Synthèse globale des invasions de poissons d'eau douce, et identification des facteurs influençant leur succès

Camille Bernery

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Synthèse globale des invasions de poissons d'eau douce, et identification des facteurs influençant leur succès

Global synthesis of freshwater fish invasions, and identification of factors influencing their success

Thèse de doctorat de l'université Paris-Saclay

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Thèse préparée dans l'unité de recherche **ESE** (Université Paris-Saclay, CNRS, AgroParisTech), sous la direction de **Franck COURCHAMP**, directeur de recherche CNRS, la co-direction de **Céline BELLARD**, chargée de recherche CNRS, et le co-encadrement de **Boris LEROY**, maître de conférences du Museum National d'Histoire Naturelle.

Thèse soutenue à Paris-Saclay, le 15 Décembre 2022, par

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THESE DE DOCTORAT

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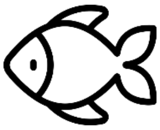


1. INTRODUCTION GÉNÉRALE

1.1. La biodiversité, essentielle mais en danger

1.1.1. Définition

La diversité biologique, ou biodiversité, est la diversité de toutes les formes vivantes sur Terre et de leurs interactions. Cette biodiversité se décline en trois grands niveaux d'organisation. Premièrement, la diversité génétique qui désigne la diversité entre les individus au sein d'une même espèce (Ellegren & Galtier 2016). Une grande diversité génétique est par exemple synonyme d'une forte capacité d'adaptation de l'espèce aux changements de leur environnement (Ellegren & Galtier 2016). Deuxièmement, la diversité spécifique qui représente le nombre d'espèces dans une communauté. Troisièmement, la diversité des écosystèmes qui désigne la diversité des conditions biotiques et de leurs interactions, ainsi que des conditions abiotiques dans lesquelles les espèces évoluent (Ellegren & Galtier 2016). La diversité spécifique est l'échelle la plus étudiée en écologie (Chiarucci et al. 2011). Cette tendance peut être confirmée par une recherche sur Web Of Science : les articles associés au terme « s*pecies diversity* » sont deux fois plus nombreux que ceux associés au terme « *genetic diversity* » (Fig. 1). Cette définition espèce-centrée à l'avantage d'offrir une discrétisation relativement simple et facilement observable de la biodiversité (Fleishman et al. 2006). Elle peut aussi être corrélée à d'autres composantes de la biodiversité (*e.g.*, la diversité génétique ; Fleishman et al. 2006). Par ailleurs, un grand nombre de bases de données sont aujourd'hui disponibles à cette unité d'analyse (*e.g., Global Biodiversity Information Facility,* GBIF 2022 ; *the International Union for Conservation of Nature,* IUCN 2022), en permettant une comparaison spatiale et temporelle lorsqu'elle est estimée de façon standardisée (Fleishman et al. 2006). Aujourd'hui, on estime que la diversité spécifique s'élèverait à 8,7 millions d'espèces eucaryotes sur Terre, mais une grande partie reste encore inconnue (*i.e.*, 86% des espèces terrestres et 91% des espèces marines seraient encore inconnues ; Mora et al. 2011). Toutefois, la biodiversité étant très complexe, ces trois grands niveaux ne sont pas suffisants pour la décrire. Par exemple, la diversité fonctionnelle est aussi une composante de la biodiversité, et permet de décrire la diversité des caractéristiques des espèces ayant une influence sur le fonctionnement des écosystèmes (Tilman 2001).

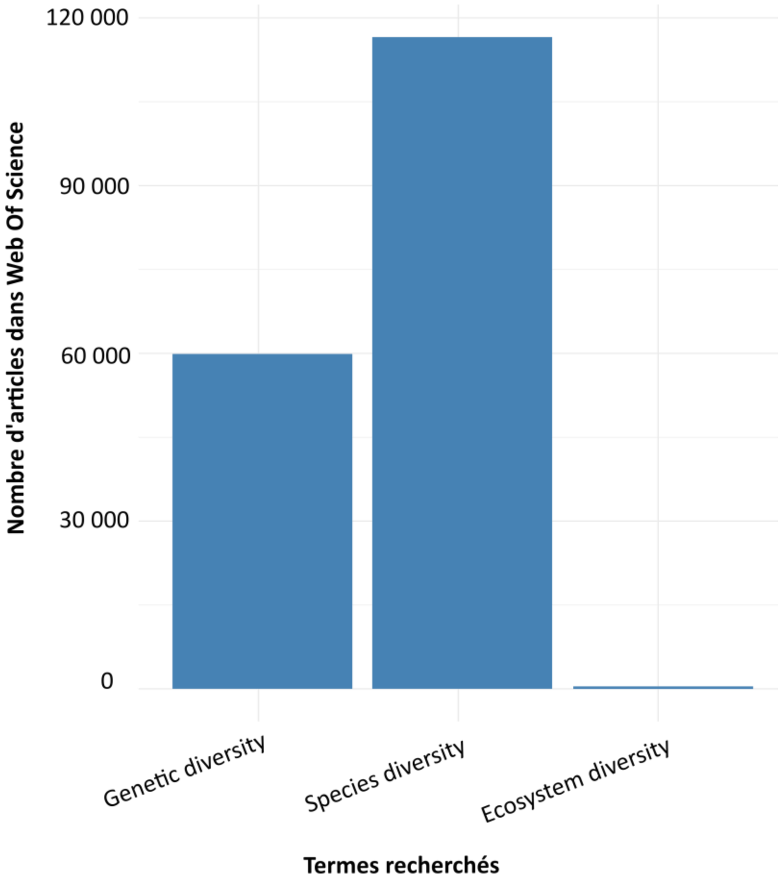
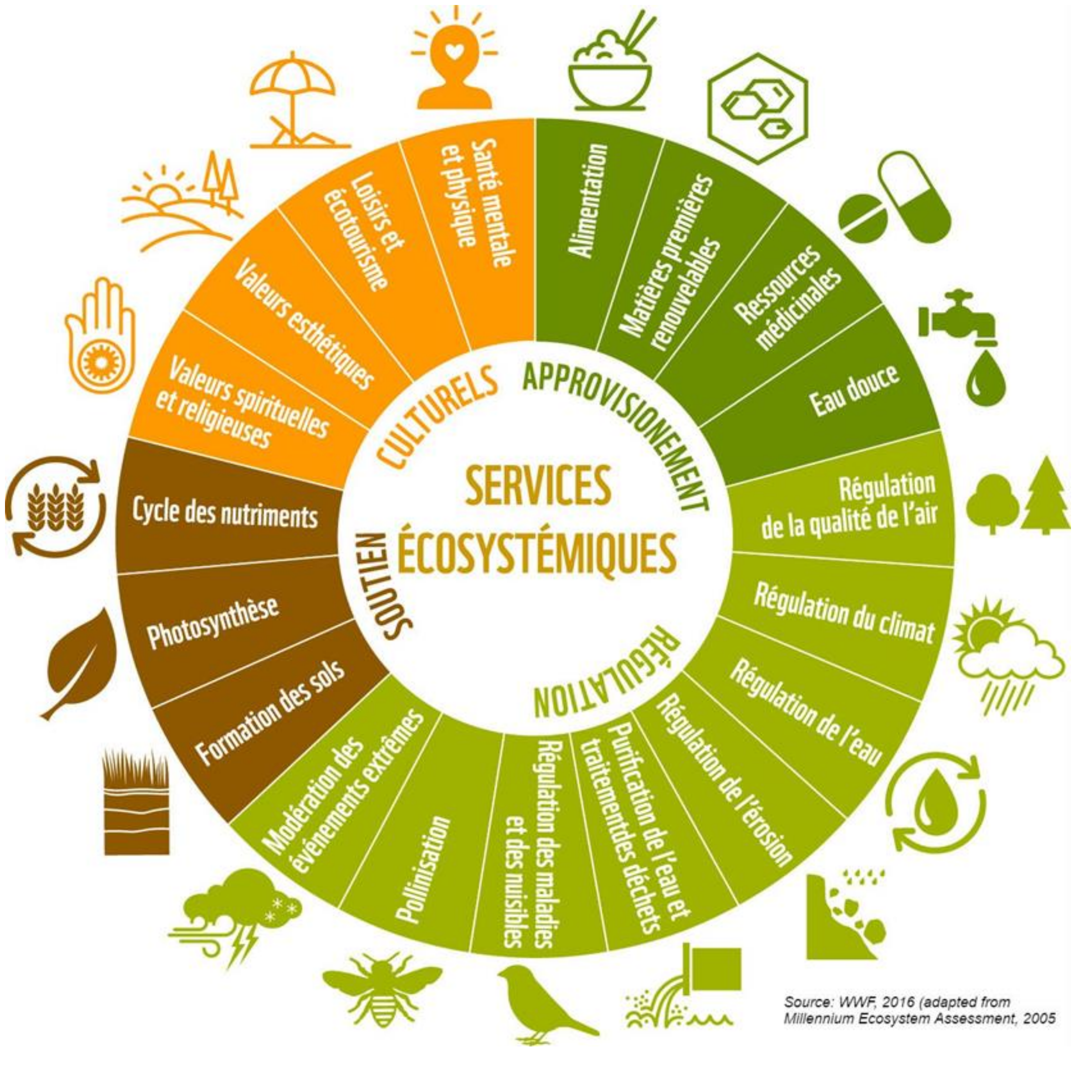


Figure 1 : Nombre d'articles dans Web of Science associés avec les termes : « ***genetic diversity*** **», «** ***species diversity*** **», «** ***ecosystem diversity*** **». La recherche a été effectuée pour le domaine «** ***Environmental Science Ecology*** **», le 11/07/2022.**

1.1.2. Importance de la biodiversité

La biodiversité a une valeur importante pour l'humanité (Guiral 2013). Elle est à l'origine des services écosystémiques, appelés aujourd'hui « *nature contribution to people* », c'est-à-dire les bénéfices que les humains retirent des écosystèmes. Ces valeurs se déclinent en services culturels, d'approvisionnement, de régulation, et de soutien (Millenium Ecosystem Assessment, 2005) (Fig. 2). En effet, la biodiversité est importante dans la culture ou l'identité de nombreuses sociétés, et permet aussi le développement du tourisme. La biodiversité génère aussi des biens et ressources utilisés par l'humanité (*e.g.*, ressources alimentaires, médicales, biocarburants). Par exemple, l'Organisation Mondiale de la Santé estime à 40% les substance pharmaceutiques étant issues de substances naturelles (Organisation Mondiale de la Santé 2022). La biodiversité est aussi source de nouvelles molécules et donc de nouveaux traitements potentiels. Lavergne et al. (2015) ont ainsi identifié 3 305 nouvelles toxines dans une seule espèce d'escargot cône (*Conus episcopatus*), dont plusieurs de ces molécules pourraient avoir des applications thérapeutiques. Il existe plusieurs centaines d'espèces d'escargots cônes, toutes contenant des molécules ayant elles aussi un potentiel thérapeutique (Bouchet & Gofas 2015). La biodiversité est aussi liée à des services de régulation, et permet par exemple la régulation du climat : les forêts et les sols permettent la régulation des teneurs en CO_2 et O_2 dans l'atmosphère, grâce à leur capacité de stockage du carbone (Lal et al. 2018; Robert & Saugier 2003). Enfin, les services de soutien permettent la production des autres services, au travers par exemple de la production de sols fertiles (*e.g.*, vers-de-terre) et de production primaire (photosynthèse) qui sont essentiels au bon fonctionnement de la planète.



Source: WWF, 2016 (adapted from Millennium Ecosystem Assessment, 2005

Figure 2 : Vue d'ensemble des différents services écosystémiques et exemples associés. Tiré de WWF, 2016 et adapté de Millennium Ecosystem Assessment, 2005.

Les valeurs instrumentales ci-dessus sont souvent celles mises en avant pour souligner l'importance de la biodiversité, parfois au détriment de la valeur intrinsèque (Ghilarov 2000). La valeur intrinsèque de la biodiversité implique que les espèces et la nature en général peuvent exister simplement pour ce qu'elles sont, indépendamment de leur utilité directe pour l'humanité (Alho 2008). Une meilleure mise en avant et considération de cette valeur pourrait aussi aider à la prise de conscience du grand public sur la crise environnementale et à comprendre les enjeux de la biologie de la conservation (Piccolo 2017).

1.1.3. Menaces pesant sur la biodiversité

Le sommet de la Terre de Rio en 1992 marque un tournant dans la prise de conscience de la dégradation de la biodiversité due aux activités humaines, et du danger que cela représente pour l'utilisation durable des ressources biologiques et pour le maintien de la vie humaine sur Terre. La préservation de la biodiversité est aujourd'hui un sujet important en politique. Ainsi, durant le sommet de la Terre, 196 pays ont signé la Convention sur la diversité biologique dont le but est la conservation et la durabilité de la biodiversité à toutes ces échelles. Leurs réunions régulières (*e.g.*, la COP 15 sur la biodiversité prévue en décembre 2022 au Canada) permettent aux politiques du monde entier de mettre en place des stratégies concernant la préservation de la biodiversité.

En effet, même si l'extinction des espèces est un phénomène naturel, dont le taux naturel est estimé entre 0.1 et 2 extinctions par millier d'espèces et par millénaire (Barnosky et al. 2011; Ceballos et al. 2015), un taux de disparition d'espèces anormalement élevé menace le bon fonctionnement des écosystèmes et nous entraîne vers une nouvelle crise de la biodiversité. Ces dernières décennies, le rythme d'extinction des espèces s'est accéléré, pour atteindre aujourd'hui 1000 fois le rythme dit naturel (Millenium Ecosystem Assessment 2005). Aujourd'hui, 13% des oiseaux, 27% des mammifères et 41% des amphibiens sont menacés d'extinction (IUCN 2022). Il est prédit que le rythme d'extinction augmente encore dans les années à venir, pour atteindre 10 000 fois le rythme naturel (Millenium Ecosystem Assessment 2005 ; De Vos et al. 2015). Il est déjà arrivé par cinq fois que la biodiversité subisse des extinctions de masse, la dernière en date étant l'extinction Crétacé il y a environ 65 millions d'années, et ayant mené au déclin et à la disparition de 76% des espèces existantes (Barnosky et al. 2011). Une extinction de masse est définie par trois critères différents : elle doit mener à l'extinction d'au moins 75% des espèces sur Terre, être un phénomène d'échelle mondiale, et être brève à l'échelle des temps géologiques (c'est-à-dire se dérouler en moins de deux millions d'années) (Barnosky et al. 2011). D'après la définition et les données, nous entamons probablement une 6$^{\text{ème}}$ extinction de masse, si les espèces actuellement menacées d'extinction viennent à disparaitre (Barnosky et al. 2011; Ceballos et al. 2015).

Les premiers effets supposés de l'humain sur la biodiversité remontent à plusieurs dizaines de milliers d'années, au travers de la maîtrise du feu, de la chasse et de la pêche puis de l'agriculture (Pereira et al. 2012). D'autres facteurs directs de changements globaux (*i.e.*, l'ensemble des changements sociétaux et environnementaux engendrés par les activités humaines, Longaretti 2017), se sont développés durant ces 500 dernières années (Maxwell et al. 2016; Pereira et al. 2012), entraînant des extinctions d'espèces. Aujourd'hui, nous pouvons identifier cinq types de facteurs responsables de cette crise, directement imputables aux activités humaines :

(i) La pollution (MacLeod et al. 2021; Rosa & Dietz 2012). La pollution est définie comme la contamination des composants physiques et biologiques du système terre/atmosphère par l'excès de substances (présentes naturellement ou non), affectant le bon fonctionnement des processus environnementaux (Muralikrishna & Manickam 2017). Par exemple, Kühn & van Franeker (2020) ont montré que les débris plastiques impactaient 914 espèces marines par ingestion ou enchevêtrement.

(ii) La destruction des habitats. Cette destruction est synonyme de disparition complète, de fragmentation ou de dégradation de l'habitat (WWF 2016). Par exemple, plus des 2/3 des forêts Méditerranéennes et des zones boisées ont été perdues depuis 1990, principalement à cause de l'agriculture qui est la première cause de destruction des habitats à l'échelle mondiale (Millenium Ecosystem Assessment 2005, Laurance 2010).

(iii) La surexploitation, c'est-à-dire l'exploitation intense des espèces ne leur permettant pas de se régénérer. La surexploitation peut résulter d'une exploitation intentionnelle, qu'elle soit légale (*e.g.*, la surpêche ; Du et al. 2021) ou illégale (*e.g.*, le braconnage des éléphants ; Ngcobo et al. 2018). Elle peut aussi être accidentelle. Par exemple, Loss et al. 2014 rapportent qu'au minimum 365 millions d'oiseaux meurent chaque année du fait de collisions avec des vitres de bâtiments aux Etats-Unis.

(iv) Le changement climatique, c'est-à-dire l'augmentation moyenne des températures et le bouleversement des régimes météorologiques en place. Par exemple, les projections climatiques de Román-Palacios & Wiens (2020) sur 538 espèces animales et végétales ont permis d'estimer que 57 à 70% de ces espèces ne pourront pas se disperser assez rapidement pour suivre leur niche climatique actuelle et éviter l'extinction à l'horizon 2070.

(v) Les invasions biologiques. Dans la suite de cette thèse, une invasion biologique sera définie suivant l'IUCN 2000, c'est-à-dire par la succession de trois étapes principales (Fig. 3) :

(1) **Le transport et l'introduction** (volontaire ou involontaire) d'une espèce en dehors de son aire géographique native par un moyen humain. L'espèce est alors une espèce exotique dans son nouveau milieu ;

(2) **L'établissement et la propagation :** l'espèce exotique est capable de se reproduire par elle-même et de s'étendre dans son nouvel environnement ;

(3) **Les impacts** : l'espèce exotique établie est responsable d'impacts écologiques (*e.g.*, déclin ou disparition d'espèces natives, dégradation de l'habitat, homogénéisation des assemblages d'espèces à l'échelle globale), socio-économiques (*e.g.*, dégradation d'infrastructures humaines, impact sur les activités économiques comme le tourisme ou les pêcheries, dégradation des services écosystémiques) et/ou sanitaires (*e.g.*, vecteurs de maladie ou de parasites, ou parasites eux-mêmes) dans son nouvel environnement (Pyšek & Richardson 2010). Par exemple, Bellard et al. (2021), un article auquel j'ai participé en tant que co-autrice, ont ainsi estimé que les invasions biologiques menacent 14% de la diversité de trait chez les mammifères, et 40% de celle des oiseaux (Annexe 1). Diagne et al. (2021) ont aussi mis en évidence que les coûts totaux reportés pour les invasions biologiques de 1970 à 2017 s'élèvent à au moins 2 168 milliards de dollars à l'échelle mondiale (voir Leroy et al. 2022). Enfin, le moustique tigre (*Aedes albopictus*), envahissant dans plusieurs pays dont la France, est vecteur de plusieurs virus dont la dengue, le chikungunya, la fièvre jaune et le Zika (Kraemer et al. 2019).

Une espèce responsable d'une invasion biologique et ayant donc réussi ces trois étapes est appelée espèce exotique envahissante. Il est important de noter qu'il existe plusieurs variations de la définition d'une espèce exotique envahissante (Heger et al. 2013). Ces variations portent surtout sur le lieu d'introduction qui, pour certains auteurs, doit être éloigné d'une grande distance de leur milieu natif (Valéry et al. 2008). Les variations peuvent aussi porter sur la présence d'impacts à l'issue de l'invasion (Blackburn et al. 2011).

Les invasions biologiques sont une menace en plein essor (Pereira et al. 2012). En effet, le rythme d'établissement d'espèces exotiques s'est intensifié depuis l'augmentation des échanges internationaux dans les années 1800, et a ensuite continué de s'accélérer (Seebens et al. 2017). Ainsi, alors que l'on répertoriait environ sept nouveaux établissements d'espèces exotiques par an en 1800, on en répertorie plus de 585 en 1996 (Seebens et al. 2017). Malgré leur nombre grandissant et leurs impacts importants à l'échelle globale, les espèces envahissantes ne bénéficient pas d'un grand intérêt sociétal, et certains aspects des invasions sont peu étudiés par rapport à d'autres menaces tel que le changement climatique (Courchamp et al. 2017; Jarić et al. 2020a; Lawler et al. 2006). Toutefois, les espèces exotiques envahissantes dans les écosystèmes insulaires sont bien documentées par rapport aux écosystèmes continentaux, de par le fait que les îles sont des points chauds d'invasion (Dawson et al. 2017), où les espèces exotiques envahissantes ont des impacts particulièrement importants par rapport aux milieu continentaux (Bellard et al. 2016; Russell et al. 2017). En revanche, les invasions en écosystèmes d'eau douce sont moins bien étudiées qu'en écosystèmes terrestres, malgré leurs impacts particulièrement importants (Jeschke & Heger 2018). En effet, plusieurs concepts et hypothèses liés aux invasions sont surtout abordés avec des modèles terrestres, et restent à tester pour les écosystèmes d'eau douce (Francis & Chadwick 2012; Ricciardi & Macisaac 2010). Par exemple, les effets des perturbations ou la composition des communautés réceptrices sur le succès d'invasion sont beaucoup moins abordés dans la littérature pour les écosystèmes d'eau douce que pour les terrestres (Ricciardi & Macisaac 2010). De la même façon, les facteurs influençant le succès d'invasion des espèces sont souvent abordées au travers d'espèces terrestres, alors que ces caractéristiques peuvent varier en fonction des écosystèmes (Francis & Chadwick 2012; Pyšek et al. 2020a). Dans la suite de cette thèse, nous allons nous intéresser aux invasions dans les écosystèmes d'eau douce.

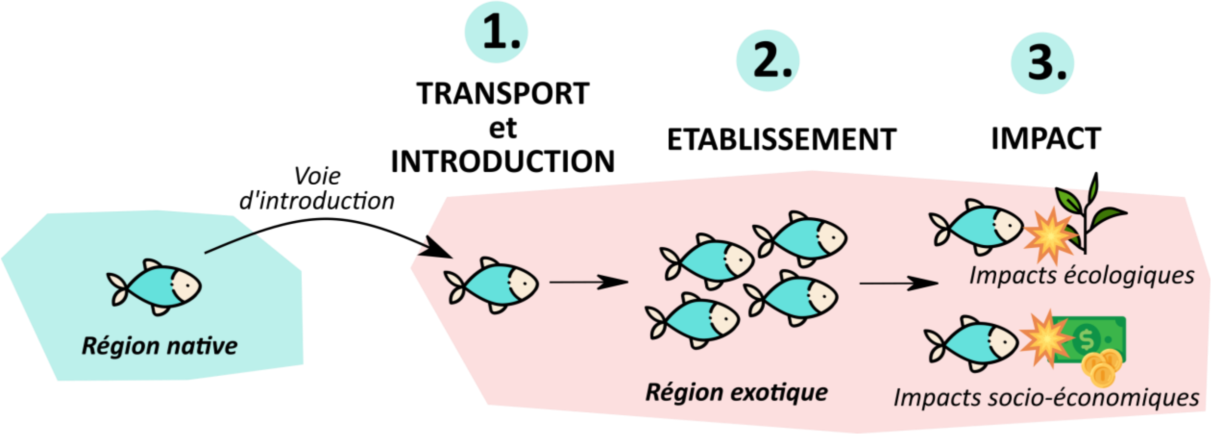


Figure 3 : Schématisation des différentes étapes de l'invasion prise en compte dans cette thèse.

1.2. Les invasions biologiques dans les écosystèmes d'eau douce

Les écosystèmes d'eau douce sont caractérisés par leur grande concentration en espèces : ils représentent 0.8% de la surface terrestre mais concentrent au moins 1/3 des espèces de vertébrés. Tous taxons confondus, environ 100 000 espèces vivent en eau douce, sur environ 2 millions d'espèces connues, soit 5% de la diversité d'espèces présentes sur Terre (Dudgeon et al. 2006). De plus, les écosystèmes d'eau douce sont caractérisés par des taux d'endémisme élevés. Le taux d'endémisme des poissons d'eau douce dans leur région biogéographique est bien plus élevé que pour les autres vertébrés terrestres, attestant de leur niveau d'isolement (Leroy et al. 2019). En plus de leur grand nombre d'espèces, ces écosystèmes fournissent un grand nombre de services écosystémiques. Par exemple, ils permettent la régulation du climat par l'évapotranspiration et le stockage du carbone, et le développement de nombreuses activités touristiques (*e.g.*, activités nautiques) et commerciales (*e.g.*, pêche, UICN France 2015). Ainsi, en France, les écosystèmes d'eau douce abritent 2/3 des poissons consommés (UICN France 2015). Toutefois, ces écosystèmes sont particulièrement sensibles aux perturbations, et voient leur diversité disparaitre plus rapidement que les écosystèmes terrestres et marins (Williams-Subiza & Epele 2021). Environ une espèce d'eau douce sur trois est menacée d'extinction, et en moins de 60 ans, les populations d'eau douce ont décliné de 84% (WWF 2020). Les invasions biologiques sont l'une des principales causes de perte de biodiversité des écosystèmes d'eau douce (Ricciardi & Macisaac 2010). En effet, à l'image des écosystèmes insulaires, les écosystèmes d'eau douce sont des systèmes fermés (*e.g.*, les bassins versants) où les impacts des espèces envahissantes peuvent donc être exacerbés notamment car les espèces natives ne peuvent pas échapper à la menace, et parce qu'elles peuvent être particulièrement naïves aux prédateurs, compétiteurs ou parasites exotiques, due à leur isolation dans les bassins versants (Cox & Lima 2006; Vilà & Hulme 2017). Ainsi, Ricciardi (2006) a montré la présence de plus de 180 espèces exotiques dans les grands lacs Américains, et de nouvelles espèces exotiques y sont découvertes tous les ans (Carpenter et al. 2011). Parmi ces espèces, la moule zébrée (*Dreissena polymorpha*) est une espèce envahissante et emblématique en raison de ses impacts. Envahissante en Amérique du Nord et en Europe de l'Ouest, elle est connue pour réduire la biomasse de phytoplancton de par ses capacités de filtration, ce qui entraîne des modifications de l'habitat (*e.g.*, augmentation de la clarté de l'eau), des cycles de nutriments, et une réduction des espèces suspensivores natives par compétition. Les impacts des moules zébrées sont aussi économiques, car elles encrassent les infrastructures humaines comme les coques de bateaux et bouchent les canalisations (Dölle & Kurzmann 2020). Parmi la grande variété d'espèces exotiques envahissantes d'eau douce, nous allons nous intéresser plus précisément aux poissons d'eau douce dans le cadre de cette thèse.

1.3. Les poissons d'eau douce envahissants : distributions, impacts et facteurs influençant leurs invasions.

1.3.1. Distribution des invasions de poissons d'eau douce

Le nombre d'introductions et d'établissements d'espèces de poissons exotiques dans le monde a connu une augmentation importante à partir de la moitié du 20ème siècle, augmentation qui a ralenti ces dernières années, potentiellement dû au délai de détection des espèces exotiques (Seebens et al. 2017 ; Chapitre 1 – Annexe 1). Malgré ce ralentissement, les poissons d'eau douce sont parmi les taxons les plus introduits en dehors de leur zones natives (Gozlan, 2008). Alors que 78 espèces d'amphibiens, 198 espèces de reptiles et 359 espèces d'oiseaux exotiques sont répertoriés comme établis dans le monde (Capinha et al. 2017; Pyšek et al. 2020b), ce chiffre monte jusqu'à 551 pour les poissons exotiques (Tedesco et al. 2017, en comptant seulement les données avec un fort taux de fiabilité). La région biogéographique Néarctique est la plus envahie, avec 293 espèces de poissons exotiques établies dans ses bassins (Chapitre 1 – Figure 1). Au contraire, la région biogéographique Ethiopienne est la moins envahie avec seulement 44 espèces de poissons d'eau douce établies (Chapitre 1 – Figure 1). Cette tendance s'explique en partie par le niveau de développement des régions concernées, les régions plus développées faisant plus de commerce et d'échanges avec d'autres régions, mais aussi par des biais de détection et de recherche, la région Néarctique étant la région du monde bénéficiant généralement d'un gros effort de recherche (Bellard & Jeschke 2016). Toutefois, les récents travaux de Tedesco et al. (2017) et la base de données Fishbase (Froese & Pauly 2019) permettent désormais d'avoir un premier état des lieux de la distribution des poissons exotiques dans les bassins versants à l'échelle mondiale.

La carpe commune (*Cyprinus carpio*) est l'espèce de poisson exotique la plus largement établie à l'échelle mondiale, puisqu'elle est établie dans 720 bassins versants, soit 23% des bassins versants dans le monde. La carpe commune fait aussi partie de la liste des 100 espèces exotiques envahissantes parmi les pires, avec sept autres espèces de poissons (Fig. 4) qui sont : la Gambusie (*Gambusia affinis*), la perche du Nil (*Lates niloticus*), l'Achigan à grande bouche (*Micropterus salmoides*), la truite commune (*Salmo trutta*), la truite arc en ciel (*Oncorhyncus mykiss*), le tilapia du Mozambique (*Oreochromis mossambicus*) et le silure grenouille (*Clarias batrachus*). Ces poissons exotiques envahissants se démarquent par l'importance de leur distribution, leurs impacts écologiques et leurs impacts sur les sociétés humaines ou par d'autres composantes marquantes liées aux invasions biologiques (*e.g.*, vitesse d'invasion, difficulté de gestion) (Lowe et al. 2000) (Figure 4):

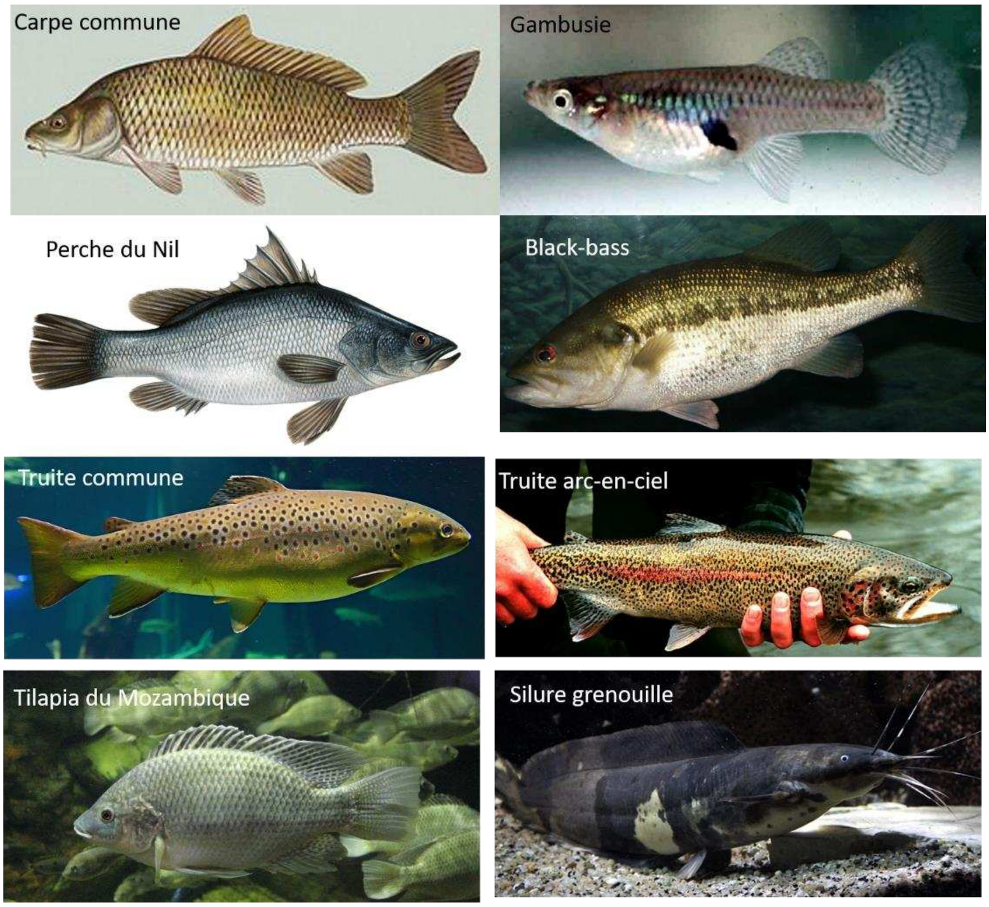


Figure 4 : Illustration des huit espèces envahissantes de poissons d'eau douce faisant partie de la liste « 100 espèces exotiques envahissantes parmi les pires au monde » (Lowe et al. 2000) .

1.3.1 Impacts des poissons exotiques envahissants

La présence de poissons exotiques dans les bassins versants est à l'origine de nombreux impacts à l'échelle mondiale (Cucherousset et Olden, 2011). Ces impacts peuvent survenir à différentes échelles écologiques, et comprennent des altérations génétiques des populations natives via l'hybridation (Blackwell et al. 2020), la transmission de pathogènes (Spikmans et al. 2020), le déclin ou la disparition d'espèces natives, l'altération d'habitats, ou l'homogénéisation taxonomique et fonctionnelle à l'échelle mondiale (Cucherousset & Olden 2011; Villéger et al. 2011). Par exemple, la carpe commune impacte les habitats natifs en augmentant la concentration de sédiments et de nutriments dans la colonne d'eau par bioturbation (GISD

2022a). L'invasion du lac Victoria par la Perche du Nil a entrainé la disparition d'au moins 200 espèces d'haplochromines endémiques, représentant ainsi la première et la plus grande extinction de masse de vertébrés que les scientifiques n'aient jamais eu l'occasion d'observer (Kaufman 1992). Plus largement, Light & Marchetti (2007) ont démontré que les invasions biologiques de poissons d'eau douce étaient la principale cause d'extinction et de déclin des espèces de poissons natifs en Californie. Cependant, il reste difficile de caractériser les impacts des espèces exotiques envahissantes, notamment pour les poissons d'eau douce. Ces difficultés proviennent entre autres de problèmes de compréhension du concept d'invasion biologique, mais aussi de problèmes pour démontrer les changements induits par les espèces exotiques envahissantes (Courchamp et al. 2017). Par ailleurs, il peut exister une longue période entre l'introduction de l'espèce exotique et ces premiers impacts écologiques (Rouget et al. 2016). Ces spécificités rendent ainsi difficile la récolte des données d'impact (Courchamp et al. 2017; Pyšek & Richardson 2010). Toutefois, un cadre récemment développé permet la classification efficace de la portion d'impacts récoltés : la classification EICAT (*Environmental Impact Classification for Alien Taxa*) (Blackburn et al. 2011). Le cadre EICAT permet de standardiser les impacts écologiques de différents taxons et espèces, et d'aider à mettre en place des priorités de gestion (Hawkins et al. 2015). Bien que EICAT ait été déjà appliqué à différents taxons (Canavan et al. 2019; Evans et al. 2016; Galanidi et al. 2018; Hagen & Kumschick 2018; Kesner & Kumschick 2018; Kumschick et al. 2017), aucune classification des impacts des poissons d'eau douce n'existe à ce jour. La revue synthétique portant sur les différents impacts des poissons de Cucherousset & Olden (2011) relate différents exemples d'impacts et démontre l'ampleur de ces impacts qui peuvent affecter les différents compartiments de la biodiversité. Cependant, en dehors de cas d'étude célèbres (*e.g.*, Nile perch, Aloo et al. 2017; *Pseudorasbora parva* ; (Spikmans et al. 2020), il n'existe pas de revue synthétique quantitative des différents types d'impacts des poissons exotiques envahissants d'eau douce. Pourtant, les synthèses sont des outils importants en recherche, car en plus de permettre une vue d'ensemble d'un sujet, elles mettent en avant les points de contradiction et les manques de littérature afin de guider les futures questions à traiter en recherche. Nous avons mené ce travail de synthèse sur les invasions biologiques des poissons d'eau douce dans les Chapitres 1 et 2 de la thèse. Le but de ce travail était de proposer à la fois une vue globale des voies d'introductions des poissons exotiques d'eau douce, et une quantification des différents impacts écologiques et économiques et de leurs principaux mécanismes.

En parallèle, les impacts économiques des poissons exotiques envahissants sont encore très mal documentés à grande échelle. Pourtant, plusieurs études montrent des coûts économiques importants des poissons d'eau douce envahissants. C'est par exemple le cas de la lamproie marine (*Petromyzon marinus*), envahissante dans les Grands Lacs Nord-Américains, qui parasite des poissons ayant une valeur économique pour la pêche, tels que les salmonidés, et environ 22 millions de dollars sont dépensés chaque année par les gouvernements du Canada et des Etats-Unis d'Amérique pour contrôler les populations exotiques de lamproies (Colautti et al. 2006). Cependant, ces études traitent aussi bien de taxons, que d'échelles ou bien de monnaies différentes, rendant la synthèse de ces coûts économiques compliquée. Pourtant, communiquer autour des coûts économiques de ces espèces pourrait augmenter la prise de conscience sociétale envers les invasions. Les coûts économiques sont une métrique familière, parlant aussi bien aux scientifiques qu'aux non-scientifiques, et permettent de chiffrer et de se représenter l'ampleur des dégâts plus facilement que les impacts écologiques (Courchamp et al. 2017; Diagne et al. 2020b). La base de données InvaCost (Diagne et al. 2020b) découle de ces constats pour l'ensemble des taxons envahissants. Cette base de données a fait l'objet d'un workshop rassemblant 47 chercheurs du monde entier sur les invasions biologiques, et auquel j'ai eu la chance de participer (Diagne et al. 2020a). Le but de ce workshop était d'explorer cette première base de données à l'échelle globale sur les coûts économiques des espèces envahissantes. Grâce à cette opportunité, j'ai pu synthétiser les coûts économiques des poissons envahissants à l'échelle mondiale, au travers d'une étude où je suis co-première autrice publiée dans *Science of The Total Environment* (voir Chapitre 2).

1.3.2 Facteurs influençant le succès des invasions de poissons d'eau douce

Finalement, la réussite des invasions de poissons d'eau douce à chaque étape de l'invasion dépend de plusieurs facteurs (Fig. 5). En particulier, trois types de facteurs se distinguent :

(i) **Les facteurs liés à l'évènement d'introduction.** Dans cette catégorie, se trouvent principalement les facteurs socio-économiques telles que les voies d'introductions et la pression de propagule (*i.e.*, le nombre d'individus étant introduits ; Simberloff 2009). Les voies d'introduction des poissons d'eau douce sont nombreuses, les deux principales étant l'aquaculture et le commerce de poissons d'aquarium (Dey 2016; Froese & Pauly 2019; Kerr et al. 2005). Par exemple, concernant la pression de propagule, plus elle est élevée, plus il y a d'individus introduits, plus la diversité génétique, la probabilité de survie et donc la probabilité d’invasion augmente (Woodford et al. 2013). En outre, ces différents facteurs sont susceptibles d’interagir, la voie d’introduction pouvant avoir une influence sur la pression de propagule

(ii) **Les traits des espèces de poissons exotiques**. Différents traits peuvent influencer le succès de l’invasion, suivant l’étape de l’invasion concernée, la voie d’introduction des espèces, ou encore les conditions présentes dans le milieu d’introduction (Kolar & Lodge 2002; Su et al. 2020; Vila-Gispert et al. 2005). Toutefois, les espèces dites généralistes sont connues pour avoir des facilités à envahir. Par exemple, il est généralement admis que les espèces étant tolérantes aux changements de températures et de salinité ont plus de facilités à envahir que les autres (Kolar & Lodge 2002; Snyder et al. 2014) car elles peuvent plus facilement s’adapter au nouveau milieu dans lequel elles sont introduites. Pour les mêmes raisons, les espèces qui ont une régime alimentaire varié envahissent aussi plus facilement (Ruesink 2005).

(iii) **Les caractéristiques du milieu d’introduction**, au travers de trois principaux aspects : la préadaptation des espèces exotiques au milieu (Nekola & White 1999), les perturbations du milieu (Zhang et al. 2006) et la communauté d’espèces en place dans le milieu (Enders et al. 2020). Ainsi, si les caractéristiques du milieu d’introduction (*e.g.*, température, salinité) sont trop différentes du milieu d’origine de l’espèce introduite, cette dernière voit ses probabilités de devenir envahissante diminuer. Par exemple, les poissons d’aquarium provenant de régions tropicales ne peuvent pas facilement s’établir dans les eaux froides des Grands Lacs Nord-Américains (Gertzen et al. 2008). La préadaptation au milieu est donc un facteur important de réussite des invasions (Tonella et al. 2018). Les perturbations jouent aussi un rôle important puisqu’elles libèrent des niches écologiques au travers de l’extinction locale d’espèces natives (Clavero et al. 2013; Havel et al. 2005). Par exemple, les estuaires, qui sont des milieux très exposés aux perturbations anthropogéniques, sont plus enclins à être envahis (Moyle & Light 1996). Enfin, la présence ou l’absence de certaines espèces dans le milieu envahi influence le devenir d’une introduction. Par exemple, l’absence d’un parasite de l’espèce introduite dans le nouveau milieu est un avantage pour l’invasion (Roche et al. 2010). La diversité des communautés natives joue aussi un rôle, les communautés avec des redondances fonctionnelles pouvant réduire la susceptibilité aux invasions (Habit et al. 2012).

Il faut noter qu’un seul de ces facteurs, pris indépendamment des autres, ne permettrait pas à lui seul d’expliquer le succès d’une invasion. Ces facteurs interagissent entre eux (Fig. 5). Ainsi, la voie d’introduction par lequel est introduite l’espèce exotique peut influencer les traits de l’espèce en question. Par exemple, les espèces introduites via l’aquaculture sont généralement de grande taille et compressées latéralement (Su et al. 2020). De même, un écosystème perturbé ou ayant des conditions très variables (*e.g.*, changements saisonniers du débit fluvial d'une rivière) permettra l'invasion d'espèces ayant des traits différents de ceux dans un écosystème avec des conditions stables (Vila-Gispert et al. 2005). L'importance relative de ces facteurs dans la réussite de l'invasion peut aussi être dépendante de l'étape de l'invasion considérée (Snyder et al. 2014). Ainsi, les petits poissons ont plus de chance d'être introduits via les eaux de ballast (Wonham et al. 2000), mais les gros poissons prédateurs ont plus de chances de s'établir (Tonella et al. 2018; Vila-Gispert et al. 2005). En outre, et au sein même d'une étape d'invasion, différents traits sont susceptibles d'expliquer le succès relatif d'une espèce à s'établir dans différents bassins et à grandes échelles (Catford et al. 2016; Su et al. 2020).

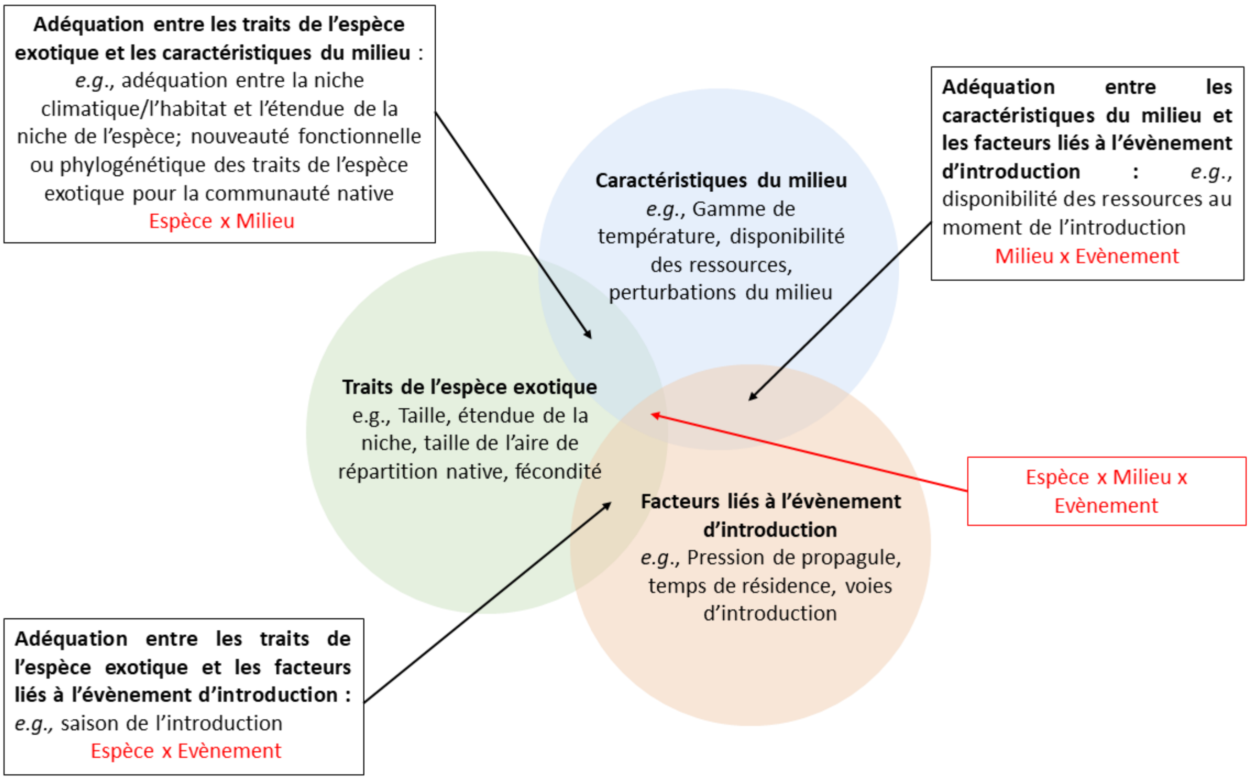


Figure 5 : Facteurs influençant la réussite des invasions et leurs interactions. Les intersections entre deux (ou toutes) ces classes principales de facteurs indiquent des situations où leurs combinaisons déterminent les invasions, par exemple, le climat d'un lieu doit correspondre aux exigences de niche de l'espèce exotique pour que l'invasion soit réussie. Tiré de Pyšek et al. (2020a).

Toutefois, les facteurs de succès de chaque étape de l'invasion sont encore mal connus à l'échelle globale pour les poissons d'eau douce. En effet, les études actuelles sur le sujet sont majoritairement à des échelles locales, ou portent sur l'étape d'établissement (García-Berthou 2007; Marchetti et al. 2004a; Ribeiro et al. 2008; Vila-Gispert et al. 2005), qui est l'étape la mieux renseignée dans les bases de données (*e.g.*, Froese & Pauly 2019). Pourtant, comprendre l'importance relative de l'ensemble de ces facteurs à chaque étape de l'invasion est essentiel pour développer des modèles de prédiction des invasions futures et pour déterminer les espèces ayant de grandes probabilités de s'établir et d'avoir des impacts dans les milieux ciblés (Novoa et al. 2020).

1.5. Problématique et plan de thèse

Cette thèse a pour objectif principal de synthétiser les principaux aspects des invasions biologiques de poissons d'eau douce, et de s'appuyer sur ce travail de synthèse pour ensuite étudier les facteurs expliquant le succès des invasions de poissons d'eau douce. Plus spécifiquement, j'ai souhaité en premier lieu proposer une vision synthétique des invasions de poissons d'eau douce envahissants à l'échelle globale à travers la rédaction d'une revue de la littérature (Chapitre 1), puis ensuite de me concentrer plus spécifiquement sur la synthèse des coûts économiques de ces invasions (Chapitre 2). Répondre à ces objectifs ont permis, entre autres, de faire un état de l'art global des connaissances sur les invasions de poissons dans la littérature scientifique actuelle, et d'identifier les principales lacunes de la recherche dans ce domaine. C'est donc dans ce contexte que j'ai souhaité m'intéresser aux caractéristiques de succès des invasions de poissons d'eau douce. En effet, la synthèse de la littérature a notamment mis en évidence que la compréhension relative des facteurs influençant les invasions de poissons d'eau douce est un des aspects encore mal connus à l'échelle globale. Par exemple, l'étape d'impact est particulièrement peu étudiée en raison du manque de données, et la majorité des études se déroulent à l'échelle locale, en ne prenant en compte qu'un panel de facteurs réduits (*e.g.*, seulement les traits des espèces introduites, alors que d'autres facteurs, tels que des facteurs socio-économiques, peuvent entrer en jeu dans la réussite de l'invasion ; voir Fig. 5). Ainsi, nous nous sommes intéressés, dans le Chapitre 3, au profil des espèces envahissantes à chaque étape de l'invasion (*i.e*, introduction, établissement et impact), en utilisant des données liées à l'écologie de l'espèce, à ses traits, à sa morphologie ou bien à son usage économique. L'établissement des espèces peut être un succès à la seule échelle locale et à proximité de l'aire native ou bien dans de nombreux bassins versants et à distance de l'aire native. On peut ainsi définir un gradient de succès d'établissement des espèces, suivant les deux modalités de succès que sont l'étendue de l'établissement et la localisation de l'établissement de l'espèce. Dans le Chapitre 4, nous avons testé si différentes caractéristiques écologiques et morphologiques étaient liées à ce gradient d'établissement.

AXE 1 : Synthèse globale des principaux aspects des invasions biologiques de poissons d'eau douce

Nous avons ainsi rédigé une revue de la littérature dont l'objectif était d'avoir une vision globale de tous les différents aspects des invasions de poissons d'eau douce à l'échelle mondiale, depuis les voies d'introduction des poissons exotiques, en passant par les facteurs influençant les succès des invasions, les impacts des poissons d'eau douce envahissants, et enfin les techniques de gestion de ces invasions. Nous avons notamment identifié les principaux facteurs présents dans la littérature permettant d'expliquer le succès des invasions à travers les différentes étapes d'invasion, mais aussi les biais existants dans les données et les lacunes de la littérature sur les différents aspects de ces invasions (*e.g.*, biais géographiques et manque d'exploration des facteurs de succès de l'étape d'impact des invasions, dû à un manque de données sur cette étape). Enfin, nous proposons des recommandations sur les principales questions qui devraient être traitées dans les études futures (*e.g.*, l'influence du changement climatique dans le succès de nouvelles invasions de poissons d'eau douce). Par ailleurs, la publication récente de la base InvaCost répertoriant les coûts des espèces envahissantes à l'échelle mondiale nous a donné l'opportunité de faire un état de l'art des connaissances mondiales sur les coûts économiques des espèces de poissons d'eau douce envahissantes. Dans ce chapitre, nous avons ainsi répertorié et analysé les coûts de 27 espèces de poissons ayant des coûts répertoriés dans la littérature, et mis en avant les biais et les manques liés à ces données.

Cette première partie est composée de deux articles :

Chapitre 1 : **Bernery, C.**, Bellard, C., Courchamp, F., Brosse, S., Gozlan, R. E., Jarić, I., ... & Leroy, B. (2022). Freshwater fish invasions: A comprehensive review. *Annual Review of Ecology, Evolution, and Systematics*, *53*.

Chapitre 2 : Haubrock, P. J*., **Bernery, C.***, Cuthbert, R. N.*, Liu, C., Kourantidou, M., Leroy, B., ... & Gozlan, R. E. (2022). Knowledge gaps in economic costs of invasive alien fish worldwide. *Science of the Total Environment*, *803*, 149875**.**

*Co-premiers auteurs

AXE 2 : Etude des facteurs expliquant le succès des invasions de poissons d'eau douce.

Une des questions centrales qui a animé mes recherches tout au long de ma thèse était aussi de mieux comprendre les facteurs qui influencent le succès des invasions de poissons d'eau douce, et si ces facteurs variaient selon les étapes d'invasion, les voies d'introduction, ou encore selon un gradient de succès de l'établissement des espèces.

Nous avons cherché à identifier les caractéristiques spécifiques importantes à la réussite de chaque étape de l'invasion (introduction, établissement, impact écologique), à l'échelle mondiale et en considérant des facteurs écologiques, socio-économiques, ou liés à l'espèce. Nous nous sommes aussi intéressés aux voies d'introduction des espèces envahissantes (*i.e.*, commerce ornemental et aquaculture) sur la sélection et l'importance relative de ces facteurs.

En outre, nous avons poursuivi ces travaux en nous focalisant plus spécifiquement sur l'étape d'établissement des espèces exotiques. Cette étape est souvent étudiée en tant que variable binaire : soit l'espèce est considérée comme établie, ou alors elle ne l'est pas (*e.g.*, Ribeiro et al. 2008; Ruesink 2005). Cependant, il se peut qu'au sein des espèces réussissant à s'établir, plusieurs profils ressortent, suivant la localisation et l'étendue de leur milieu d'établissement. En utilisant des traits morphologiques, écologiques, et de comportement, nous avons donc exploré cette question en considérant le nombre de bassins versants dans lesquels les espèces s'étaient établies, ainsi que la localisation d'établissement (au sein ou en dehors de leur biorégion native).

Chapitre 3 : Publication soumise – **C. Bernery**; C. Bellard; F. Courchamp; S. Brosse; B. Leroy. Important characteristics to become a successful freshwater fish invader.

Chapitre 4 : Travail en cours – **C. Bernery***, C. Marino*, C. Bellard. Differences in exotic species characteristics along an establishment gradient.

*Co-premiers auteurs

1.6. Modèle d'étude et bases de données

1.6.1. Modèle d'étude : les poissons d'eau douce envahissants

Cette thèse porte sur les poissons d'eau douce exotiques, qui sont connus pour leurs introductions partout dans le monde, et leur impact écologique important sur les communautés natives (Cucherousset & Olden 2011). Nous considérerons comme poissons d'eau douce les espèces qui appartiennent aux groupes Actenopterigii et Cyclostomata, et dont l'eau douce est un de leurs habitats répertoriés dans FishBase (Froese & Pauly 2019). Ainsi, certains poissons migrateurs sont considérés comme poissons d'eau douce même s'ils passent une partie de leur cycle de vie dans les eaux marines (*e.g.*, la lamproie marine). Les poissons ne vivant qu'en eaux marines ou saumâtres ne seront pas considérés. Ainsi, cette description correspond à 17,251 espèces dans FishBase (Froese & Pauly 2019), réparties en 41 ordres et 232 familles. Cinq ordres représentent à eux seul plus de 87% des espèces considérées : les Cypriniformes (4501 espèces), les Siluriformes (3738 espèces), les Perciformes (3379 espèces), les Characiformes (2169 espèces), et les Cyprinodontiformes (1316 espèces).

1.6.2. Bases de données

Pour répondre aux différents objectifs de la thèse, nous avons utilisé différentes variables liées aux invasions de poissons d'eau douce, que ce soient leurs impacts, les traits écologiques, morphologiques, ou bien leurs lieux d'invasions. Ces variables ont principalement été extraites de quatre bases de données :

(i) **FishBase.** La base de données FishBase (Froese and Pauly, 2019) est la plus grande base de données en libre accès portant sur les poissons. Elle comporte des données entre autres sur la taxonomie, l'écologie, l'habitat, le commerce ou la reproduction de 34,800 espèces de poissons.

(ii) **Fishmorph** (Brosse et al. 2021b), qui est une base de données en libre accès comportant 10 mesures morphologiques pour 8,342 espèces de poissons d'eau douce (Actinopterygii). Ces mesures se rapportent à différents aspects fonctionnels des poissons, tels que la locomotion ou l'alimentation.

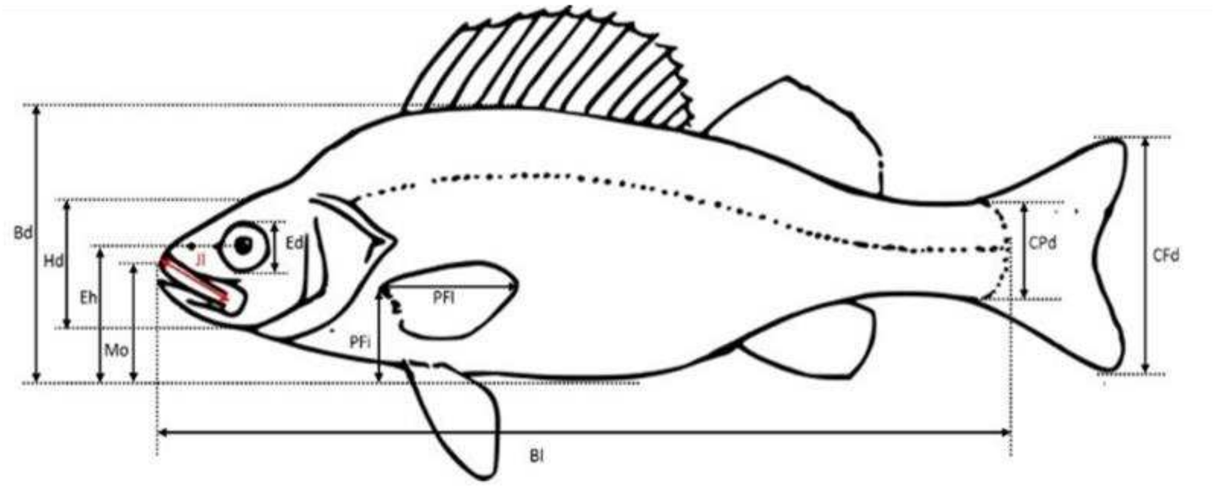


Figure 6 : Schématisation des différentes mesures présentes dans la base Fishmorph. Tiré de Brosse et al. 2021b.

(iii) **La base de données des occurrences de poissons d'eau douce dans les bassins versants** (Tedesco et al. 2017)**.** Cette base de données rassemble la liste des espèces présentes dans 3,119 bassins versants du monde (soit 80% sur la surface terrestre). Elle compte ainsi 14,953 espèces, dont le statut exotique ou non est renseigné pour chaque bassin. Dans la suite de cette thèse, nous avons couplé cette base de données aux régions biogéographiques des poissons d'eau douce identifiées par Leroy et al. (2019).

(iv) **InvaCost.** InvaCost (Diagne et al. 2020b) est une base de données publique, régulièrement mise à jour, et rassemblant les coûts économiques des espèces envahissantes présents dans la littérature scientifique et dans la littérature grise (Voir Fig. 7 pour la construction de la base). Ainsi, lors de sa parution, cette base de données rassemblait les coûts économiques de 343 espèces envahissantes à l'échelle mondiale, parmi lesquelles plusieurs espèces de poissons envahissants.

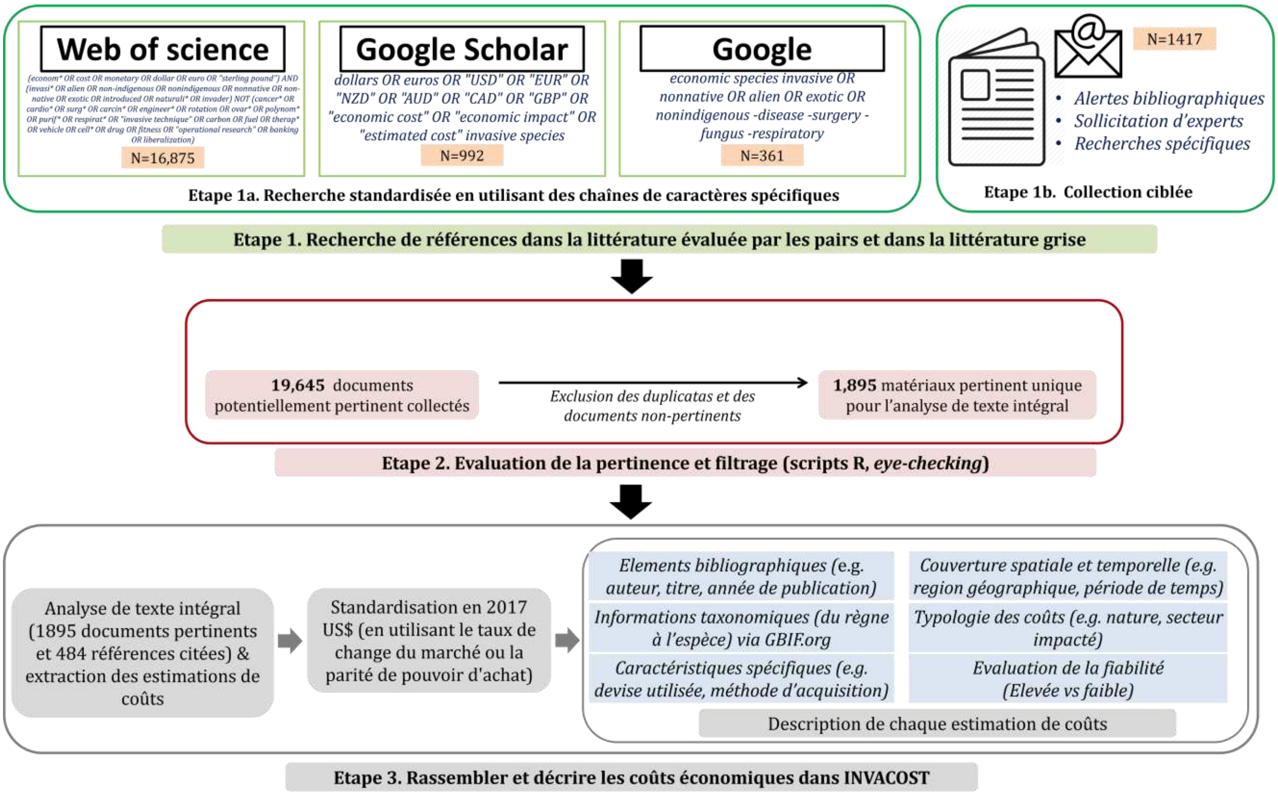
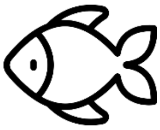
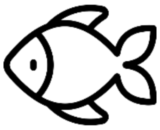


Figure 7 : Schéma de la construction de la base de données InvaCost. Tiré de Diagne et al. (2020b).



AXE 1 : Synthèse globale des principaux aspects des invasions biologiques de poissons d’eau douce



Chapitre 1 : Les invasions des poissons d’eau douce : une revue globale de la littérature

Annual Review of Ecology, Evolution, and Systematics

Freshwater Fish Invasions: A Comprehensive Review

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Keywords

pathways, life history traits, impacts, management, characteristics

Abstract

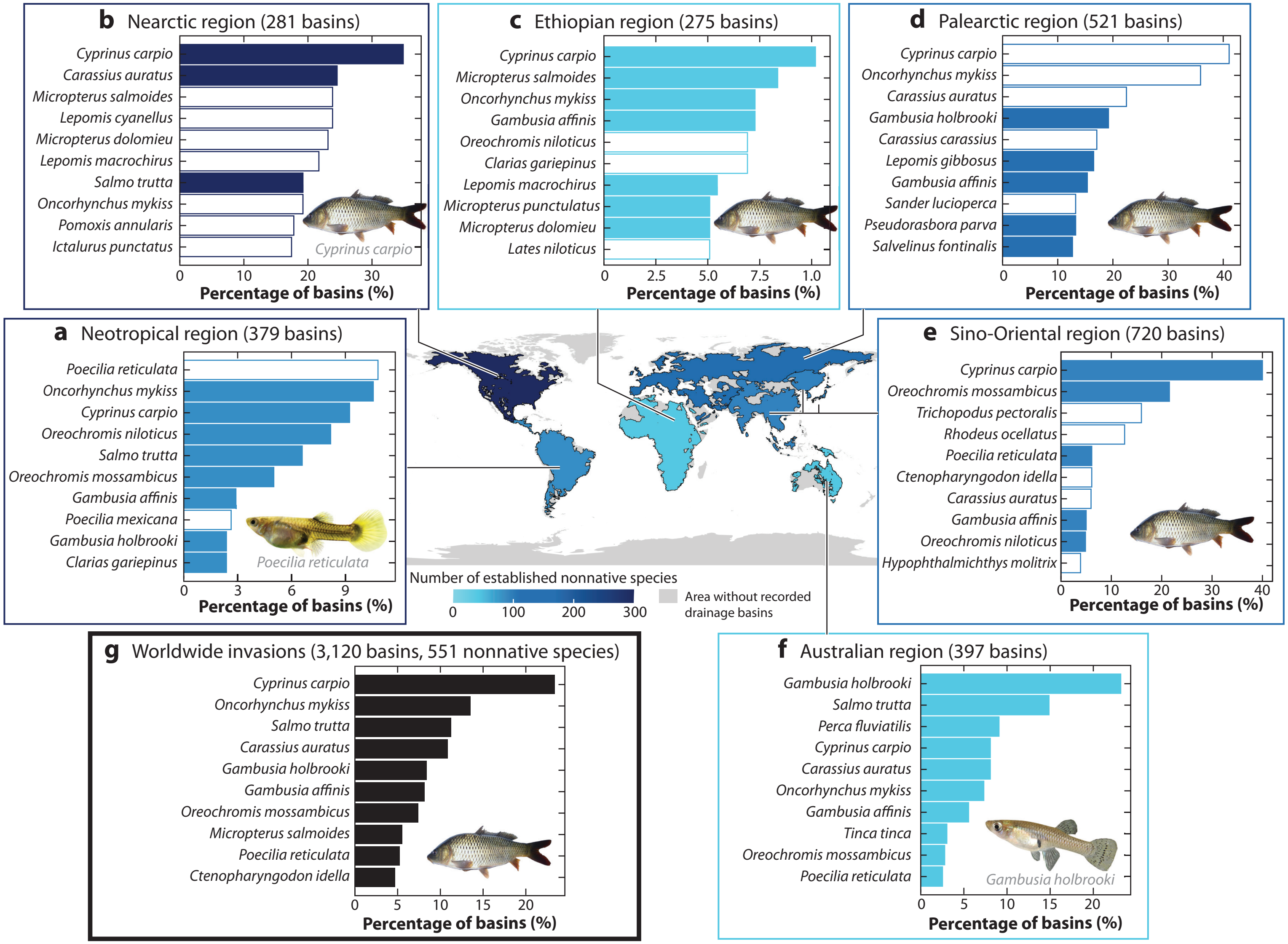
Freshwater fish have been widely introduced worldwide, and freshwater ecosystems are among those most affected by biological invasions. Consequently, freshwater fish invasions are one of the most documented invasions among animal taxa, with much information available about invasive species, their characteristics, invaded regions, invasion pathways, impacts, and management. While existing reviews address specific aspects of freshwater fish invasions, there is still a gaping lack of comprehensive assessments of freshwater fish invasions that simultaneously address pivotal and connected elements of the invasion process. Here, we provide a holistic review, together with quantitative assessments, divided into four major parts: (*a*) introduction pathways, (*b*) characteristics of nonnative species and invaded ecosystems that explain successful invasion processes, (*c*) invasion impacts and their mechanisms, and (*d*) management. We highlight data gaps and biases in the current databases and highlight a basic lack of understanding of several aspects of freshwater fish invasions. In addition, we provide recommendations for future studies.

1. INTRODUCTION

The growth of global trade has resulted in the intentional and unintentional displacement of many species beyond their natural geographic ranges (Seebens et al. 2017). From 1800 to 2000, new species introductions increased worldwide, and this trend is expected to continue over the next few decades (Seebens et al. 2017, 2021). These new species introductions can lead to biological invasions, which are a major source of change and decline in global biodiversity (Bellard et al. 2016), as well as a major source of economic loss (Haubrock et al. 2022). The invasion process is often divided into five successive stages (Moyle & Light 1996a, Blackburn et al. 2011): (*a*) transport of a species beyond its native range through human-mediated pathways, (*b*) introduction into a new environment, (*c*) establishment (i.e., generation of a self-reproducing population), (*d*) spread, and (*e*) impacts (i.e., changes induced by the invasive species in the receiving ecosystem).

Although the history of fish transportation dates back to at least the Zhou Dynasty (1046–256 BCE) in China (Zhao et al. 2015) and the Roman Empire in Europe (first and second century CE) (Balon 1995), the rate of global transportation and introduction of fish has substantially increased since the industrial revolution (eighteenth century). Seebens et al. (2017) reviewed the first records of established nonnative freshwater fish species per country, and this data suggest a massive increase in the cumulative number of first records during the mid-twentieth century followed by a short period with fewer additions (**Supplemental Figure 1**). Nowadays, freshwater fish species are among the most introduced taxa (Gozlan 2008), and they occur in all biogeographic regions (Leprieur et al. 2008) (**Figure 1**). At the global scale, 551 nonnative freshwater fish species have been recorded as established, with the common carp (*Cyprinus carpio*) being the most widely established species (**Figure 1**). Once established, nonnative fish can proliferate, spread, and cause ecological and/or socioeconomic impacts, in which case we define them as invasive following (Lewis et al. 2016). Note that the definition of invasiveness can vary in the literature, depending on whether or not the impact is included (Pyšek & Richardson 2010, Blackburn et al. 2011), be it ecological or socioeconomic. Invasive freshwater fish have been an important driver of biodiversity changes over the past two centuries (Su et al. 2021). Indeed, a wide range of ecological impacts due to invasive nonnative fish have been reported, including declines in native fish populations and species extinctions (Aloo et al. 2017), which cause profound changes in food webs and even an overall trend toward biotic homogenization (Villéger et al. 2011). Freshwater fish invasions also result in economic and human health impacts (Gozlan et al. 2010b, Cucherousset & Olden 2011, Haubrock et al. 2022). Globally, freshwater ecosystems are among the most affected by biological invasions (Ricciardi & MacIsaac 2010), which is particularly problematic given their importance in terms of ecosystem services (e.g., water supply, food, and economic productivity through fisheries and aquaculture) (Carpenter et al. 2011).

Fish invasions have been well documented around the world (Rahel 2000), with several reviews focusing on notorious invaders such as mosquitofish (*Gambusia* spp.) (Pyke 2008) and Nile perch (*Lates niloticus*) (Aloo et al. 2017) or on specific regions of ecological or economic importance such as Spain (Elvira & Almodóvar 2001), Poland (Grabowska et al. 2010), South Africa (Ellender & Weyl 2014), and the North American Great Lakes (Escobar et al. 2018). Other reviews focus on certain stages of the invasion process such as entry routes, impact, and management (Gozlan et al.



(Caption appears on following page)

Figure 1 (*Figure appears on preceding page*)

Percentage of basins in which introduced nonnative freshwater fish species have established at the bioregional (*blue gradient*) and global (*black*) scales. Only the ten species with the highest percentage of invaded basins are represented for each bioregion; the most common species for each bioregion is illustrated. Solid bars indicate introductions of species not native to the biogeographical region, whereas open bars indicate introductions of species within their native biogeographical region (i.e., a species can be native to part of a region but introduced elsewhere in that region). We used data from Tedesco et al. (2017), which were filtered to include only species for which freshwater is recorded as one of their habitats in FishBase (Froese & Pauly 2022). We used the freshwater fish biogeographical regions defined by Leroy et al. (2019). Photo in panels *a–e* reproduced from BlueBreezeWiki/Wikimedia (**https://upload.wikimedia.org/wikipedia/commons/5/5f/190729_Guppy_01.jpg**) (CC-BY SA 3.0). Photo in panel *b* reproduced from George Chernilevsky/Wikimedia (**https://upload.wikimedia.org/wikipedia/commons/3/3b/Cyprinus_carpio_2008_G1_%28cropped%29.jpg**) (CC-BY SA 3.0). Photo in panel *f* reproduced from MarshBunny/Wikimedia (**https://upload.wikimedia.org/wikipedia/commons/d/d3/EasternMosquitoFishJG_Female.jpg**) (CC-BY SA 4.0).

2010b); fisheries and aquaculture pathways (Gozlan 2017); or ecological impacts (Cucherousset & Olden 2011). Alongside these species-, region-, or process-focused reviews, several studies went beyond fish and considered freshwater invasions more broadly (Fuller 2015, McKnight et al. 2017), which makes it difficult to isolate information that specifically pertains to freshwater fish. Consequently, a comprehensive review of introduction pathways and the factors influencing invasion success, impacts, and management is still lacking. Such an integrated overview is necessary to understand the role and importance of different introduction pathways, to characterize the key drivers of invasion success, and to summarize the different impact mechanisms and management plans implemented to counter freshwater fish invasions. This overview facilitates integrative analyses, combining the pathways of introduction, the life history traits of nonnative species, and the characteristics of the receiving ecosystems (Novoa et al. 2020), which allows us to better predict invasions and their impacts and to set up effective management actions (Elbakidze et al. 2018).

In this review, we focus on fish (i.e., Actinopterygii and Cyclostomata) that have freshwater listed as one of their habitats in FishBase (Froese & Pauly 2022). Fish living only in brackish water and/or saltwater were not considered (e.g., *Sparus aurata*). Specifically, we assess four aspects of freshwater fish invasions:

1. The pathways by which nonnative freshwater fish species are introduced around the world and their relative importance in terms of the number of established nonnative fish species
2. The characteristics of nonnative species and receiving ecosystems, which can affect the success of each stage of the invasion process
3. The main impacts and the impact mechanisms of invasive nonnative freshwater fish species and their relative importance according to the Global Invasive Species Database (GISD) (ISSG 2015)
4. The methods and techniques used for management, with special attention paid to recently developed or emerging approaches

This review provides a state-of-the-art assessment of the key aspects of freshwater fish invasions worldwide, while identifying gaps and limitations in the current literature, and can serve as a roadmap for future studies.

2. PATHWAYS OF INTRODUCTION

The globalization of trade and the value of imported products are known to be linked to the introduction of nonnative fish worldwide (Turbelin et al. 2017). In this section, we describe the pathways by which nonnative freshwater fish species enter receiving environments. Further information and examples of introduction pathways are available in **Supplemental Appendix 1**.

2.1. Aquaculture

Aquaculture, which primarily refers to the farming of fish and other aquatic species (Kerr et al. 2005), contributes to a substantial share of establishment events for nonnative freshwater fish species worldwide: Out of the 1,649 freshwater fish establishment events listed in FishBase (Froese & Pauly 2022), 42% are the result of species introduced through aquaculture (**Supplemental Figure 2**).

Legal aquaculture stocking can introduce undesirable nonnative species due to fish escaping from the aquaculture facilities where they are reared. They may also be accidentally released instead of or along with the intended fish, following the misidentification or careless culling of stocks (Mandrak & Cudmore 2010). The composition of species escaping from aquaculture facilities depends on the species cultivated in the region (Center of Food Safety 2012). For example, in Australia, fish escaping from aquaculture facilities resulted in the introduction of several nonnative species such as the shortfin eel (*Anguilla australis*) and Australian bass (*Macquaria novemaculeata*) (Lintermans 2004).

Aquaculture also involves the trade in live freshwater fish, which consists of their import, transfer, and distribution (Kerr et al. 2005). The live fish trade is a significant vector for the transportation of nonnative fish, but there is no clear evidence of its role in introducing nonnative fish apart from a few anecdotal examples (see Rixon et al. 2005).

The importance of the aquaculture pathway is expected to increase in the future, with predicted growth in supplementary hatchery stocking programs worldwide and in nonnative fish aquaculture in most tropical developing countries (Britton & Orsi 2012, Bezerra et al. 2019, Vitule et al. 2019).

2.2. Ornamental Trade

The ornamental fish trade is a growing, multi-billion dollar industry involving more than 125 countries and 2,500 fish species, with 60% of these species being of freshwater origin (Dey 2016). It is well recognized that the ornamental fish trade is a major pathway for the introduction and establishment of fish (Strecker et al. 2011, Fuller 2015). According to FishBase data, 17% of establishment events are the result of species introduced through the ornamental trade (**Supplemental Figure 2**). Indeed, most ornamental fish sold in pet shops are nonnative and can become invasive if released into suitable habitats (Strecker et al. 2011).

The frequency of ornamental species introductions depends on their popularity, with popular species being discarded more frequently and in greater numbers (Duggan et al. 2006, Gertzen et al. 2008). Currently, 90% of fish species in the ornamental trade are of tropical origin (Evers et al. 2019), including the most popular species, Poeciliidae and tetras (Characiformes) (Duggan et al. 2006, Strecker et al. 2011). The tropical origin of ornamental fish species makes their establishment and spread unlikely in temperate countries, where most ornamental trade has historically taken place (Gozlan et al. 2010b). However, there are major invasion risks in tropical countries with significant levels of ornamental trade (e.g., China, Malaysia), as some are trade hubs where the reexportation of their imports occurs (Dey 2016). Climate change may also create new invasion opportunities for tropical species in temperate areas in the near future (e.g., Herborg et al. 2007).

Introduction threats from the ornamental trade are increasing with the recent development of online trade, which has contributed to the transport of over a million fish worldwide in recent years (Olden et al. 2020). Online markets also increase the diversity of traded species and facilitate trade in prohibited species, thereby increasing the risk of invasive species introductions.

2.3. Release of Bait for Angling

Recreational fishing, most often through angling, involves catching animals that are not a primary source of food and that are not usually sold or traded (Arlinghaus et al. 2012). Anglers frequently use live fish as bait, and the majority discard any unused bait (Kilian et al. 2012). Many anglers erroneously believe that releasing bait is beneficial to ecosystems and game fish populations, despite the existence of prohibitory laws (Kilian et al. 2012, Drake & Mandrak 2014). Therefore, bait release is an important pathway of introduction into areas where angling is common, with high reported rates of establishment (Gascho Landis et al. 2011). According to FishBase, 14% of nonnative freshwater fish establishment events worldwide are the result of species introduced through angling and bait release (**Supplemental Figure 2**). The causes of this high rate of establishment are twofold. First, environmental conditions are usually suitable for the released bait due to the physical proximity of the angling and source sites. Indeed, baiting fish are either caught by anglers themselves or purchased from local retailers and then transported to a nearby angling site (Gascho Landis et al. 2011, Drake & Mandrak 2014). Second, the propagule pressure resulting from this pathway can be significant [e.g., in Maryland, USA, 65% of anglers using live fish as bait discarded any unused bait (Kilian et al. 2012)]. Recreational fishing is currently growing in popularity in some regions such as Central Europe (Lyach & Čech 2018), Brazil (Freire et al. 2012), and India (Gupta et al. 2015), and other developing countries will likely follow. This increase may lead anglers to visit a higher number and greater diversity of fishing grounds, thereby increasing the likelihood of introducing nonnative fish (Lyach & Čech 2018). Nevertheless, this trend could be reversed by increasing awareness through the introduction of more appropriate restrictions and controls by fishery guards (Lyach & Čech 2018).

2.4. Biological control

Nonnative fish species have been introduced as biological control agents to control weeds or mosquitoes, among other pests (Beisel & Lévêque 2010). However, some nonnative species used as biological control agents have become established and invasive, leading to catastrophic ecological impacts (Copp et al. 2005). According to FishBase, 9% of freshwater fish establishment events are the result of species introduced through biological control (**Supplemental Figure 2**). Typical examples are the mosquitofish species (*Gambusia affinis* and *Gambusia holbrooki*), which were introduced worldwide to control the mosquito populations responsible for malaria epidemics (Lintermans 2004). Biological control has been a major pathway for invasion in the past (Beisel & Lévêque 2010). Regulations preventing such introductions have increased in the last few years, although there is a lack of evidence regarding their effectiveness. In the near future, climate change is likely to favor the emergence of mosquito-borne pathogens in new locations, leading to the possible introduction of nonnative fish to control mosquitoes (Azevedo-Santos et al. 2017). For these two reasons, biological control is likely to remain an important introduction pathway in the future (Pyke 2008, Azevedo-Santos et al. 2017).

2.5. Stocking for Fisheries

Fish stocking is the practice of supplementing wild stocks with hatchery-reared fish to establish new fisheries, bolster threatened or overfished native populations, or support recreational fisheries. This global management practice has existed for over a century (Gozlan et al. 2010b, Fuller 2015). Most stocking occurs with native species, but it can also be used to introduce new species for economically valuable fisheries (Mandrak & Cudmore 2010, Fuller 2015, Teletchea 2019). Stocking has led to biological invasions worldwide, with disastrous ecological and economic impacts, such as the invasions caused by the enrichment of wild fisheries in China (Hulme 2015) or invasions by Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*) in Lake Victoria in Africa (Cucherousset & Olden 2011) (**Supplemental Appendix 2**). According to FishBase, 7% of nonnative freshwater fish establishment events result from species introduced for fishing (**Supplemental Figure 2**). As it is generally difficult to disentangle legal and illegal stocking, the extent of illegal stocking is unknown. However, several examples suggest that it can be substantial at a local level (e.g., Lintermans 2004, Kerr et al. 2005, Johnson et al. 2009). For example, a single person introduced 15,000 nonnative fish into New Zealand and irreversibly changed the country's freshwater ecosystems (Mitchell 2020). Legal frameworks to regulate illegal stocking are increasingly being adopted, although they have been widely criticized for their ineffectiveness (Johnson et al. 2009), which is still demonstrated by recent examples (Fernández et al. 2019).

2.6. Ballast Transport

Since the 1800s, ballast water has been used to increase the stability and maneuverability of ships during voyages. This procedure involves taking on very large volumes of water as a ship leaves port and discharging them in the port of arrival. Although fish constitute only a small proportion of the transported organisms (Wonham et al. 2000, Bailey 2015), it is well established that ballast water is a nonnegligible pathway for the unintentional introduction of fish, even if it is less significant for freshwater than for marine fish (Wonham et al. 2000, Fuller 2015). So far, there are unconfirmed examples, such as the yellow-finned goby (*Acanthogobius flavimanus*) and the streaked goby (*Acentrogobius pflaumii*) (Francis et al. 2003, Lintermans 2004). However, this pathway is less likely to lead to future fish introductions. Legislation to reduce ballast water introductions, particularly for large ships, has been implemented worldwide, with the inclusion of quotas of viable organisms per cubic meter of ballast water and the obligation to conduct mid-oceanic ballast water exchange (Verna & Harris 2016) to kill any freshwater organisms in the ballast water.

2.7. Interconnected Waterways

Human activities can break down natural geographic barriers through the construction of canals or other structures linking two contiguous basins that were originally completely independent (Galil et al. 2007). For example, over the last two centuries, the surface of the catchment areas connected to the Rhine River by inland canals has increased 21.6-fold (Leuven et al. 2009). These connections facilitate freshwater invasions in two ways. First, they allow fish to move between previously inaccessible basins, and second, they allow nonnative fish species introduced via another pathway to expand into previously independent river basins. Well-known examples include *Gobiidae*, which can now reach new areas through canals connected to the Danube (Rabitsch et al. 2013, Zoric et al. 2014), and several species from the Panama canal region. Indeed, construction of the Panama canal allowed the connection of the Rio Chagres and the Rio Grande drainage basins, leading to species exchanges between them (Smith et al. 2004). In addition to canals, dams can also connect waterways, as evidenced by the construction of a hydroelectric dam that allowed 33 fish species to reach the upper part of the Rio Paraná in South America after flooding waterfalls that acted as a natural barrier (Júnior et al. 2009). Even today, new canal construction projects are underway, such as the One Belt One Road project (Wong et al. 2017). One Belt One Road is a major construction strategy adopted in 2013 by the Chinese government to develop roads across Asia, reaching as far as Africa and Southern Europe, with planned infrastructure including ports, canals, and dams. These new structures are expected to become a driver of future freshwater fish introductions and expansions.

2.8. Other Pathways of Introduction

2.8.1. Prayer animal releases. Animal releases, as a part of prayer rituals and offerings or as a means of protecting living organisms, are practiced in some religions such as Buddhism or Taoism (Everard et al. 2019). Successful introductions of invasive freshwater fish have been attributed to this pathway in China (Everard et al. 2019), Canada (Lintermans 2004, Beisel & Lévêque 2010, Liu et al. 2012), and the United States (Fuller 2015). Overall, this pathway appears to be less notable than the other pathways, and there is no evidence to suggest it is increasing.

2.8.2. Acclimatization societies. Acclimatization societies aimed not only to establish in colonized countries the species that were familiar and representative of European colonizing countries but also to promote the spread of nonnative species throughout Europe (Arthington & McKenzie 1997). These societies have been responsible for introducing nonnative fish into Australia (Arthington & McKenzie 1997, García-Díaz et al. 2018), Russia, Britain, Europe (Gherardi et al. 2009), and New Zealand (McDowall 1994). Although this pathway was a major cause of fish introductions before 1970, it is now of minor importance due to global recognition of the negative impacts of nonnative species (García-Díaz et al. 2018) leading to laws banning such introductions in several countries (Copp et al. 2005).

2.8.3. Biodiversity conservation. Anecdotally, introductions of nonnative freshwater fish can result from translocation programs to prevent species extinctions. This is the case for the huchen (*Hucho hucho*) in Poland (Witkowski et al. 2013) and the Pedder galaxias (*Galaxias pedderensis*) in Australia, both of which have been moved outside of their native range to prevent extinction (Chilcott et al. 2013). Nevertheless, future translocations associated with climate change initiatives could increase the number of species established outside their native range through this pathway (Thomas 2011).

2.8.4. Unintentional transport via fishing gear or animals. Aquatic animals can be transported from one water body to another on equipment such as boat hulls or fishing gear, as well as on animals. The importance of this pathway for fish has been illustrated only anecdotally in the literature. For example, it was shown that the nets of eel fishermen in Tasmania, Australia, may be responsible for moving redfin perch between adjacent water bodies (Lintermans 2004).

3. FACTORS INFLUENCING THE INVASION SUCCESS OF NONNATIVE FISH

The invasion success of a nonnative species is governed not only by the likelihood of the species being transported and introduced but also by its ability to survive and spread in the new environment. Therefore, the success of the invasion may result from one of several interacting factors: the propagule pressure of the nonnative species, life history traits, residence time, and characteristics of the receiving ecosystem. In the following sections, we discuss these factors separately, although invasion success may be driven by multiple factors simultaneously (e.g., Woodford et al. 2013). Further details and examples of these factors are described in **Supplemental Appendix 1**.

3.1. Propagule Pressure

Propagule pressure has two features: propagule size, which is the number of fish individuals arriving during an introduction event, and propagule number, which is the number of introduction events (Simberloff 2009). Propagule pressure has been shown to significantly increase establishment success, as the larger number of introduced individuals increases both the genetic diversity and the survival probability of the introduced population (e.g., due to reduced risk of stochastic extinctions and increased probability of having individuals with a high dispersal and reproduction capacity) (Woodford et al. 2013). Although a large propagule size facilitates establishment, it is not always necessary. For example, the life history traits of the topmouth gudgeon (*Pseudorasbora parva*) mean that its population can grow rapidly in uncompetitive environments (e.g., fishless environments), thus allowing the species to establish with only a few introduced individuals (Britton & Gozlan 2013). Indeed, the influence of propagule pressure on invasion success is highly dependent on the life cycle and life history traits of the introduced species, as well as on the suitability of the receiving habitat (Gertzen et al. 2008). Propagule pressure also depends on the pathways of introduction, and future trends in propagule pressure should follow the expected trends for each pathway.

3.2. Life History Traits

Each stage of the invasion process is influenced by life history traits, although the relative importance of specific traits varies between stages (Kolar & Lodge 2002). Indeed, the traits associated with the transport and introduction stages are highly diverse and depend on whether or not the introduction was intentional. Intentionally introduced species can be expected to have traits selected in relation to their utility to humans. For example, species intentionally introduced for stocking are often large fish, which are preferred by anglers and consumers (Fuller 2015, Su et al. 2020). By contrast, the morphological and ecological traits of unintentionally introduced species depend on the nature of the pathway. Species that are transported and introduced by ballast water are generally small, with preadapted traits that allow them to survive in ballast water, such as a specialized lateral line for hunting in the dark [e.g., *Gobiidae* (Wonham et al. 2000, Fuller 2015)]. Other examples can be found in **Supplemental Appendix 3** (see also García-Berthou 2007).

Traits associated with successfully established species appear to be less diverse than those of transported or introduced species due to the environmental filtering effect (Su et al. 2020). Existing evidence suggests that established species tend to have a generalist diet, broad environmental tolerance, and high plasticity (i.e., traits that allow them to adapt to a wide range of environmental conditions) (Kolar & Lodge 2002, Tonella et al. 2018). This is the case with the invasive topmouth gudgeon, which is found in 32 countries and characterized by high phenotypic plasticity in its growth and reproductive traits (Gozlan et al. 2010a). However, specialist species may occasionally become established due to their ability to exploit specific resources that are not limited in the environment [e.g., detritivores (Moyle & Light 1996a, Tonella et al. 2018)]. In addition to these general patterns, there is an interaction between the traits of the established species and the environmental conditions of the receiving ecosystem. Species established in highly variable environments tend to have higher fecundity, earlier maturity, faster growth, and smaller adult size compared to those established in stable environments (Moyle & Marchetti 2006). For example, invasive species in the Iberian Peninsula colonized different types of streams depending on the seasonal flow patterns: Small species with high offspring numbers preferentially colonized streams with high seasonality, while large fish with delayed maturity and a lower spawning rate invaded streams with regular flows (Vila-Gispert et al. 2005).

Traits associated with the spread and impact of nonnative species have rarely been studied, except in predictive and profiling studies, which means that assumptions about the underlying mechanisms remain unresolved and speculative (Kolar & Lodge 2002; Marchetti et al. 2004a, 2004b; Moyle & Marchetti 2006; Ribeiro et al. 2008). In general, the successful spread and impact of species seem to depend on their broad physiological tolerance and origin from a nearby region; this highlights the importance of preadaptation to invaded ecosystems. However, studies are inconsistent regarding the impact measures; hence, the relationship between traits and impacts remains unresolved for freshwater fish (Howeth et al. 2016). Some studies predict that small species produce greater impacts than large ones (e.g., Marchetti et al. 2004b), although existing evidence suggests that large fish can cause catastrophic ecological impacts, as in the cases of the Nile perch (Aloo et al. 2017) (**Supplemental Appendix 2**) and largemouth bass (*Micropterus salmoides*) (Gratwicke & Marshall 2001). The correlative nature of the existing studies means that our understanding of the underlying mechanisms is speculative or limited. For example, species with small eggs are correlated with high impacts, although this correlation is poorly understood (Kolar & Lodge 2002, Snyder et al. 2014).

3.3. Residence Time

The residence time of nonnative species, or the time since the first recorded introduction, plays an important role in the spread and impact stages (Wilson et al. 2007). Residence time has been shown to be linked to the spread of nonnative species via colonization success (Buckwalter et al. 2020) and the size of the introduced range (Rabitsch et al. 2013). Species impacts may evolve over time and can sometimes increase even without new introductions (Rabitsch et al. 2013); for example, the impacts of the Nile perch increased significantly 20 years after its first introduction (Taabu-Munyaho et al. 2016) (**Supplemental Appendix 2**). The mechanisms by which residence time may affect establishment, spread, and impacts can be linked to various hypotheses from invasion science, including adaptation, evolution of increased competitive capacity, defense displacement, windows of opportunity, and biotic acceptance (Jeschke et al. 2018).

3.4. Inherent Characteristics of Invaded Ecosystems

3.4.1. Proximity between donor and receiving environments. Apart from propagule pressure, life history traits, and residence time, the characteristics of the receiving environment are also very important in explaining invasion success. Therefore, the ecological and geographic proximity between the donor and recipient ecosystems is likely to contribute to the establishment of nonnative species, with these two components often being linked (Nekola & White 1999). Species originating from a nearby region are most likely to encounter the same abiotic conditions (e.g., temperature) in the receiving environment and therefore be preadapted there (Moyle & Light 1996b, Moyle & Marchetti 2006). Most introduced species are introduced into the same biogeographic region as their native region, where they experience similar climatic conditions (Blanchet et al. 2009; B. Leroy, unpublished data). For example, fish that are intentionally introduced for economic or recreational reasons tend to be released in places where they are expected to thrive (Ruesink 2005). Nevertheless, some species can become invasive in climatically different regions due to their high plasticity and adaptability [e.g., topmouth gudgeon, goldfish, and mosquitofish (Fletcher et al. 2016)].

3.4.2. Anthropization and perturbations. Abrupt environmental changes are also known to facilitate biological invasions (Zhang et al. 2006). When disturbances occur too rapidly, many native species cannot cope, leading to their lower abundance, local extinction and the creation of unoccupied niches left free for nonnative species (Havel et al. 2005, Clavero et al. 2013). Aquatic ecosystems that are heavily or frequently disturbed by humans therefore seem to be highly susceptible to invasions. For example, dam density and reservoir area, which are related to the alteration, destruction, and fragmentation of freshwater habitats, as well as to hydrological changes (Leprieur et al. 2008, Clavero et al. 2013), are positively associated with the number of nonnative aquatic species (Marchetti et al. 2004a, Clavero et al. 2013, Su et al. 2021). Artificially created habitats such as water impoundments may also facilitate invasions, because they are more accessible to humans than natural lakes and also because they reduce the distance between invaded and noninvaded areas, thus increasing the likelihood that natural lakes will in turn be invaded (Johnson et al. 2008). Water consumption for energy production or irrigation also generates water-level fluctuations and temperature changes that profoundly alter aquatic habitats and exclude some native species, which are often replaced by more tolerant nonnative species (Hudon 1997).

At a larger scale, climate change may also influence freshwater fish invasions by causing temperate zones to match the climatic requirements of tropical or subtropical species, thus creating new niches for nonnative species, as is the case for tropical snakeheads (Channidae) in the USA (Herborg et al. 2007). In addition, climate change may also affect other aspects of freshwater invasions, ranging from pathways (e.g., emergence of a new optimal area for aquaculture) to their impacts [e.g., shifts in competitive dominance (Rahel & Olden 2008)].

3.4.3. Native community diversity. Species diversity in recipient communities also plays an important role in invasion success, via three main mechanisms detailed in the following sections: biotic resistance, enemy release, and invasion meltdown. Other mechanisms have also been hypothesized to explain the effects of native community diversity on invasion processes such as indirect biotic effects, novel associations, and missed mutualisms (Jeschke et al. 2018, Enders et al. 2020). However, these hypotheses are not well described or explored in the literature on freshwater fish.

3.4.3.1. Biotic resistance. The biotic resistance hypothesis suggests that richer communities are characterized by higher functional redundancy, stronger competition, and fewer unoccupied niches than poorer communities, which reduce their susceptibility to invasion (Gozlan et al. 2010b, Havel et al. 2015, Pelletier et al. 2020). However, the biotic resistance hypothesis for freshwater fish has not yet been validated. Of the nine studies examining this issue for freshwater fish between 2001 and 2015, four supported the biotic resistance hypothesis, four questioned it, and one neither supported nor rejected it (Jeschke et al. 2018). We speculate that these divergent observations may be explained by the scale of the studies: Those supporting the hypothesis were conducted at local or regional scales (Habit et al. 2012), while those not supporting it were conducted at larger scales at which the species–area relationship may have had stronger effects (Fitzgerald et al. 2016).

3.4.3.2. Enemy release. The enemy release hypothesis states that an introduced species often experiences a reduction in predators, parasites, or pathogens in its new ecosystem compared to its native range (Torchin et al. 2003). Of the twelve studies examining the enemy release hypothesis for freshwater fish between 2008 and 2016, seven supported the hypothesis, one questioned it, and four neither supported nor rejected it (Jeschke et al. 2018). However, only parasitism was studied. Native parasites may have difficulties adapting to new hosts, and introduced fish tend to be parasitized by fewer individuals than native fish, in part because of the low probability of invasive species introducing their parasites (Torchin et al. 2003, Roche et al. 2010). Moreover, even when introduced fish do not avoid infection with parasites, they can avoid their negative effects, as shown by Lacerda et al. (2013). Overall, the enemy release hypothesis has been recognized as an important factor for explaining the success of invasions, although the amount of published evidence regarding fish remains incomplete (Roche et al. 2010, Jeschke et al. 2018).

3.4.3.3. Invasional meltdown. Although the presence of some established nonnative species can negatively affect or prevent new invasions, others may directly or indirectly increase the chances of success for new invasive species, through a process known as invasional meltdown

(Simberloff 2006). Of the twenty-three studies investigating invasional meltdown for freshwater fish between 2008 and 2016, nine supported the hypothesis, twelve questioned it, and two neither supported nor rejected it (Jeschke et al. 2018). For example, the invasive topmouth gudgeon carries the rosette agent parasite *Sphaerothecum destruens* without being affected by it. This intracellular parasite can, however, cause massive declines in native fish populations, which in turn allows the topmouth gudgeon to overcome native competition, establish, and invade environments (Ercan et al. 2015).

4. IMPACTS

Invasive freshwater fish are directly responsible for ecological impacts in natural ecosystems, as well as economic damage to fisheries, aquaculture, and human infrastructure and health (Haubrock et al. 2022). Although the ecological and socioeconomic impacts have very different effects, they share common mechanisms (Levine et al. 2003). In this section, we first explore the main mechanisms responsible for the impacts of invasive freshwater fish and then discuss the associated ecological and socioeconomic impacts (**Supplemental Appendix 4**).

4.1. Mechanisms

Several mechanisms are described in the GISD, each related to how invasive freshwater fish species interact with native and other invasive species (e.g., competition, predation, disease and parasite transmission, and hybridization), as well as with the native habitat (e.g., burrowing and browsing) (ISSG 2015). The main mechanisms involve interactions with native species (96% of 198 described cases), followed by interactions with the native habitat (3% of cases described) (**Figure 2*a***).

4.1.1. Competition. Competition is the main mechanism described in both the GISD (53% of cases) (**Figure 2*a***) and the literature on ecological impacts. Indeed, field data and experiments have repeatedly shown that the trophic niches of invasive and native fish species overlap (Schleuter 2007, Sampson et al. 2009, Minder et al. 2020). In addition, invasive fish also compete with organisms found outside their freshwater habitats, such as riparian spiders and birds (Epanchin et al. 2010, Jackson et al. 2016). Specific traits of some invasive fish such as aggressive behavior or increased foraging abilities help invasive species to outcompete native species for food, particularly in degraded ecosystems (Bergstrom & Mensinger 2009, Abrahams et al. 2017). Overall, the indirect and cascading effects of competition from invasive fish on ecosystems have been suggested in a limited number of studies (Eby et al. 2006) but remain anecdotal at this time.

4.1.2. Predation. Predation is the second most frequently described mechanism for the ecological and socioeconomic impacts of invasive freshwater fish (30% of cases described) (**Figure 2*a***). Many examples illustrate the strong influence of predation such as the case of peacock bass (*Cichla monoculus*) introduced in Lake Gatun, Panama. This example suggests that invasive predatory fish can have irreversible consequences on the composition and functional diversity of native ecosystems (Sharpe et al. 2017). Another famous example is the predation by the invasive Nile perch in the Lake Victoria, which led to "the first mass extinction of vertebrates that scientists have ever had the opportunity to observe" (Kaufman 1992, p. 846) (**Supplemental Appendix 2**).

4.1.3. Hybridization. Hybridization involves the mating of individuals from two genetically distinct populations (Harrison & Larson 2014) (8% of cases described) (**Figure 2*a***). Hybridization between closely related invasive and native fish species is common due to their external mode of fertilization (Olden et al. 2004, Ludwig et al. 2009, Blackwell et al. 2020). For example, in the

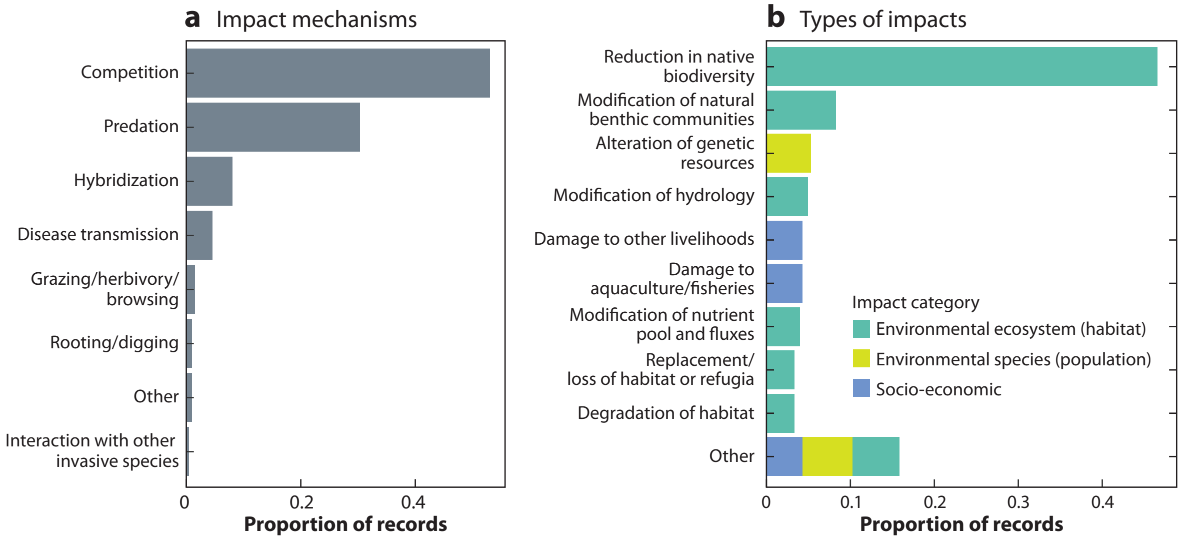


Figure 2

Bar charts illustrating the relative proportion of records of (*a*) impact mechanisms (198 records) and (*b*) types of impacts (303 records) for nonnative freshwater fish. Data are taken from the Global Invasive Species Database (GISD) (ISSG 2015). The GISD compiles impacts and mechanisms of invasive species worldwide with geographic and temporal details. Each record is defined here as the documented observation of (*a*) a mechanism or (*b*) an impact of one species in one location. The spatial resolution of records is variable; some records were recorded at the country level, whereas others were recorded at the scale of a drainage basin. Note that a species can have multiple records in each panel, either in the same category or in different categories.

United Kingdom, approximately 40% of the British population of crucian carp (*Carassius carassius*) consists of hybrids with goldfish (Hänfling et al. 2005). In the Pecos River in Texas, the nonnative sheepshead pupfish (*Cyprinodon variegatus*) has hybridized with the native Pecos pupfish (*Cyprinodon pecosensis*). Hybrids were shown to replace Pecos pupfish populations, due to better swimming endurance and rapid growth rate (Rosenfield et al. 2004). In some cases, low rates of introgression can also have important impacts on the population. For example, hybrids between bull trout (*Salvelinus confluentus*) and brook trout (*Salvelinus fontinalis*) are often sterile, involving only a little introgression risk, as their genes are not passed to the next generation. However, this hybridization led to local declines of the bull trout, due to their loss of reproductive potential (Kanda et al. 2002) (**Supplemental Appendix 4**). Hybridization between native and invasive fish is likely to increase in the coming years due to shifts in species distributions as a result of climate change (Muhlfeld et al. 2017) and to the increased transportation and introduction of fish from aquaculture and fisheries. Stocking nonnative populations that are genetically distant from locally adapted native populations of the same species can also cause inbreeding or outbreeding depression, and as a result, impact the fitness of individuals (Ludwig 2006, Ludwig et al. 2009).

4.1.4. Disease and parasite transmission. Invasive fish can carry diseases and parasites from their native ranges that are transported and introduced along with their host into the new territory (Kuchta et al. 2018, Spikmans et al. 2020). Cointroduced parasites become invasive if they spread into native host populations in the new area (Lymbery et al. 2014). These co-invasive parasites are generally simple life-cycle parasites with no requirement for intermediate hosts (Sheath et al. 2015). Coinvasive parasites of freshwater fish are the fourth most common impact mechanism described in the GISD (5% of cases described) (**Figure 2*a***). Coinvasive parasites can be spread by multiple invaders such as the Asian fish tapeworm (*Schyzocotyle acheilognathi*), which has been co-introduced around the world with carps, guppies, and mosquitofish (Kuchta et al. 2018). Coinvasive parasites are considered to be disproportionately important for freshwater fish: Studies on host fish accounted for more than 50% of all studies on co-introductions (Lymbery et al. 2014). Evidence suggests that co-invasive parasites tend to have more detrimental effects in native fish populations than in their introduced vectors due to the lack of resistance in native hosts (Kirk 2003, Lymbery et al. 2014). For example, the nematode *Anguillicola crassus*, introduced into Europe with Japanese eels, has had a greater impact on native eels than it had on Japanese eels (Kirk 2003). However, the true impact of co-invasive parasites may be underestimated, because many parasites tend to go unnoticed and because their nonnative origin is often unresolved. Furthermore, their effects on native fish populations are difficult to demonstrate (Jarić et al. 2019).

We also note the mechanism of direct parasitism, which involves the parasitism of a native species directly by an invasive fish. However, direct parasitism is a rare mechanism for freshwater fish, as it has been demonstrated, to our knowledge, only for sea lampreys, a major invader in the North American Great Lakes (Cucherousset & Olden 2011, Siefkes 2017).

4.1.5. Interaction with native habitats: Digging and grazing or browsing. Ecosystem engineers are species that modify the resources and abiotic conditions of habitats, which, in turn, influence community composition (Emery-Butcher et al. 2020). Some invasive fish are known to be ecosystem engineers and to impact habitats through their foraging and reproductive behavior (**Figure 2*a***). For example, some invasive carp are responsible for suspending sediments due to their burrowing feeding habits, thereby increasing turbidity and erosion and releasing pollutants trapped in the soil (Matsuzaki et al. 2009, Emery-Butcher et al. 2020). The same behavior has been described for the invasive pumpkinseed (*Lepomis gibbosus*) during their nest construction (Beisel & Lévêque 2010).

4.2. Ecological and Socioeconomic Impacts

Ecological impacts are the most frequently described impact category for nonnative freshwater fish (87%) (**Figure 2*b***). These impacts have mainly been documented at the ecosystem level (76% of 303 cases) (**Figure 2*b***), although they can occur at all biological levels (genetic, individual, population, ecosystem, and biogeographic) (**Figure 2*b*, Supplemental Appendix 4**). For example, in Montana, USA, rainbow trout are known to hybridize with the native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), thus reducing the fitness of the latter species by lowering reproductive success and altering genetic resources (Muhlfeld et al. 2009). At the ecosystem level, invasive fish can be responsible for modifying nutrient fluxes (Matsuzaki et al. 2009). At biogeographic levels, introductions have caused an overall increase in fish species richness throughout basins worldwide by exceeding extinction rates (Villéger et al. 2011). This increase in richness has been associated with an increase in the functional diversity of assemblages (Toussaint et al. 2018). However, these changes in biodiversity were mainly caused by the introduction of a limited number of widespread species (Toussaint et al. 2016), leading to an increase in both taxonomic and functional similarity among aquatic systems and regions (Villéger et al. 2011, Su et al. 2021). This process, known as biotic homogenization, has been intensively studied in recent years (Rahel 2000, Villéger et al. 2011, Pool & Olden 2012, Villéger et al. 2014, Vargas et al. 2015, Campbell & Mandrak 2020) (**Supplemental Appendix 4**).

The socioeconomic impacts of nonnative fish are less studied and constitute only a minor part (13%) of the 303 cases described in the GISD (**Figure 2*b***). Nonnative fish can damage aquaculture, fisheries, and infrastructure, thus adding to the costs of management plans implemented to prevent ecological impacts and economic damage. For example, the sea lamprey eradication plan in the North American Great Lakes in 2001 cost US$13.5 million (Smith & Swink 2003). A recent study showed that impact costs have been estimated for only 27 invasive fish species, but these totaled approximately US$37 billion between 1960 and 2020 (Haubrock et al. 2022). As most species lack cost studies, these records are not only severely underestimated but also geographically and taxonomically biased. Most costs were recorded in North America; in addition, the majority of costs pertained to damage and resource loss (e.g., impacts on native fish stocks through predation), with very few management-related costs. However, most of these costs were based on extrapolations, while the observed costs were only US$2.28 billion. The discrepancy between cost estimates and reporting reflects the critical underreporting of economic costs for freshwater fish and the difficulty of estimating the cost of lost ecosystem services (Gozlan et al. 2010b, Haubrock et al. 2022). The substantial underestimation of nonnative fish costs may partly be related to the economic benefits associated with nonnative fish species [e.g., farmed fish, sport fishing (Gozlan 2008)]. In this uncertain context, Leprieur et al. (2009) and Vitule et al. (2009) have argued for a precautionary principle against introducing nonnative freshwater fish.

5. MANAGEMENT

Management techniques for dealing with freshwater fish invasions are numerous and depend on the stage of the invasion process. While prevention and early detection plus a rapid response can limit the introduction and establishment of invasive nonnative fish species, respectively, control and eradication techniques are required when the invasion is at a more advanced stage (Robertson et al. 2020).

5.1. Prevention, Early Detection, and Monitoring

Prevention entails acting before introduction takes place by avoiding the transport of fish species or their introduction into the wild (Robertson et al. 2020). For freshwater fish, legal frameworks have been implemented to mandate the treatment of ballast waters and thereby reduce the transport of species through this pathway (Werschkun et al. 2014, Robertson et al. 2020). In addition, laws have been passed to prohibit the illegal stocking of fish (Johnson et al. 2009). Risk assessment tools, such as the fish invasiveness scoring kit are also used by policymakers to distinguish between potentially invasive and noninvasive species of nonnative fish and provide an aid for developing legislation (Copp et al. 2008). Barriers can also be set up to avoid the introduction of fish species after the construction of a canal (Noatch & Suski 2012). The GISD contains information about the management approach used for 27 species through 40 records. A record is defined here as a management plan implemented for one species in one location. Based on these 40 records, prevention is the second most common management strategy, with 15 records linked to such management actions.

Once a nonnative species is introduced, it is important to detect it as early as possible. In addition to traditional techniques (e.g., netting, trapping, and electrofishing), which have limited effectiveness when the target species is represented by only a few individuals, several monitoring techniques can detect and track trends in nonnative species. For example, bioacoustic sensors are a noninvasive method that has been used to detect nonnative fish species [e.g., spotted Tilapia (*Tilapia mariae*) in Australia (Kottege et al. 2012, 2015)]. Another noninvasive technique is the use of environmental DNA (eDNA), which involves analyzing DNA from an environmental sample to detect species (Rees et al. 2014). The eDNA technique is more sensitive at detecting rare introduced fish species than traditional detection methods (Jerde et al. 2011) but cannot always provide the accurate location of target species in fast-flowing environments (Pont et al. 2018).

Detection techniques can also be used to study the invasion history of species and identify the introduction pathway. For example, Reshetnikov et al. (2011, 2017) used parasitological analysis to detect and study the introduction pathways of the invasive Amur sleeper (*Perccottus glenii*). Indeed, the detection of the specific parasite *Nippotaenia mogurndae* led to the detection of an invasive population of Amur sleeper and supported the hypothesis that it came from a nonaquarium introduction, as this parasite cannot survive with prolonged aquarium maintenance.

Additionally, citizen science and internet data are also promising monitoring tools for early detection and rapid response. For example, mobile phone applications such as Find a Pest or Invasive Alien Species Europe are monitoring, tracking, identification, and information tools for the general public (Pawson et al. 2020). Similarly, posts and conversations on social media can also be useful sources of information, as they may contain photos, species names, and/or geo-references (Daume & Galaz 2016). For example, the introductions of nonnative buffalo fish (*Ictiobus cyprinellus* and *Ictiobus niger*) into Czech rivers were detected from anglers' posts on online forums and websites (Kalous et al. 2018). Prevention and early response are recognized as the most effective (and cheapest) ways to manage invasive nonnative species (Leung et al. 2002). However, these measures obviously require the public's prior awareness of biological invasions. Monitoring tools used for early detection can also be useful for monitoring the abundance of the nonnative population after an eradication effort. Unfortunately, monitoring is the least documented management strategy for freshwater fish according to the GISD, as it was used for only 2 out of 40 records.

5.2. Eradication, Containment, and Suppression

As long as the area of invasion is very limited, and the nonnative population is small, eradication using several possible methods may be logistically and financially feasible. Chemical treatments such as rotenone have been widely used for years to eradicate species rapidly and efficiently, but they are also toxic to nontarget species (Knapp & Matthews 1998, Britton et al. 2011, Rytwinski et al. 2019) and not well accepted by the public (Bremner & Park 2007). Nevertheless, some chemical methods known for their selectivity and effectiveness are still used, such as lampricides to control sea lampreys (Siefkes 2017). Electrofishing and gill netting can be effective eradication methods, although they are far more expensive and time consuming than chemical treatments (Knapp & Matthews 1998, Bosch et al. 2019). More recently, new management techniques have been explored, such as genetic biocontrol methods to alter the sex ratio within a population, but they are still under development (Teem & Gutierrez 2014). In North America, a Trojan Y chromosome strategy is used to produce YY males of the invasive brook trout (Schill et al. 2016). Field evaluations of the efficiency of stocking YY male brook trout are ongoing in North American lakes and streams with encouraging results (Roth et al. 2020). Biological eradication techniques using specific viruses to control populations have also been considered for freshwater fish [e.g., common carp in Australia, using the host-specific CyHV-3 virus (McColl et al. 2014)]. This method remains risky due to the potential spillover of the virus to other species and requires a thorough knowledge of the targeted species as well as the epidemiology, virulence, and transmissibility of the virus (McColl et al. 2014, 2016).

In addition, when nonnative fish reproduce, spread over larger areas, and establish large populations, eradication ceases to be possible (Ahmed et al. 2022). In this case, management responses involve mitigating the invasive species or its impacts. Indeed, the control of freshwater fish is currently the main management measure that has been used for 23 of the 40 records listed in the GISD. For instance, containment measures can be implemented to limit the spread of invasive species. Species can be contained using physical barriers [e.g., common carp in New Zealand (Tempero et al. 2019)] or nonphysical barriers that alter the behavior of invasive species, e.g., electrical barriers, altered flow regimes, magnetic fields, or the addition of carbon dioxide and oxygen to create low oxygen zones (Noatch & Suski 2012). Suppression actions (i.e., reducing the distribution or abundance of the nonnative population in an area) can also be implemented (Robertson et al. 2020), as can selective capture, which can be promoted through public awareness and incentives. In addition the exploitation of invasive freshwater fish as a food source can be an effective suppression technique (Seaman et al. 2022). For example, in Lake Victoria, fishing of Nile Perch has led to a decline in these fish (Yongo et al. 2018). More recently, Bouska et al. (2020) showed that, with sufficient market demand, harvest could be an effective way to control the invasive bighead carp (*Hypophthalmichthys nobilis*) in the Mississippi River basin. In addition, management techniques formerly used for terrestrial invasions are beginning to be applied to freshwater fish (Simberloff 2021). This is the case with the sterile male technique (Bravener & Twohey 2016, Simberloff 2021), which has been recently applied to sea lampreys in the Great Lakes (Bravener & Twohey 2016) and with pheromones, which have great potential, as fish use pheromones to communicate. The pheromone technique has been tested for sea lampreys and common carp in order to reduce mating and reproductive success, redirect migratory invasive fish, or mass trap fish, with some encouraging results (Sorensen & Johnson 2016).

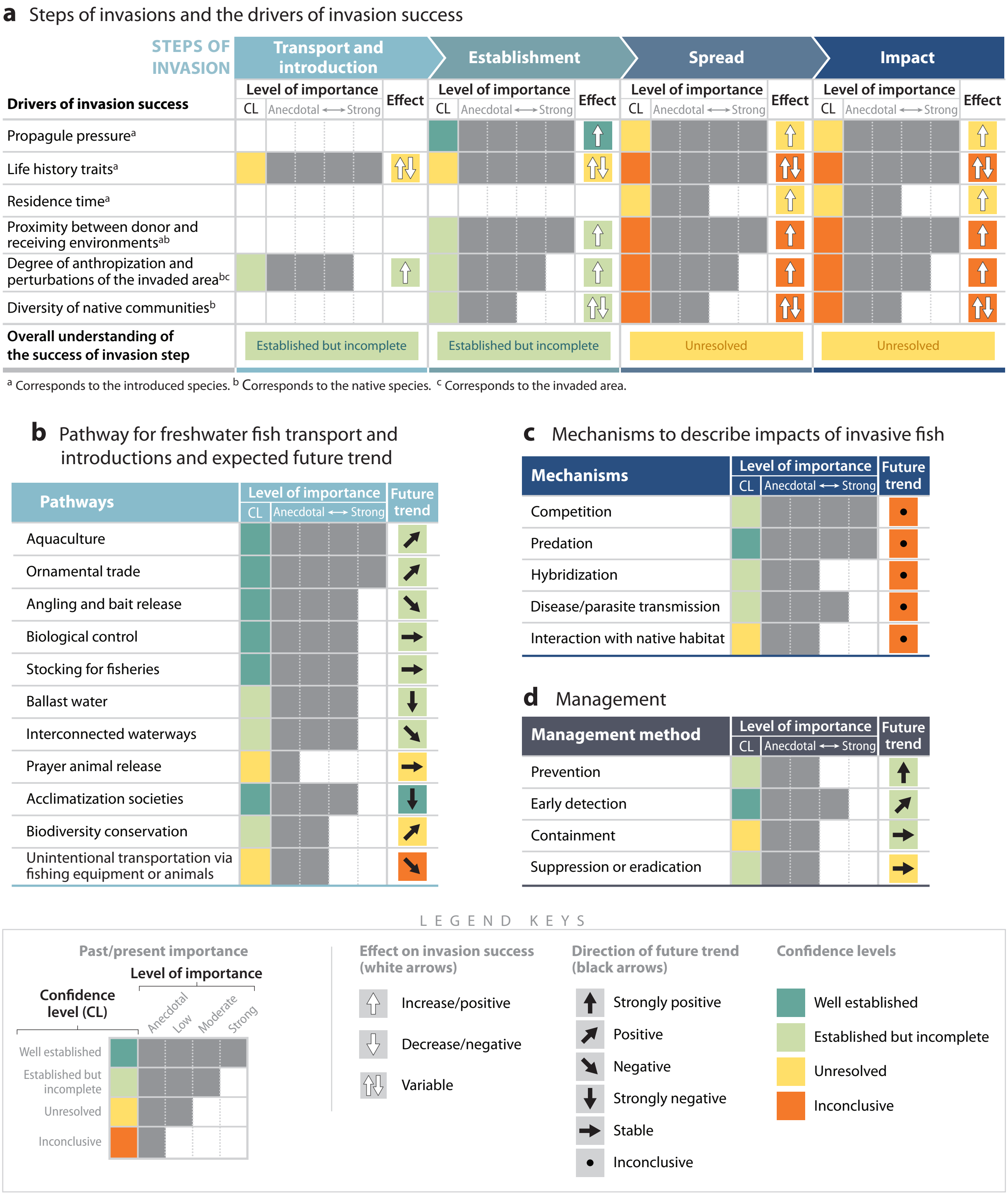
Overall, it remains very challenging to control freshwater fish invasions despite new management options (e.g., genetic biocontrol methods). Consequently, legal frameworks are urgently required at a global scale, since prevention is by far the most effective and least costly management approach.

6. SHORTFALLS, GAPS, AND BIASES IN KNOWLEDGE AND DATA

More than 60 years after Elton's seminal work on invasions [Elton 2020 (1958)], much has been learned about invasion records and spatial patterns. Since then, a large amount of theoretical knowledge has been amassed regarding invasion processes and mechanisms for freshwater fish. In short, nonnative freshwater fish are introduced through several pathways, two of which stand out, namely aquaculture and the ornamental trade. These two trade sectors are likely to grow further in the future and may involve even more species if no regulation is implemented (**Figure 3**). The main factors associated with successful invasions are propagule pressure, the life history traits of introduced species (e.g., a broad physiological tolerance facilitates the establishment, spread, and impact of the invasion), and the characteristics of the receiving environment (e.g., strong anthropogenic disturbances facilitate invasions). We demonstrate that the success of an invasion is most often explained by a combination of factors such as high propagule pressure combined with proximity between donor and receiving environments. Invasive freshwater fish affect native ecosystems through multiple mechanisms, especially competition and predation. These mechanisms are mainly related to ecological impacts, although their economic impacts are still greatly underestimated. The most widely used method to address freshwater fish invasions is population control, even though prevention would be the most effective to implement. New management techniques are constantly being developed, thus allowing for efficient and targeted eradications that were previously impossible without impacting the entire ecosystem. Despite the abundance of studies on freshwater fish invasions, there is still a clear lack of understanding of certain aspects that stems from inadequate exploration of certain key hypotheses, a lack of available data, and geographic and temporal biases.

6.1. Lack of Exploration of Key Hypotheses

Our review highlights the fact that although some aspects of freshwater fish invasions are well known (e.g., pathways of introduction), several important aspects and hypotheses have not been sufficiently explored (**Figure 3**), notably with regard to the ecological hypotheses proposed to



(Caption appears on following page)

Figure 3 (*Figure appears on preceding page*)

Summary of the state of knowledge regarding freshwater fish invasions. The content of this summary figure was derived from an expert-based assessment from all coauthors based on the reviewed literature. We evaluated the level of confidence in our assessments on the basis of both the amount of scientific evidence and the degree of convergence in evidence among studies. (*a*) Our assessment of the past and present importance of each driver for the success of invasion (indicated by the length of the *gray bars*), shown for each step of the invasion process (*top row*), as well as the perceived effect of the driver on invasion success (positive, negative or variable; indicated by the direction of the *white arrows*). The last row of panel *a* indicates the level of overall understanding of each step of the invasion; the transport and introduction and establishment steps are relatively well documented in the literature, whereas the spread and impact steps are still insufficiently documented in the literature. (*b*) The past and present importance of each pathway (*gray bars*) for freshwater fish transport and introductions, with an assessment of the expected future trend (*black arrows*) for each pathway. (*c*) The past and present importance of the known and documented mechanisms by which invasive fish impact native ecosystems (*gray bars*), with an assessment of the expected future trend (*black arrows*). Note that the future trend for all mechanisms was deemed inconclusive because of the lack of literature addressing this aspect. (*d*) The past and present importance of management methods (*gray bars*), with an assessment of the expected future trend (*black arrows*) for each method.

explain invasion success (Jeschke et al. 2018). For example, among the 39 hypotheses about invasion success and impacts proposed by Enders et al. (2020), only a few have been investigated with regard to freshwater fish invasions (biotic resistance, invasional meltdown, and enemy release). Another example is the effect of life history traits on the spread and impacts of invasive fish, which remains unresolved because it has been explored only in a limited number of modeling studies. Because of these unresolved hypotheses, we still struggle to link mechanisms to observations. We are also unable to fully profile invaders while taking into account all the characteristics that influence invasion success (i.e., species traits, environment, and socioeconomic characteristics), and thus to predict the outcome when a new nonnative species is established in a receiving ecosystem (Marchetti et al. 2004b, Pyšek et al. 2020). This inability hinders the development of effective actions to manage biological invasions.

6.2. Gaps in Data Coverage

There is a severe lack of data on several aspects of freshwater fish invasions, including essential aspects such as the number of invasion occurrences, particularly in specific regions that are poorly documented. For example, there are limited data on the propagule pressure of freshwater fish species (García-Berthou 2007). Only minimal figures on fish production and commerce are given by the Food and Agriculture Organization of the United Nations (Food Agric. Org. UN 2016), while statistics on ornamental fish releases are restricted to North America and based on predictive models (Strecker et al. 2011). There is also a lack of data regarding the economic impacts of freshwater fish invasions despite the potential high costs associated with them (Haubrock et al. 2022). Likewise, invasive freshwater fish have not been classified in the SocioEconomic Impact Classification of Alien Taxa (Bacher et al. 2018). The same paucity applies to their ecological impacts. While the ecological impact classification of invasive species exists for several taxa through the Environmental Impact Classification for Alien Taxa (EICAT) database (Hawkins et al. 2015), this classification is not available for freshwater fish species. Likewise, the only database that lists management plans implemented for invasive freshwater fish species by country is the GISD. However, this database is incomplete, as it contains management information for only 27 nonnative freshwater fish species in 14 countries, even though at least 551 nonnative freshwater fish are established worldwide (**Figure 1**). For example, some iconic invasive species with known management plans are not included in the database (e.g., sea lamprey). Previous studies such as that by Rytwinski et al. (2019) have already raised the issue of poorly documented evaluations of eradication methods.

However, several other databases reporting information on freshwater fish invasions do exist [e.g., economic impacts (Diagne et al. 2020), occurrence in drainage basins (Tedesco et al. 2017)].

Nevertheless, these databases do not cover all the aforementioned data gaps. They are also affected by unquantified incompleteness biases, which necessarily affect predictions and conclusions relating to freshwater fish invasion patterns.

6.3. Geographic and Temporal Biases

Our knowledge of the success of biological invasions of freshwater fish is heavily biased toward developed countries, with a large concentration of studies conducted in North America. For example, studies on the traits and characteristics influencing invasion success mainly focus on invasive freshwater fish in North America, while only a few studies explore other locations such as Iberian rivers (Ribeiro et al. 2008), Mediterranean streams (Vila-Gispert et al. 2005), and South America (Tonella et al. 2018) (see **Supplemental Appendix 3**). The same bias was demonstrated for the economic impacts of freshwater fish species by Haubrock et al. (2022). Nevertheless, it is important to observe that this trend is not specific to freshwater fish, as it has already been demonstrated for other taxa in the context of biological invasions (Bellard & Jeschke 2016). As the characteristics of recipient ecosystems (e.g., climatic conditions) are an important factor influencing invasions, the accumulated knowledge on North American species is not representative of invasive species in other regions of the world. In particular, we know that the African region is heavily exposed to invasive freshwater fish, but studies are still severely lacking in this region (Pyšek et al. 2020, Haubrock et al. 2022).

Furthermore, the available databases on invasions are not updated within a sufficient timeframe to allow for real-time monitoring of invasions. For example, Tedesco et al. (2017) list only a few introductions in the Amazon drainage basin, even though recent reports show an increase in invasions (Vitule et al. 2019, Magalhães et al. 2020). Similarly, Guianese rivers have long been considered among the most pristine, but recent reports point to introductions of several nonnative fish species that must be considered an early sign of potential invasions (Brosse et al. 2021). These examples are not documented in the Tedesco et al. (2017) database, thereby preventing users from obtaining up-to-date and accurate information on invasions. This problem can even be quantified in the database of first records of established species created by Seebens et al. (2017). Indeed, the first-record rate of nonnative established fish species declined after 2000, partly due to the detection delay (Seebens et al. 2017). Comprehensive and up-to-date databases are therefore essential for building reliable invasion models, especially as ecosystems and the global economy are likely to face major changes in the coming years. One solution might be the development of long-term projects with sufficient funding to ensure the regular updating of such important databases.

6.4. Future Trends

The maintenance or development of human activities in the coming years will certainly lead to changes in future patterns of freshwater fish invasions. While the majority of introduction pathways are expected to decline, some are predicted to retain the same importance, such as the prayer animal release pathway, while others will increase, as is the case for pathways related to biodiversity conservation, aquaculture, and the ornamental trade (**Figure 3**). The latter two are documented as the two main pathways of introduction of nonnative species, and they will certainly become increasingly important due to the growth in online trade and their development in developing countries [e.g., the increase in the aquarium trade in South America (Magalhães & Jacobi 2013, Magalhães et al. 2020)]. For example, as described in Section 2.7, the One Belt One Road project includes plans to build ports, canals, and dams across Asia and into Africa and Southern Europe (Wong et al. 2017). This construction project is a major potential pathway for further introductions of invasive species from East Asia to the West.

Climate change will also drive changes in the near future. However, the literature on the influence of climate change on future invasions of freshwater fish species remains scarce. Nonetheless, we can expect that climate change will affect introduction pathways. Areas with optimal temperatures for the aquaculture of some fish are expected to shift, possibly leading to changes in the regions in which species are reared, thus bringing about new species introductions (Rahel & Olden 2008). Climate change will also continue to open new niches for invasive species and may even create new opportunities for the establishment of species currently unable to establish in temperate countries (Vilizzi et al. 2021). These niche shifts could also create new possibilities for hybridization (Muhlfeld et al. 2017).

To avoid the potential impacts of new invasions, management plans need to be strengthened. In view of current trends toward the development of laws and expansion of citizen science, we expect that prevention and early detection methods will evolve and be increasingly useful (**Figure 3**).

6.5. Recommendations

In this review, we provide an overview of different aspects of freshwater fish invasions, from pathways of introduction to management techniques. We also highlight several research gaps that need to be filled. Here, we provide a few recommendations on the main issues that should be addressed in future studies.

First, data collection efforts should focus on specific areas (e.g., Africa, South America) and aspects of fish invasions where data are poor or nonexistent. Comprehensive data on the propagule pressure of introduced fish could be collected and gathered in a single comprehensive database. We are aware that gathering this information is difficult, but the collection of proxies for propagule pressure such as import data or ballast water volume could also be a potential solution to fill this gap (Drake et al. 2015). Regarding impacts, tremendous progress in research could be achieved by classifying the ecological impacts using the EICAT classification and completing the data on economic impacts with a specific focus on less-studied species and regions [e.g., the Nile perch is known to impact local communities of fishermen in East Africa, but its costs are not recorded (Haubrock et al. 2022)] (**Supplemental Appendix 2**). In addition, it is well known that some invasive freshwater fish species can simultaneously bring benefits to the economy (Gozlan 2008), but the balance between impacts and benefits is still unresolved. The development of a comprehensive database of the positive and negative economic and ecological impacts of freshwater fish invasions could help clarify the benefits of certain species and consequently inform management decisions (Vimercati et al. 2020). Regarding the lack of management data, the large number of articles on the management of freshwater fish species could provide the basis for a comprehensive database.

Second, the further study of some aspects of freshwater fish invasions should be a priority. For example, several hypotheses regarding freshwater fish invasions are yet to be explored (see Jeschke et al. 2018) or fully understood (e.g., the enemy release and biological resistance hypotheses). More generally, the spread and impact stages of the invasion process are less well studied than the other stages, and they could benefit from a better understanding if reliable data were collected (**Figure 3**).

Third, the prediction of future invasion trends using predictive models and scenarios must consider all the drivers of invasion success. Indeed, a comprehensive framework with a combination of socioeconomic characteristics, ecological characteristics, and life history traits of species, along with global drivers of change (e.g., climate change), would allow us to better predict future trends in freshwater fish invasions (Novoa et al. 2020). Reliable predictions are essential for global conservation reports such as the Global Assessment Report on Biodiversity and Ecosystem Service (Brondizio et al. 2019) to advise managers and decision makers at the international level and to guide international and national public policies concerning freshwater fish invasions.

In conclusion, biological invasions of freshwater fish are among the most important invasions worldwide, and many aspects have already been addressed in the literature, ranging from the introduction pathways of nonnative freshwater fish species to their impacts and management methods. Nonetheless, data gaps and biases remain, and unresolved aspects of freshwater fish invasion should be addressed in future studies to better understand and manage them more effectively.

DISCLOSURE STATEMENT

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Conclusion : Dans cette revue, nous avons synthétisé les connaissances publiées sur les différentes facettes des invasions de poissons d'eau douce, depuis les voies d'introduction des poissons exotiques jusqu'aux techniques de gestion des espèces exotiques envahissantes. Le but de cette revue était aussi de donner des recommandations pour les travaux futurs sur les invasions de poissons d'eau douce. Ainsi, nous avons notamment mis en avant la diversité des facteurs influençant chaque étape des invasions de poissons d'eau douce (*e.g.*, pression de propagule, traits d'histoire de vie, voies d'introduction), mais aussi le manque d'exploration de certains d'entre eux. Par exemple, l'influence des traits d'histoire de vie sur le succès de chaque étape de l'invasion n'est pas encore résolue. De même pour les facteurs influençant certaines étapes de l'invasion, tel que l'impact, ce qui s'explique en partie en raison du manque de données qui s'applique aussi bien aux impacts écologiques qu'aux impacts économiques, et pour lesquels il n'existe aucune classification standardisée à grande échelle. Ainsi, parmi les différentes pistes d'amélioration évoquées dans la revue de synthèse, nous avons mentionné une évaluation des impacts économiques des poissons d'eau douce envahissants. En effet, les poissons d'eau douce envahissants n'ont pas fait l'objet d'une documentation dans la base SEICAT (*SocioEconomic Impact Classification of Alien Taxa*) (Bacher et al. 2018) classifiant les impacts socio-économiques des espèces envahissantes. Pourtant, certaines espèces ont des coûts économiques importants. Par exemple, 13,5 millions de dollars US ont été dépensés pour l'éradication de la lamproie marine (*Petromyzon marinus*) dans les Grands Lacs Nord-Américains (Smith & Swink 2003). Une vision synthétique de l'ensemble des coûts répertoriés à l'échelle globale est essentielle, en plus d'être est une information permettant de compléter celles portant sur les impacts écologiques, et ainsi d'optimiser la mise en place de la gestion des espèces exotiques envahissantes (Diagne et al. 2020b). Cependant, la synthèse et la standardisation des coûts économiques des poissons exotiques est compliquée en raison de la nature des coûts (espèces différentes, secteurs d'impacts variés) des échelles de mesure (spatiales et temporelles) et même des unités de mesures (monnaies différentes). La base InvaCost remédie en partie à ces problèmes en répertoriant les coûts liés aux espèces exotiques envahissantes dans la littérature grise et scientifique, en homogénéisant ces coûts dans une même monnaie corrigée pour l'inflation (US$ 2017), et en liant à ces coûts une localisation et des secteurs impactés. Grace à cette base, nous avons ainsi pu synthétiser les coûts connus dans la littérature des poissons envahissants (n= 384 entrées de coûts annualisées liés à 27 espèces). Cette étude parue pendant la phase d'écriture la revue, est abordée dans cette dernière et est pour l'instant la seule évaluation synthétique des coûts économiques pour les poissons exotiques envahissants à l'échelle globale.

Chapitre 2 : Évaluation des coûts économiques des poissons envahissants, et des manques de données

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Knowledge gaps in economic costs of invasive alien fish worldwide

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HIGHLIGHTS

- Invasive alien fish species have cost at least $37.08 billion globally since 1960s.
- Annual costs increased from <$0.01 million in the 1960s to $1 billion since 2000.
- Reported costs are unevenly distributed, with a bias towards North America.
- Impacts are less reported than other taxa based on research effort.
- Gaps in available data indicate underestimation and a need to improve cost reporting.

GRAPHICAL ABSTRACT

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ABSTRACT

Invasive alien fishes have had pernicious ecological and economic impacts on both aquatic ecosystems and human societies. However, a comprehensive and collective assessment of their monetary costs is still lacking. In this study, we collected and reviewed reported data on the economic impacts of invasive alien fishes using InvaCost, the most comprehensive global database of invasion costs. We analysed how total (i.e. both observed and potential/predicted) and observed (i.e. empirically incurred only) costs of fish invasions are distributed

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geographically and temporally and assessed which socioeconomic sectors are most affected. Fish invasions have potentially caused the economic loss of at least US$37.08 billion (US2017 value) globally, from just 27 reported species. North America reported the highest costs (>85% of the total economic loss), followed by Europe, Oceania and Asia, with no costs yet reported from Africa or South America. Only 6.6% of the total reported costs were from invasive alien marine fish. The costs that were observed amounted to US$2.28 billion (6.1% of total costs), indicating that the costs of damage caused by invasive alien fishes are often extrapolated and/or difficult to quantify. Most of the observed costs were related to damage and resource losses (89%). Observed costs mainly affected public and social welfare (63%), with the remainder borne by fisheries, authorities and stakeholders through management actions, environmental, and mixed sectors. Total costs related to fish invasions have increased significantly over time, from <US$0.01 million/year in the 1960s to over US$1 billion/year in the 2000s, while observed costs have followed a similar trajectory. Despite the growing body of work on fish invasions, information on costs has been much less than expected, given the overall number of invasive alien fish species documented and the high costs of the few cases reported. Both invasions and their economic costs are increasing, exacerbating the need for improved cost reporting across socioeconomic sectors and geographic regions, for more effective invasive alien fish management.

1. Introduction

Invasive alien fish introductions are increasing in number globally (Leprieur et al., 2008; Avlijaš et al., 2018). In turn, the drivers of these invasions are also rising (Turbelin et al., 2017; Zieritz et al., 2017), with the potential to intensify future impacts. In particular, the increase in anthropogenic activities, especially in emerging market economies, is expected to facilitate new introductions of invasive alien fish species and subsequent invasions through pathways such as tourism, trade (e.g. aquaculture and aquarium trade) and infrastructure development (e.g. waterways/channel construction) (Hulme, 2015; Haubrock et al., 2021a).

Ecological impacts of invasive alien fishes (Cucherousset and Olden, 2011) include the displacement and extinction of native species (Mills et al., 2004; Haubrock et al., 2018), alteration of trophic interactions (Martin et al., 2010; Cuthbert et al., 2018; Haubrock et al., 2019), and disruption of ecosystem functioning (Capps and Flecker, 2013). Invasive alien fish can also transmit new pathogens (Gozlan et al., 2005; Waicheim et al., 2014; Boonthai et al., 2017; Ercan et al., 2019) and threaten native species' genetic diversity through hybridization (Oliveira et al., 2006; Gunnell et al., 2008). However, despite evidence for increasing numbers of fish invasions worldwide and their growing ecological impacts (Leprieur et al., 2008; Seebens et al., 2020; Raick et al., 2020), their economic impacts remain poorly understood, largely due to a lack of data for numerous sectors and difficulties in monetizing ecological impacts. This paucity of cost data has led to debate among scientists about previous estimates of invasion costs (Cuthbert et al., 2020), which have often relied on over-extrapolation and presented untraceable sources. In the context of fisheries, this could involve projecting costs from local scales to entire fisheries.

This lack of knowledge of costs of invasive alien fish, in turn, hampers decision-making and severely limits the ability of policymakers to design cost-effective management strategies (Britton et al., 2010; Hyytiäinen et al., 2013). In cases where invasive alien fish populations may have a positive value, understanding the trade-offs and designing socially optimal management are also hampered by the lack of cost data. Examples of such positive values include invasive alien fishes with commercial benefits (Gollasch and Leppäkoski, 1999), aesthetic and/or cultural values associated with recreational uses (Downing et al., 2013; Schlaepfer et al., 2011; Katsanevakis et al., 2014; Gozlan, 2015, 2016), or other perceived ecosystem benefits (Gozlan, 2008; Pejchar and Mooney, 2009; Britton and Orsi, 2012).

Despite the potential benefits of some taxa, recent works have highlighted the increasing negative economic impacts of invasive alien species globally (Bradshaw et al., 2016), with economic costs of invasions exceeding US$1.2 trillion in recent decades across all habitat types (Diagne et al., 2021). In a first global synthesis of the cost of aquatic invasive alien species (Cuthbert et al., 2021), impacts have reached $345 billion worldwide, which is likely an underestimate given that impacts of aquatic invasions are generally underrepresented compared to terrestrial taxa. That is because their costs are lower than expected based on numbers of alien species between those habitats (Cuthbert et al., 2021). Further, Cuthbert et al. (2021) found that the ruffe *Gymnocephalus cernua* was the second most costly invasive aquatic taxon in the world, considering total costs which include predictions and extrapolations. In addition, significant gaps in reporting on the costs of aquatic invasions were found in Asia and Africa, with many countries reporting no invasion costs, despite the presence of known harmful invasive alien species (Cuthbert et al., 2021). While the increasing economic impacts of aquatic invasions are alarming, there remain knowledge gaps at more granular scales regarding the specific nature of impacts of key taxonomic groups, such as fish, which must be filled to fully understand biases and inform taxon-specific management (Haubrock et al., 2021b; Cuthbert et al., 2021; Kouba et al., 2021).

Following recent advances addressing costs of invasive alien species at different regional scales (Bradshaw et al., 2021; Crystal-Ornelas et al., 2021; Haubrock et al., 2021c; Kourantidou et al., 2021; Liu et al., 2021) and across taxonomic groups (Cuthbert et al., 2021), we aim to better understand costs of fish invasions. To provide a necessary baseline for the economic impact of this taxon, we have therefore characterised, for the first time, the current status of knowledge on the global costs of invasive alien fishes using the InvaCost database (Diagne et al., 2020a). This database contains detailed information on reported costs (e.g. types of costs, sectors affected, regional attributes, reliability of cost estimates, etc.) over the last 60 years, associated with ~1000 invasive alien species from all ecosystem types worldwide (i.e. impacts occurring outside their native range). Invasive alien species included in the InvaCost database are thus those that spread outside of their geographic range of origin (Blackburn et al., 2011) and have a negative economic impact that was quantified in monetary terms. Our aims were to describe the reported global costs associated with invasive alien fish species, to explore the structure of these costs, and to identify gaps and potential biases in the estimation of past and current economic impacts.

2. Methods

2.1. Cost data sourcing and filtering

To estimate the cost of fish invasions reported globally, we considered cost data from the latest version of the InvaCost database (version 4.0, https://doi.org/10.6084/m9.figshare.12668570; released in June 2021). This version of the database compiles 13,123 cost entries reported from both English and non-English sources in a sufficiently detailed manner to allow a large-scale synthesis of the costs associated with invasive alien species at different spatial, taxonomic and temporal scales (Diagne et al., 2020a; Angulo et al., 2021). These cost data were primarily retrieved using a series of search strings entered into the Web of Science platform (https://webofknowledge.com/), Google Scholar database (https://scholar.google.com/) and the Google search engine (https://www.google.com/) to identify and collate relevant references on invasion costs. Local stakeholders and experts on invasions were also contacted as part of the search process. All references were thoroughly evaluated to identify their relevance and to extract information on costs. In the invasive alien species literature, there is a wide variety of costing practices which have an associated risk of misunderstandings and causing discrepancies among reported costs (Diagne et al., 2021). These may include, for example, differences in discounting across studies or in cost estimation methodologies. Despite the obvious challenges of standardizing heterogeneous costs, InvaCost is the most comprehensive database on the economic costs of IAS that has largely succeeded in resolving the problems associated with standardisation over time and across countries where they have been reported (Diagne et al., 2020b). In addition, this database is public and regularly updated with either corrections if mistakes are detected and/or new data as they become available. With regard to monetary units, all costs published in the literature and included in the database were converted to 2017 US$ values (see Diagne et al., 2020a and Supplementary Material 1 for detailed information). The database used for this analysis includes information on monetary costs across taxonomic, regional and sectoral descriptors, and allows for a distinction between *observed* (i.e. costs of a realized impact) and *potential* costs (i.e. costs of a predicted/expected impact over time within or beyond the actual distribution area of the IAS). It also allows for a classification based on the reliability of the source and the methodologies used for the cost estimates (*high* or *low* reliability, with *high* implying that the source is from pre-assessed material such as peer-reviewed articles and official reports or from grey material but with documented, repeatable and traceable methods, and with *low* referring to all other estimates).

We filtered the InvaCost database to retain costs related to fishes belonging to the classes Cephalaspidomorphi and Actinopterygii; these were the only fish taxa in the database with reported costs, but also included an entry listed as "Osteichthyes" (see Pimentel et al., 2000). Because the available information did not allow us to distinguish this entry among ray-finned fish (Actinopterygii) and lobe-finned fish (Sarcopterygii), it was kept as a "diverse" entry. In total, we identified 177 entries, from which 7 were excluded as no starting and/or ending year for the listed costs could be identified. After expansion, these entries resulted in 384 annualized cost entries (see expansion process below). Cost entries that were not attributable to single species, sectors or cost types within these classes were classified as "Diverse/Unspecified". All analyses were conducted for the period between 1960 to 2020, as (i) monetary exchange rates prior to 1960 were not available, and (ii) 2020 was the last year for which cost data were available in the database. The final dataset used for the analysis is provided in Supplementary Material 2.

2.2. Global cost descriptions

In order to describe the costs of invasive alien fish over time, we used the *expandYearlyCosts* function of the 'invacost' package (v0.3-4; Leroy et al., 2020) in R version 4.0.2 (R Core Team, 2020). This function facilitates consideration of the temporal dimensions of the data, with the estimated costs per year being expanded over time according to the length of time over which they occurred or were expected to have occurred (i.e. the length of time between the *Probable_starting_year_adjusted* and *Probable_ending_year_adjusted* columns). In order to obtain a comparable cumulative total cost for each estimate over the period during which costs were incurred for each invasion, we multiplied each annual estimate by the respective duration (in years). The analyses were therefore conducted on the basis of these 'expanded' entries to reflect the likely duration of the costs as reported in each study analysed. This means that costs covering several years (e.g. US$10 million between 2001 and 2010) are divided according to their duration (i.e. US$1 million for each year between 2001 and 2010). Finally, the cumulative costs of the invasion were estimated based on their classification in the following cost descriptors (i.e. columns) included in the database (Supplementary Material 1):

(i) Method_reliability: indicating the perceived reliability of cost estimates based on the publication type and estimation method. Costs are considered to be of *low* reliability in those cases where they were derived from grey literature and/or are lacking documented, repeatable or traceable methods. On the contrary, costs are considered of *high* reliability if they come from peer-reviewed articles, official documents, or grey literature but with a fully documented, repeatable and traceable method (Diagne et al., 2020a). While we acknowledge that this binary classification does not capture the widely varying methodologies of underlying studies, it provides a practical, reproducible and objective means of cost assessment and filtering;

(ii) Implementation: whether the cost estimate was actually incurred in the invaded area (*observed*; e.g. a cost directly incurred from investment in managing an invasive alien fish population, or an invasion-driven decline in a native fishery that resulted in a realised loss of income) or whether it was extrapolated or predicted over time within or beyond the actual distribution area of the IAS (*potential*), and thus not empirically incurred (Diagne et al., 2020a; see Supplementary Material 1). We emphasize that costs were compiled in InvaCost based on the information in each cost document (i.e. we did not extrapolate or predict cost estimates independently here, and simply compiled reported costs). For example, *potential* costs may include estimated reductions in fisheries income because of an invasion (Scheibel et al., 2016), known local costs that are extrapolated to a larger system than the one they occur in (Oreska and Aldridge, 2011), and costs extrapolated over several years based on estimates from a shorter period (Leigh, 1998).

(iii) Geographic_region: description of the continental geographic location of the cost;

(iv) Type_of_cost_merged: grouping of costs into categories: (i) "*Damage*" referring to damages or loss incurred by the invasion (i.e. costs of repairing damage, losses of resources, medical care), (ii) "*Management*" including expenditure related to control (i.e. surveillance, prevention, management, eradication), (iii) and "*Mixed*" including mixed cost of damage and control (cases where the reported costs were not clearly distinguishable);

(v) Impacted_sector: the activity, societal or market sector that was affected by the cost. Seven sectors are described in the database: *agriculture*, *authorities-stakeholders* (official structures allocating efforts to manage biological invasions), *environment*, *fishery*, *forestry*, *health*, and *public and social welfare* (Diagne et al., 2020a; see Supplementary Material 1).

2.3. Temporal cost accumulations

To assess temporal trends of invasive alien fish species, we considered 10-year averages since 1960. We examined the costs in terms of the *year of impact*, which reflects the time at which the invasion cost likely occurred and extended it over years in which the costs were realised using the *summarizeCosts* function of the 'invacost' R package (using the *Probable_starting_year_adjusted* and *Probable_ending_year_adjusted* columns; see Leroy et al., 2020). This allowed the estimation of average annual costs over the whole period considered, as well as over decadal increments, for both *observed* and *potential* costs.

2.4. Comparison with other taxonomic groups

In order to put the costs of invasive alien fish species in a broader taxonomic perspective, we compared the economic costs of invasive alien fish with other invasive vertebrates: birds and mammals. The comparison was based on the total cost and the number of documents reporting costs in the InvaCost database, coupled with the number of invasive alien species per taxon, and the numbers of scientific publications in the field of invasion science. First, total monetary costs and number of entries for birds and mammals were calculated following the same methods and database version as for fishes (as detailed above). Secondly, we estimated the number of publications available for each group using the same search protocol as for the InvaCost database (see Diagne et al., 2020a), excluding words referring to costs and adding the name of the biotic group (i.e. "fish", "mammal", or "bird"), in order to obtain a comparative approximation of the research effort in invasion ecology for these three taxa. The exact search strings used can be found in Supplementary Material 3. The information considered in this comparison was collected using the Web of Science Core collection. Thirdly, the numbers of alien species for each of the three taxonomic groups mentioned above was estimated using the IUCN Red List database (https://www.iucnredlist.org/). We classified a species as alien according to the IUCN legends of the countries where they occur. If a species is considered as introduced in at least one country, then we consider this species as alien. Finally, we used Pearson's Chi-squared test of independence to assess whether the data for the three taxonomic groups had the same distribution of values (number of alien species, number of cost entries, number of studies reporting invasion costs, and total costs).

3. Results

A total of 384 annualized cost entries for 27 invasive alien species belonging to 18 fish families were available in the database, totalling US $37.08 billion. The majority of costs was deemed as potential (US $34.79 billion; n = 88, hereafter the number of cost entries), while observed costs amounted to only US$2.28 billion (n = 296). Furthermore, the majority of costs (US$25.31 billion; n = 295) was considered of high reliability, while US$11.77 billion (n = 89) was considered of low reliability (Supplementary Material 4).

3.1. Costs across regions and taxa

North America was the region with the highest reported economic costs of invasive alien fish species, followed by Europe, Oceania, Asia and Central America (Fig. 1). Costs inferred from polar regions (e.g. French Southern and Antarctic Lands) were below US$ 1 million (no costs for invasive alien fish were reported for Arctic regions).

When considering only observed costs, the costs of invasive alien fish in North America (n = 46), were again about 10 times higher than observed costs recorded in Oceania (n = 12), and over 60 times higher than costs in Asia (n = 59; Fig. 2). Reported observed costs were attributed to several species in North America, Europe and Asia, but were least diverse in Central America, Oceania and polar regions (Fig. 2) (note that these do not include taxa at coarser groupings than species level).

The Actinopterygii class included 26 invasive alien fish species with reported costs (US$34.26 billion). The class Cephalasdomorphi, on the other hand, included only one species, the sea lamprey *P. marinus* (US $1.39 billion in North America) (Table 1). Observed costs listed for the class Osteichthyes (i.e. bony fish; US$1.42 billion) were deemed diverse, as this cost entry could not be assigned to a lower taxonomic level (see Pimentel et al., 2000 for details). Globally, the ruffe *G. cernua* was the costliest species, followed by the topmouth gudgeon *Pseudorasbora parva*, the sea lamprey *P. marinus*, the common carp *Cyprinus carpio*, the red lionfish *Pterois volitans*, unspecific species belonging to *Tilapia* sp., the silver-cheeked toadfish *Lagocephalus sceleratus*, the black bass *Micropterus salmoides*, white bass *Morone chrysops*, the brown trout *Salmo trutta*, and common minnow *Phoxinus phoxinus* (Table 1). All other species contributed less than US$ 1 million (Table 1).

Considering total costs (*potential* and *observed*) inferred in North America, the ruffe *G. cernua* was the costliest species (US$28.93 billion), followed by *P. marinus* (US$1.39 billion), white bass *M. chrysops* (US $3.39 million) and brown trout *S. trutta* (US$1.78 million). All other species, such as the northern pike *Esox lucius* and the northern snakehead *Channa argus*, contributed less than US$1 million.

Considering only observed costs globally, *P. marinus* was the costliest species, followed *by C. carpio*, *P. volitans*, *Tilapia* sp., *L. sceleratus*, *M. salmoides*, *M. chrysops*, *S. trutta*, and *P. phoxinus* (Table 1). All other species contributed up to US$1 million (Table 1; Fig. 2). Observed costs of *P. marinus*, *S. trutta* and *M. chrysops* were only reported in North America.

3.2. Cost types and impacted sectors

Costs related to damages and resource losses represented approximately 89% of the observed cost (n = 96; Fig. 3). Costs associated

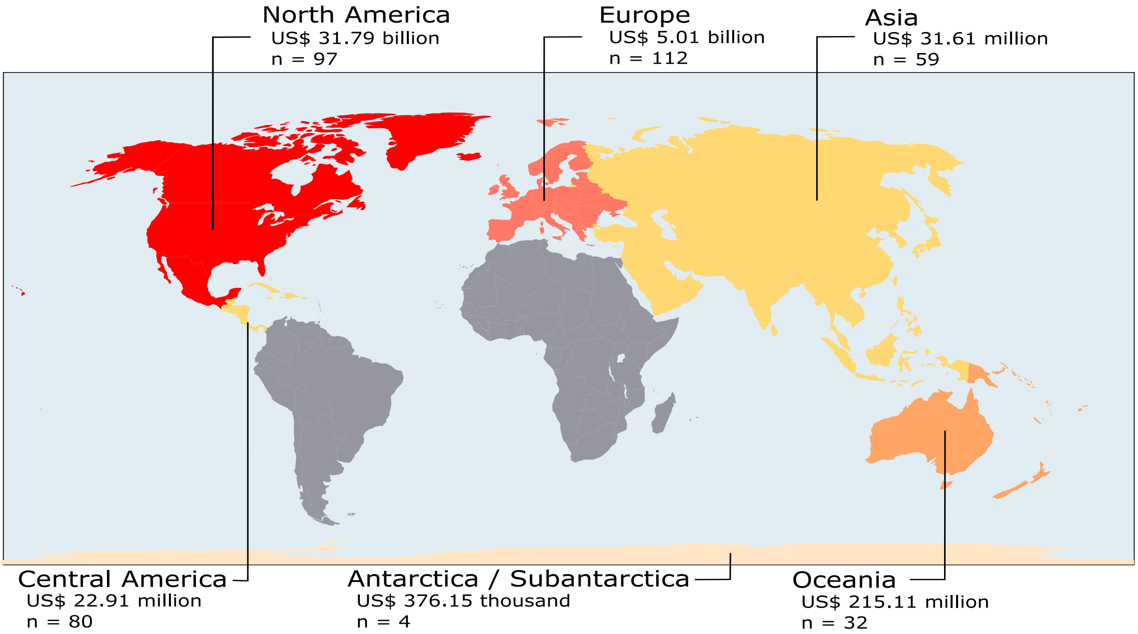

Fig. 1. Total costs (observed and potential) of invasive fishes by geographical region. Grey indicates no cost information being available for that region, yellow to red indicates the magnitude of the reported costs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with management (i.e. control, detection and eradication costs) were an order of magnitude lower, despite having more entries (n = 196), while mixed costs amounted to less than US$1 million (n = 4) (Fig. 3). In North America, most of the observed cost (US$1.77 billion) was attributed to damages and losses, with the remaining US$231.16 million (11.5%) classified as management costs.

Considering observed costs, public and social welfare was the most affected sector, followed by costs to fisheries, authorities and stakeholders, the environment and mixed sectors (Fig. 3). Inferring only observed costs to impacted sectors in North America, the distribution of costs across sectors was similar, with public and social welfare (US $1.44 billion) predominantly impacted, followed by fisheries (US $349.81 million), authorities and stakeholders (US$208.70 million), and mixed sectors (US$3.27 million).

3.3. Temporal cost accumulations

In total, costs averaged to US$607.78 million per year between 1960 and 2020 (Fig. 4), with a strong increase from <US$0.01 million per year in the 1960s to US$603.08 million per year in the 1980s, before surpassing US$1 billion by the 2000s. Observed costs averaged to US$37.43 million per year between 1960 and 2020. Annual observed costs first increased from <US$0.01 million in the 1960s to US$159.96 million per year in the 2000s, then decreased after 2010 to US$7.27 million per year. It should be noted, however, that time lags (i.e. between the occurrence of costs and official reporting) were not accounted for in the last decade (2010−2020), and thus cost estimates are therefore likely to be more underestimated in recent years.

3.4. Comparisons across biotic groups

Records for alien fishes from the IUCN Red List database (n = 147, hereafter the number of species) were 30% fewer than recorded alien birds (n = 210) and 39% more than recorded alien mammals (n = 106). Conversely, fishes were the taxonomic group with the highest number of scientific publications on alien species (17,864 papers), about twice the number of publications on birds (8759) and four times the number on mammals (4880) (Fig. 5). Nevertheless, invasive alien fish species had the lowest number of unique references reporting costs in the InvaCost database (55) compared to mammals (378) and birds (64). In turn, the total cost of invasive alien fish species (US $37.08 billion) was much lower than that of mammals (US$ 424.56 billion), but higher than that of birds (US$7.52 billion). The distribution of values for each biotic group thus differed significantly (fish *vs.* birds: $\chi2 = 2738$, df = 3, $p < 0.001$; fish *vs.* mammals: $\chi2 = 100{,}000$, df = 3, $p < 0.001$; Fig. 5), with costs and inputs for fish disproportionately lower than expected based on the number of studies and alien species.

4. Discussion

The total economic cost of invasive alien fishes was US$37.08 billion globally, from just 27 species with reported cost data. These costs are the result of reported/published estimates only which, because of the lack of reported costs in several regions (i.e. Africa and South America) and for several species, suggest that the overall cost estimate is significantly underestimated compared to the actual costs.

The reported observed costs are, in fact, very few and are mainly based on damages and resource losses to fisheries, as well as on the costs of large-scale management interventions. For example, the cost of the Eurasian ruffe invasion (*G. cernua*), which accounts for a significant portion of the total cost of invasive alien fish in North America, was extrapolated from population density estimates in Lake Superior to the types of impacts it could have if it were to spread more widely in the Great Lakes basin, resulting in economic costs (potentially reaching US$500 million by 2050) by impacting recreational fisheries and causing a decline in yellow perch (*Perca flavescens*) populations. This resulted in an estimate of US$13.6 million for a two-year control program and US$119 million to US$1.05 billion in benefits from control programmes for recreational and commercial fisheries over a 50-year time period (Lovell et al., 2006). However, because these estimated economic costs have not yet been confirmed, the limited information available on the socio-economic impacts of *G. cernua* in the Great Lakes precludes an adequate assessment of economic cost. Nevertheless, it is possible that these potential costs were not overestimated, but rather that the expected impact was mitigated by management, suggesting that the extrapolation may have been robust (and useful) at the time it was made. Other harmful invasive alien fish, such as Asian carp species in the Mississippi River basin, have no current cost estimates, despite the expectation of potential future economic and ecological costs large enough to require the expenditure of US$831 million to try to prevent spread in the Great Lakes (USACE, 2018).

We also showed that the costs of invasive alien fish were significantly lower compared to birds and mammals and the research effort devoted to them. This could be due to a perception bias where damage to habitats or aquatic communities goes unnoticed by the public and authorities because of the difficulties in timely detection of fish invasions compared to other taxa. At the same time, the introduction of aquatic species has often been seen as beneficial to some local communities, especially those engaged in harvesting, processing or recreational tourism (Selge et al., 2011), which leads to a risk of ignoring the negative impacts of the invasion. Invasive alien fish have diverse impacts on ecosystems and understanding their indirect effects will benefit from advances in non-market valuation methods to infer the full range of their impacts (e.g. decline of native species, displacement, extinctions, disease, etc.) (Hanley and Roberts, 2019). Compared to mammals and birds, fish invasions and their vectors of introduction are well studied, with a high number of publications in the natural sciences and reports on the number of invasive alien species (Semmens et al., 2004; Castellanos-Galindo et al., 2020). The low number of reported costs for fish invasions, despite this wealth of literature documenting their presence, likely reflects the difficulties in quantifying their costs and possibly in some cases the fact that certain fish have a long history of intentional introductions (Gozlan, 2008).

4.1. Taxonomic, regional and environmental biases

In total, economic costs were available for only 27 out of the more than 147 invasive alien fish species worldwide (IUCN, 204 according to FishBase (Froese and Pauly, 2019), with some highly invasive and impactful fish species being completely absent. For example, observed costs have not been reported for the Chinese or Amur sleeper (*P. glenii)* in Europe, although it is a known vector of parasites (Reshetnikov et al., 2011; Kvach et al., 2013) which may have an important impact on the aquaculture sector (Ondracková et al., 2012).

Documented costs of invasive alien fish species also show marked regional disparities, with the majority of reported costs attributed to North America and significantly lower costs reported elsewhere. These regional disparities are not only reflected in the massive differences in costs, but also in the spatial scale of their reporting; a higher proportion of costs in North America was reported at the national level (89 %) compared to costs at the regional (1 %) or local level (10%). These large-scale estimates likely increase the magnitude of reported costs and underscore the need for large-scale estimates outside North America. Despite the fact that a number of fish species have been intentionally introduced to meet the rapidly increasing demand for farmed fish (Lin et al., 2015; Xiong et al., 2015; Grosholz et al., 2015; Zhao et al., 2015; Gozlan, 2016), costs of only five invasive alien fish species have been reported in Asia. This is amidst evidence that multiple introduced fish species escape from aquaculture facilities or are released into the wild (Marchetti et al., 2004; Saba et al., 2021). Similarly, the total lack of reporting on the costs of fish invasions in South America and Africa is surprising given the multiple high-profile examples of fish invasions on these

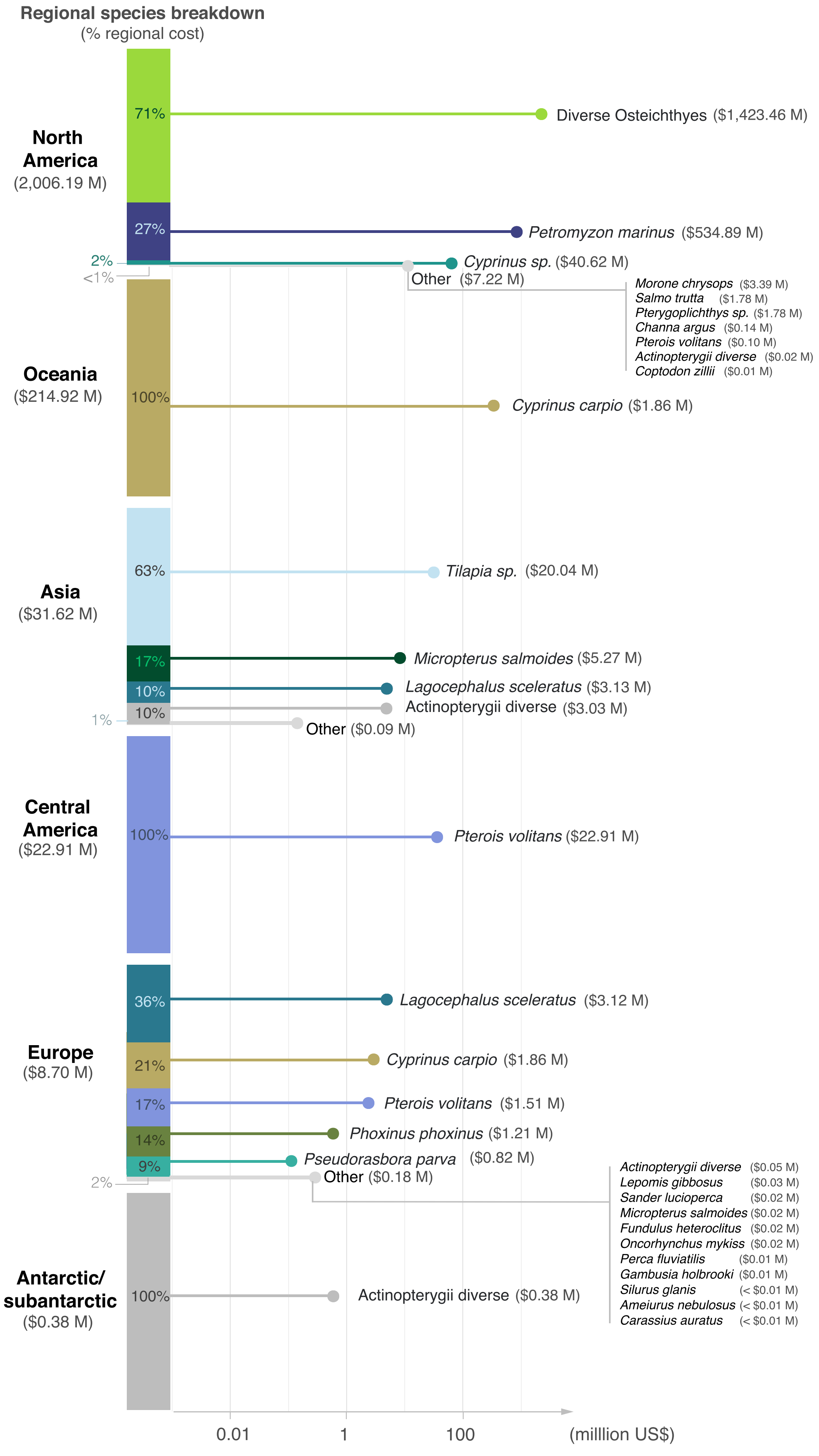
Regional species breakdown
(% regional cost)
North America
(2,006.19 M)
71%
Diverse Osteichthyes ($1,423.46 M)
27%
Petromyzon marinus ($534.89 M)
2%
Cyprinus sp. ($40.62 M)
<1%
Other ($7.22 M)
Morone chrysops ($3.39 M)
Salmo trutta ($1.78 M)
Pterygoplichthys sp. ($1.78 M)
Channa argus ($0.14 M)
Pterois volitans ($0.10 M)
Actinopterygii diverse ($0.02 M)
Coptodon zillii ($0.01 M)
Oceania
($214.92 M)
100%
Cyprinus carpio ($1.86 M)
Asia
($31.62 M)
63%
Tilapia sp. ($20.04 M)
17%
Micropterus salmoides ($5.27 M)
10%
Lagocephalus sceleratus ($3.13 M)
10%
Actinopterygii diverse ($3.03 M)
1%
Other ($0.09 M)
Central America
($22.91 M)
100%
Pterois volitans ($22.91 M)
Europe
($8.70 M)
36%
Lagocephalus sceleratus ($3.12 M)
21%
Cyprinus carpio ($1.86 M)
17%
Pterois volitans ($1.51 M)
14%
Phoxinus phoxinus ($1.21 M)
9%
Pseudorasbora parva ($0.82 M)
2%
Other ($0.18 M)
Actinopterygii diverse ($0.05 M)
Lepomis gibbosus ($0.03 M)
Sander lucioperca ($0.02 M)
Micropterus salmoides ($0.02 M)
Fundulus heteroclitus ($0.02 M)
Oncorhynchus mykiss ($0.02 M)
Perca fluviatilis ($0.01 M)
Gambusia holbrooki ($0.01 M)
Silurus glanis (< $0.01 M)
Ameiurus nebulosus (< $0.01 M)
Carassius auratus (< $0.01 M)
Antarctic/ subantarctic
($0.38 M)
100%
Actinopterygii diverse ($0.38 M)
0.01
1
100
(milllion US$)

Table 1
Cost-contributing invasive fish species for total and observed costs, illustrating species, total costs and numbers of database entries; F = Freshwater, M = Marine, B = Brackish (according to the environment classification of Froese and Pauly, 2019).

Common name	Genus	Species	Environment	Total costs		Observed costs	
				Cost (US$ 2017 value) in million	Database entries	Cost (US$ 2017 value) in million	Database entries
Brown bullhead	*Ameiurus*	*Nebulosus*	F	0.001	3	0.001	3
Goldfish	*Carassius*	*Auratus*	F,B	0.001	3	0.0010	3
Northern snakehead	*Channa*	*Argus*	F	0.138	1	0.138	1
Redbelly tilapia	*Coptodon*	*Zillii*	F,B	0.011	3	0.011	3
Common carp	*Cyprinus*	*Carpio*	F,B	216.978	48	216.773	28
Northern pike	*Esox*	*Lucius*	F,B	0.021	1	–	–
Mummichog	*Fundulus*	*Heteroclitus*	M,F,B	0.017	5	0.017	5
Eastern mosquitofish	*Gambusia*	*Holbrooki*	F,B	0.009	10	0.009	10
Ruffe	*Gymnocephalus*	*Cernua*	F,B	28,933.217	47	–	–
Silver-cheeked toadfish	*Lagocephalus*	*Sceleratus*	M	6.540	15	6.247	13
Pumpkinseed	*Lepomis*	*Gibbosus*	F,B	0.030	13	0.030	13
Bluegill	*Lepomis*	*Macrochirus*	F	0.073	10	0.073	10
Black bass	*Micropterus*	*Salmoides*	F	5.293	34	5.293	34
White bass	*Morone*	*Chrysops*	F	3.394	1	3.394	1
Rainbow trout	*Oncorhynchus*	*Mykiss*	M,F,B	0.016	2	0.016	2
European perch	*Perca*	*Fluviatilis*	F,B	0.014	3	0.014	3
Chinese sleeper	*Perccottus*	*Glenii*	F,B	0.173	4	–	–
Sea lamprey	*Petromyzon*	*Marinus*	M, F, B	1389.395	15	534.887	12
Common minnow	*Phoxinus*	*Phoxinus*	F,B	1.210	3	1.210	3
Guppy	*Poecilia*	*Reticulata*	F	0.017	2	0.017	2
Topmouth gudgeon	*Pseudorasbora*	*Parva*	F,B	5004.319	22	0.818	11
Red lionfish	*Pterois*	*Volitans*	M	24.528	85	24.528	85
Janitor fish	*Pterygoplichthys*	sp.	F	0.002	1	0.002	1
Brown trout	*Salmo*	*Trutta*	M,F,B	1.782	10	1.782	10
Zander	*Sander*	*Lucioperca*	F,B	0.022	4	0.022	4
European catfish	*Silurus*	*Glanis*	F,B	0.002	1	0.002	1
Tilapia	*Tilapia*	sp.	F	20.039	1	20.039	1
Diverse/unspecified				1467.556	31	1467. 556	31

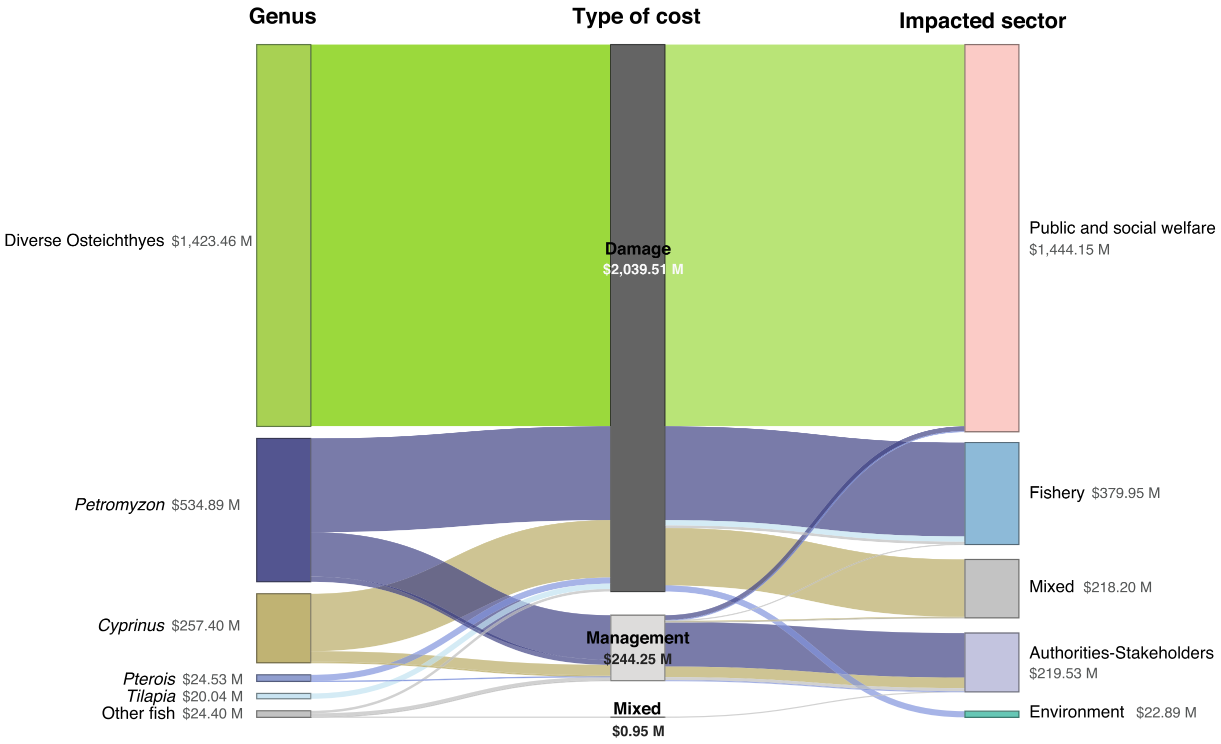

Fig. 3. Distribution of observed costs of alien fish invasions across genera, types of costs and sectors affected. Costs are shown in millions of US 2017 dollars.

Fig. 2. Observed costs of invasive fish species across regions (North America, Europe, Asia, Antarctic/Sub-Antarctic and Central America) indicating the contribution of the species to the respective total. For example, *Pterois volitans* accounts for 100% of the costs of invasive fish in Central America and contributes US$0.02 billion to the total cost of invasive species. Note that the *x*-axis is on a $\log_{10}$ scale.

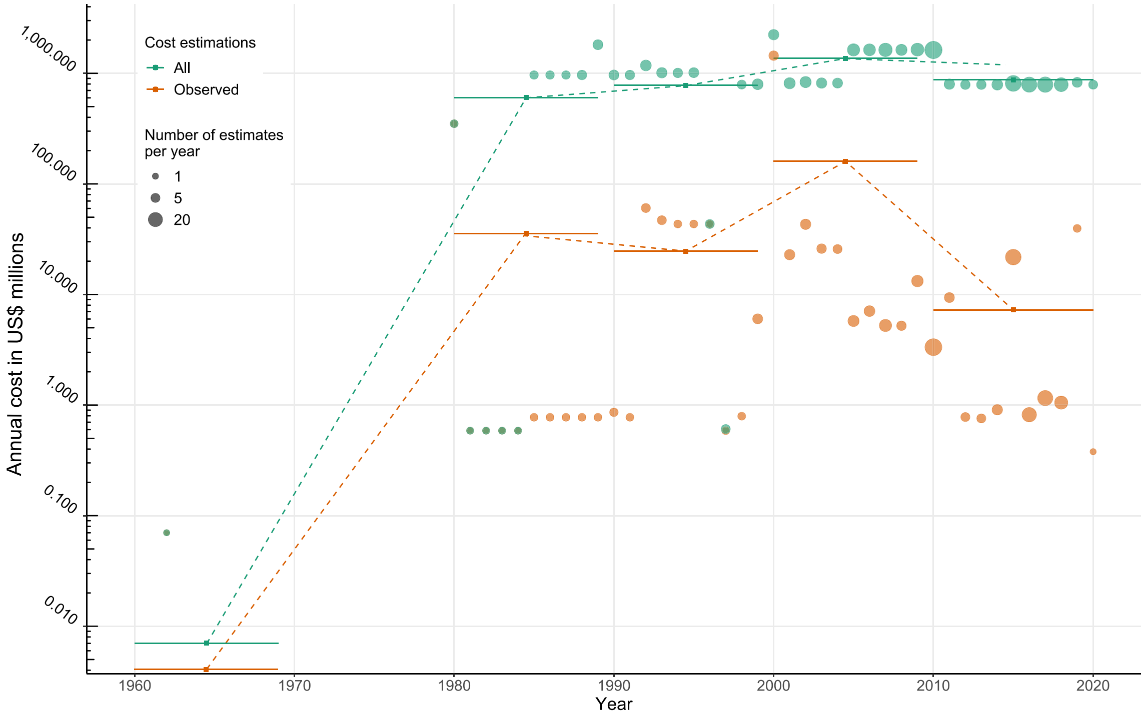

Fig. 4. Total (green) and observed (orange) average annual costs in billions of 2017 US$ resulting from global invasions by fish. Points are annual values scaled by the number of annual estimates. Note that the *y*-axis is represented on a $\log_{10}$ scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

continents. For example, in parts of South America (e.g. northern Bolivia), the introduction of *Arapaima gigas* has had serious environmental impacts and is aggressively replacing commercially valuable native fisheries (although *A. gigas* is also fished commercially) (Miranda-Chumacero et al., 2012; Liu et al., 2017; Ju et al., 2019). In East Africa, although the introduction of Nile perch has increased commercial fishing yields, stimulated fish processing and generated income from recreational tourism, it has also had negative effects on local communities by displacing small-scale fishermen and increasing food insecurity and health problems around Lake Victoria (Abila, 2000; Yongo et al., 2005; Aloo et al., 2017). The invasion has also altered the ecological community composition and food web of the lake (Witte et al., 2013), reducing

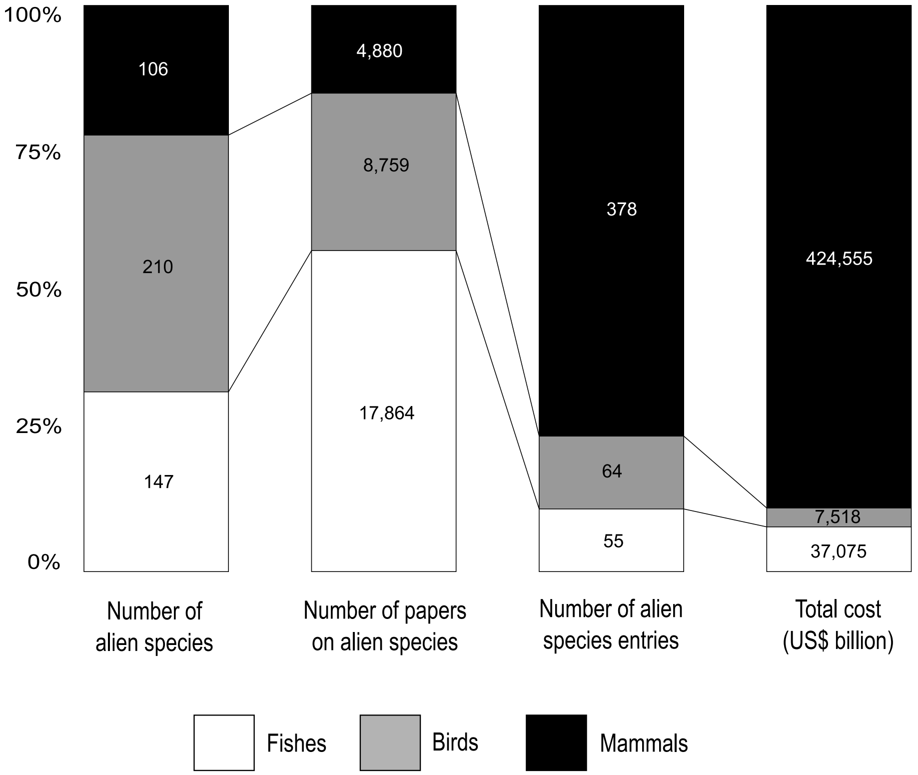

Fig. 5. Comparison among fishes, birds and mammals based on the numbers of alien species, numbers of articles on alien species, entries and costs in the InvaCost database.

water quality and causing the extinction of around 200 native species (many of them endemic), resulting in one of the largest anthropogenic ecosystem changes ever recorded (Ligtvoet et al., 1991; Kaufman, 1992; Mugidde et al., 2005).

With respect to the large difference in costs between North America and Europe, one possible contributing factor worth considering is that the fauna of the Western Palearctic is depleted due to glaciations (Oberdorff et al., 1997). While Nearctic fish faunas were less impacted by glaciations and remained relatively diverse, most fish species in European rivers were intentionally introduced or colonized as a result of anthropogenic activities e.g., the Danube (Levêque et al., 2007). Therefore, invasions in Europe might have an impact, at best, on a limited number of freshwater fishes (or might even have been economically beneficial historically), whereas invasions in North America would necessarily have an impact on a larger number of native species (Levêque et al., 2007). Therefore, compared to other regions, higher costs may also result from the economic importance of the respective freshwater fisheries, which are much more developed in North America than in Europe (e.g. especially for recreational activities such as angling and boating; Franklin, 1998; Mordue, 2009). Another potential bias may exist with respect to the regional variation in the number of researchers and institutions studying the impacts of invasive alien fish. That is, that a disproportionately large number of North American researchers may be studying invasive alien fish. This may explain the relatively large investment in management efforts in North America (e.g. for sea lampreys; Stewart et al., 2003; Twohey et al., 2003). Nevertheless, the discrepancies in invasive alien fish costs between North America and Europe cannot be fully explained by differences in economic activity or severity of impacts triggered by invasions. It is also often unclear whether management of invasive populations is driven by ecological or economic rationale between these regions or elsewhere, and InvaCost does not record this information.

In contrast to freshwater fish invasions, very few costs are associated with invasive alien marine fish species (Anton et al., 2019, 2020). This is notable given their well-known impacts on marine ecosystems (i.e. on habitat or other native species via competition for food) and on spatially-overlapping commercial fisheries for native species (i.e. costs incurred by bycatch, gear damage, injury, increased fuel consumption to reach invasive-free areas, etc.). Key examples include the angelfish *Pomacanthus* sp. (Semmens et al., 2004), the round herring *Etrumeus golanii* (Galil et al., 2019), the rabbitfish *Siganus rivulatus* and *S. luridus*, the pufferfish *L. sceleratus* in the Mediterranean (Kalogirou, 2013; Giakoumi, 2014) and the lionfish *P. miles* (Moonsammy et al., 2012). We think that the low number of entries in the database for marine fish, and for fishes in general, reflect limited knowledge of the costs being incurred, rather than their absence.

4.2. Conservative nature of reported costs

Considering the biases described above, the cost estimates presented here are likely to be very conservative, as cost data are scarce for most invasive alien fish species and for most regions of the world (see also Diagne et al., 2021 for an overview of the reasons for cost underestimation). A limited understanding of the costs of invasive alien fish is likely to hamper effective communication, investments in detection, control, prevention and management, and relegate them to the bottom of the priority list of policy makers and/or resource managers facing budgetary constraints. This is despite the fact that much of the funding used to manage invasive alien fish in North America comes directly from angling licence sales and taxes on fishing gear and boat fuel, and was therefore not reported or tracked in InvaCost. For example, in 2011, anglers in freshwater ecosystems in the US generated more than US$40 billion in retail sales, with an estimated total economic impact of US $115 billion and more than 800,000 jobs (Hughes, 2015). Although not reflected in our results for the costs of invasive marine fish, the expenditure of marine anglers is also substantial ($31 billion in 2012), as is the economic impact (US$82 billion and 500,000 jobs in 2012) (Hughes, 2015). Of course, most of these species are not invasive, but since some of them are, it contributes to the difficulty of comparing costs and benefits of invasive alien fishes.

In addition, many of the costs associated with research activities seeking to advance knowledge of invasive alien fish, controlling their populations and mitigating their impacts are generally unreported or inaccessible in the public domain, resulting in an underestimation of investment in relevant research. This is an important driver of limitations inherent in the InvaCost database. Firstly, the monetary costs recorded in InvaCost were largely based on a systematic use of research terms (Diagne et al., 2020a), however, different studies and parties use different terminology to describe invasive alien species. As a result, costs may have been missed in these searches given the pervasive differences in keywords across cost reporting documents. Another similar reason is the fact that some source documents may use the vernacular names that were not considered in the search strings. Additionally, despite the effort to include literature in multiple languages (15 additional non-English languages in InvaCost searches, see Angulo et al., 2021), it has not been possible to cover all languages that may be reporting costs for invasive alien fish globally. This may have exacerbated perceived knowledge gaps in Asia and Africa in particular for which the linguistic coverage was limited. InvaCost is further limited in that only impacts that can be readily monetised are included, resulting in the omission of potential impacts assessed via other measures and metrics, or that are non-market in nature. Furthermore, the methods used to quantify these impacts differ considerably among studies — and although InvaCost uses an objective binary classification for reliability and implementation of the method as a standardised repository for reported costs — it has not been possible to fully account for the variable methodological nature of the underlying studies. The costs in InvaCost therefore directly reflect those reported in the underlying studies, and are subject to their respective potential criticisms. It is important to stress that many of these aforementioned limitations likely make our results substantial underestimates. Considering that InvaCost is a living database meant to be updated on an ongoing basis by authors and future users (Diagne et al., 2020a), we expect that these limitations can be alleviated in the future, yielding improved and more realistic estimates of costs for invasive alien fish and other species.

Finally, we note that invasive alien fish species are also known to have economic benefits (especially when they have commercial value) as well as aesthetic and spiritual values (Gozlan et al., 2010; 2018), which requires a better understanding of the trade-offs and incentives to introduce new species and/or maintain a long-term sustainable stock of their invasive population. Considering the benefits of invasive alien fish and understanding these trade-offs was beyond the scope of both the InvaCost database and this paper. However it is an important dimension of managing these species for the greater public good, and one that deserves further exploration in future research. Nevertheless, a comprehensive understanding of the costs and benefits of invasive alien fish is difficult because fish often disperse freely across international borders in seas and rivers, and trade pathways differ greatly between neighbouring countries, while neither costs nor benefits are equally shared.

5. Conclusion

Our work highlights the known and unknown economic costs of invasive alien fish species on a global as well as regional scale. A better understanding of the costs of invasive alien fish species should contribute, for example, to more responsible aquaculture practices, increased awareness of the risk of recreational introductions, and more effective regulatory instruments to prevent accidental species introductions. While it is difficult to predict how the cost of invasive alien fish will evolve worldwide, it is certain that the numbers of introductions of invasive alien species will continue to increase over time (Seebens et al., 2017, 2020). There is accordingly an urgent need to develop more effective and proactive management strategies to prevent fish invasions and promote mitigation of their impacts.

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CRediT authorship contribution statement

Phillip J. Haubrock: Conceptualization, Data curation, Methodology, Formal analysis, Writing – original draft, Visualization. **Camille Bernery:** Formal analysis, Conceptualization, Methodology, Writing – original draft, Visualization. **Ross N. Cuthbert:** Formal analysis, Conceptualization, Methodology, Writing – original draft, Visualization. **Chunlong Liu:** Writing – review & editing. **Melina Kourantidou:** Methodology, Writing – review & editing. **Boris Leroy:** Data curation, Methodology, Writing – review & editing, Visualization. **Anna J. Turbelin:** Data curation, Methodology, Formal analysis, Writing – review & editing, Visualization. **Andrew M. Kramer:** Writing – review & editing. **Laura N.H. Verbrugge:** Writing – review & editing. **Christophe Diagne:** Data curation, Methodology, Supervision, Writing – review & editing. **Franck Courchamp:** Conceptualization, Data curation, Methodology, Supervision, Writing – review & editing. **Rodolphe E. Gozlan:** Conceptualization, Data curation, Supervision, Writing – review & editing.

Declaration of competing interest

The author have no financial/personal interest or belief that could affect their objectivity to declare.

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Conclusion : Dans cette étude, nous avons estimé les coûts économiques globaux documentés des poissons exotiques envahissants, qu'ils soient marins ou d'eau douce, sur la base d'une compilation de l'ensemble des coûts économiques évalués dans la littérature (n=384 coûts annualisés). Parmi les 27 espèces de poissons dans la base InvaCost, 25 sont des espèces de poissons d'eau douce. Les coûts observés (*i.e.*, coûts réalisés) à l'échelle mondiale de ces poissons d'eau douce s'élèvent à 36,28 milliards de dollars depuis 1970, et les coûts potentiels (*i.e.*, coûts prédits ou extrapolés) à 795,29 millions de dollars. Les espèces marines ne représentent quant à elles que 31,07 millions de dollars, tous coûts confondus. En considérant tous les taxons d'eau douce de la base InvaCost, les poissons représentent le deuxième groupe le plus coûteux, juste après les moustiques du genre *Aedes* causant majoritairement des dommages sanitaires (Cuthbert et al. 2021).

Les espèces de poissons d'eau douces les plus coûteuses sont des espèces caractérisées notamment par leur grande aire d'invasion, leurs nombreuses voies d'introduction et/ou par leurs impacts écologiques (Table 1). Les trois espèces les plus coûteuses recensées sont :

1. La grémille (*Gymnocephalus cernua* - 28,93 milliards de dollars), avec des coûts provenant majoritairement de modèles d'extrapolations de leurs impacts sur la pêche récréative, résultant aussi en coûts de gestion. Ces coûts sont majoritairement localisés en Amérique du Nord.

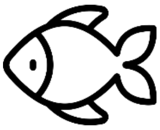
2. Le goujon asiatique *(Pseudorasbora parva* - 5 milliards de dollars), dont les coûts sont majoritairement composés de coûts de gestion (contrôle et éradication) au Royaume-Uni.

3. La lamproie marine *(Petromyzon marinus* - 1,4 milliards de dollars), avec des coûts majoritairement localisés en Amérique du Nord et composés de coûts de dommages sur les pêcheries et de coûts de gestion.

Toutefois ces résultats sont sujets à des biais, notamment dus aux manques de données d'impacts. Ces biais sont les mêmes que pour les poissons en général : les coûts répertoriés sont majoritairement situés en Amérique du Nord et associés à un petit nombre d'espèces (25) par rapport au nombre d'espèces de poissons d'eau douce exotiques établies dans le monde (551 espèces selon Tedesco et al. 2017). Ainsi, certaines espèces majeures de poissons d'eau douce envahissantes sont manquantes, comme par exemple la perche du Nil (*Lates niloticus*) qui a pourtant mené à une précarisation des pêcheurs locaux sur le lac Victoria (Aloo et al. 2017, et voir Chapitre 1 - Annexe 2). Par conséquent, les coûts réels potentiels sont probablement sous-estimés dans la base InvaCost, et pourraient être revus à la hausse avec l'augmentation des recherches sur le sujet et des introductions d'espèces exotiques dans les années à venir (Seebens et al. 2017).

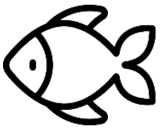
Table 1 : Informations supplémentaires concernant l'histoire d'invasion et l'écologie des espèces de poissons d'eau douce les plus couteuses actuellement connues. Crédits photos : Wikimedia Commons.

 *Gymnocephalus cernua* **28,93 milliards de dollars**	La grémille (*Gymnocephalus cernua),* originaire d'une partie de l'Europe et d'Asie, est une espèce envahissante en Europe et en Amérique du Nord (Gutsch & Hoffman 2016). Cette espèce été introduite via les eaux de ballast dans les grands lacs américains, et via les canaux, les transports maritimes et les lâchers d'appâts par les pêcheurs en Europe. Elle a des impacts sur les communautés natives par compétition pour la ressource alimentaire, et aussi par prédation (Gutsch & Hoffman 2016).
 *Pseudorasbora parva* **5 milliards de dollars**	Le goujon asiatique (*Pseudorasbora parva*) est originaire d'Asie de l'Est et a envahi 32 pays partout dans le monde. Cette espèce est principalement introduite via l'aquaculture en tant « qu'auto-stoppeuse » (*i.e.*, organisme qui a une association opportuniste avec une marchandise) de la carpe commune et via la pêche récréative (Gozlan et al. 2010a). Le goujon asiatique est caractérisé par la grande plasticité de ses traits reproductifs et développementaux (Gozlan et al. 2010a). Il est porteur sain de l'agent rosette *Sphaerothecum destruens*, connu pour causer le déclin des populations de poissons native et pour faciliter l'invasion du goujon (Ercan et al. 2015).
 *Petromyzon marinus* **1,4 milliards de dollars**	La lamproie marine *(Petromyzon marinus)* est originaire d'Europe où elle est menacée, et est envahissante en Amérique du Nord (Hansen et al. 2016). Elle a été introduite via son utilisation comme appât dans la pêche récréative, et pourrait aussi s'être répandu au travers des canaux en s'accrochant aux bateaux (GISD 2022b). La lamproie marine est un parasite des autres poissons, et contribue ainsi au déclin de grands poissons prédateurs natifs (Cucherousset & Olden 2011).



AXE 2 : Étude des facteurs expliquant le succès des invasions de poissons d’eau douce

Au cours de l'Axe 1 de cette thèse, nous avons pu décrire les processus des invasions de poissons, mais aussi attester de leurs impacts importants à l'échelle mondiale, qu'ils soient économiques ou écologiques. Comprendre les processus entrant en jeu dans le processus d'invasion est important afin d'anticiper ces impacts. Ainsi, dans la suite de cette thèse, nous avons eu pour objectif de caractériser les profils d'espèces en déterminant les facteurs associés au succès d'invasion des espèces exotiques. Toutefois, l'étude de ces facteurs demeure complexe : les facteurs sont nombreux et dépendent à la fois de l'espèce (*e.g.*, régime alimentaire, taille, tolérances physiologiques) et du milieu envahi (*e.g.*, anthropisation, caractéristiques des assemblages), et interagissent avec d'autres aspects des invasions tels que la voie d'introduction ou l'étape de l'invasion considérée. Or, les études actuelles ne s'accordent pas sur un profil type de poisson exotique. Par exemple, alors que Ribeiro et al. (2008) associent un fort succès d'établissement à une petite taille, Vila-Gispert et al. (2005) l'associent à une grande taille. De même, Kolar and Lodge (2002) associent l'impact avec une haute tolérance aux basses températures, alors que Snyder et al. (2014) l'associent à une basse tolérance aux basses températures. Des études à l'échelle globale permettraient de mettre en évidence les grandes tendances liées aux étapes d'invasion et aux voies d'introduction qui sont difficiles à détecter à l'échelle locale, mais aussi de prendre du recul et nuancer des tendances contradictoires à l'échelle locale. Afin de répondre à cette problématique, nous avons décidé dans cette partie d'étudier différentes caractéristiques des poissons exotiques envahissants à l'échelle globale, et de déterminer leur influence sur le succès des différentes étapes d'invasion : introduction, établissement et impacts. En particulier, cette partie permettra de déterminer les caractéristiques écologiques, et socio-économiques des espèces exotiques envahissantes à l'échelle globale.



Chapitre 3 : Quelles sont les caractéristiques importantes des poissons d’eau douce envahissants ?

Important characteristics determining the success of non-native freshwater fish introduction, establishment, and impact.

Running title : Characteristics of successful fish invaders

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Abstract

Aim

The invasion success of introduced freshwater fish is influenced by many factors, including ecological, species, and socioeconomic characteristics. Most studies that document the importance of one of these factors are conducted at a local scale and/or focus on a single step of the invasion process. Here, our aim is to identify the characteristics of successful invaders across the entire invasion process using ecological, species, and socioeconomic characteristics.

Location

Worldwide.

Time period

Contemporary.

Major taxa studied

Freshwater fish.

Methods

We conducted a worldwide analysis of 307 freshwater fish species and considered the number of countries in which each species was introduced, established, or had ecological impacts as a proxy of invasion step success. We applied generalized linear models to 20 variables relating to species morphology, ecology, and introduction pathways to determine the main characteristics associated with invasion success. By disentangling our results by pathways, we specifically explore the role played by aquaculture and ornamental trade pathways in the characteristic selection.

Results

We found that non-native freshwater fish with a broad diet, high parental care, and multiple introduction pathways are the most widely introduced and established worldwide. The number of countries associated with impacts was best explained by the type of introduction pathway (*i.e.*, aquaculture or fisheries). We also discovered that alien species introduced through aquaculture belonging to Cypriniformes and having a broad diet were the most widely introduced and established species. The same was observed for species introduced through ornamental pathways that were mainly native to tropical regions.

Main conclusions

Considering both intrinsic and extrinsic drivers is important when analyzing the invasion success of freshwater fish and disentangling the different invasion steps. These findings have strong implications for anticipating the profile of species with a high potential to invade a large number of countries.

Key words: aquaculture, ecology, exotic, freshwater fish, introduction pathways, invasion steps, morphology, ornamental trade, socioeconomic, traits.

Introduction

The rise of global trade has led to an increase in the introductions of invasive alien species worldwide (Seebens et al., 2017). Nowadays, biological invasions are recognized as a major threat to biodiversity (Bellard et al., 2016). Freshwater fish are among the most introduced taxa, and non-native freshwater fish are now established in all biogeographical realms (Gozlan, 2008; Leprieur et al., 2008). Established non-native freshwater fish species have diverse impacts, ranging from local hybridization with native fauna – such as between the invasive rainbow trout (*Oncorhynchus mykiss*) and native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in Canadian rivers as reported by Muhlfeld et al., (2009) – to profound changes in species assemblages, leading to taxonomic homogenization across large regions such as the Laurentian Great Lakes (Campbell and Mandrak, 2020).

Nonetheless, not all introduced non-native fish species become established or have impacts. Previous studies have shown that the success of each step of the invasion is influenced by three categories of drivers: species characteristics, ecological characteristics of the native or recipient ecosystems, and socioeconomic characteristics. Regarding species characteristics, non-native fish species with a broad food spectrum are more establish more easily than more specialized species (Ruesink, 2005). Likewise, for ecological characteristics, the size of the native range influences the establishment and spread of non-native species (Marchetti et al., 2004a). Concerning socioeconomic characteristics, some introduction pathways are known to be an important source of freshwater fish introductions and establishments such as aquaculture and ornamental trade (Gozlan et al., 2010). Socioeconomic characteristics can also relate to the human use of fish, as the development of the ornamental trade has caused a recent rise in fish introductions (Magalhães and Jacobi, 2013). Moreover, we can expect a strong interaction between species characteristics and socioeconomic drivers. For instance, species introduced through the aquaculture trade are more likely to be large species (Su et al., 2020), while those introduced through ballast waters are more likely to be small species (Wonham et al., 2000). Understanding the different characteristics that promote invasions is extremely important in order to improve predictions about future invasions (Pyšek et al., 2020).

Several papers have focused on understanding the characteristics of successful invasive freshwater fish species using quantitative analysis (*e.g.*, García-Berthou, 2007; Snyder et al., 2014; Su et al., 2020). However, species, ecological, and socioeconomic characteristics have rarely been studied together at the global scale for freshwater fish (but see (Ruesink, 2005; Pyšek et al., 2020). Indeed, most studies are conducted at a local scale with the analyses performed on a limited number of species (Marchetti et al., 2004b; Ribeiro et al., 2008), often without considering the different types of drivers (Ribeiro et al., 2008) or the steps of the invasion process (*e.g.*, García-Berthou, 2007, Ruesink, 2005; Lawson and Hill, 2021). As a result, there is currently no consensus about the drivers influencing the invasion success of freshwater fish globally (but see García-Berthou, 2007).

To address this gap, we aimed to determine the drivers of the different steps of invasions (*i.e.*, introduction, establishment, and impact) of freshwater fish species at the global scale using a statistical modeling approach. For 307 freshwater fish species, we considered their species (functional and morphological traits), ecological (features of the native ecosystems of the species), and socioeconomic characteristics (introduction pathways and human use). We investigated the link between these characteristics and the invasion patterns measured as the number of countries where each species is introduced, established, and reported to impact the native fauna or recipient ecosystem. We built our models based on initial assumptions for each invasion step. First, we hypothesized that the species characteristics influencing the introduction success are dependent on the introduction pathway (*e.g.*, given that large-bodied fishes are more interesting for consumers, they have a greater chance of being introduced through the “aquaculture” pathway; Su et al., 2020), which is itself influenced by the native region of non-native species (*e.g.*, species from the ornamental trade tend to be native in tropical countries, Gertzen et al., 2008). As the establishment step depends on the adequacy between the recipient ecosystem and the needs of the species, we hypothesize the higher success of generalist species (*i.e.*, broad diet) and species introduced in large numbers (*i.e.*, with high propagule pressure). High parental care has also been highlighted in several studies as an important characteristic influencing establishment (Marchetti et al., 2004b; Lawson and Hill, 2022). Few studies have focused on the impact step. However, it has already been demonstrated that species at the top trophic levels have a large impact, notably because prey in the new environment are naive to the new predator (Moyle and Light, 1996; Howeth et al., 2016). We can hypothesize that species with a nekton diet will have a greater impact than species at low trophic levels.

Material and methods

Species-level variables influencing the invasion success of freshwater fish

To understand the drivers of success in exotic freshwater fish introduction, establishment, and impact, we compiled species-level variables pertaining to their species, ecological, and socioeconomic characteristics. We chose these variables because they are assumed to influence species invasions (see Table 1 for justifications and hypotheses; Pyšek et al., 2020). We obtained 20 species-level variables from five data sources: (i) FishBase (Froese and Pauly, 2019, version 19.04, accessed with the "rfishbase" R package; Boettiger et al., 2012), which includes data on the invasive status, characteristics, and human use of 34,300 fish species at the global scale; (ii) the FISHMORPH morphological database (Brosse et al., 2021), which includes information on the morphological traits of 9,150 fish species; (iii) the database on freshwater fish occurrences complied by Tedesco et al. (2017), which has distribution data for 14,953 freshwater fish species in 3,119 basins worldwide; (iv) the global biogeographical regions of freshwater fish (Leroy et al., 2019); and (v) the world climate database WorldClim (Fick and Hijmans, 2017). We summarized all variables in Table 1 and describe them in detail hereafter.

Species characteristics

We defined freshwater fish as all species with a freshwater habitat listed as one of their preferred habitats in the table *species()* of the "rfishbase" R package.

Main diet and number of diets – To retrieve data on species diets, we used the 5 type of diet filled in the "FoodI" column of the *fooditems()* table of the "rfishbase" R package : Detritus, Nekton, Plants, Zoobenthos, and Zooplankton. We used two variables: (i) the most represented diet for each species as the main diet and (ii) the total number of diets (Table 1). In the rare cases (37 out of 307 species considered here) where several diets were equally represented, we chose the most represented diet within the order. We made an exception for *Megalops atlanticus* to which we had associated the "nekton" main diet, because this species, which is a known predator of crabs and small fish (Planquette et al., 1996), has two main diets that are also the two most represented diets of the order.

Swimming ability – To analyze the influence of swimming ability on invasion success, we used two variables from Su et al. (2019). First, we used the pectoral fin vertical position (*i.e.*, ratio of pectoral fin position relative to body depth), which reflects the swimming style (Table 1). Lateral pectoral fins are used for propulsion and fine movements, whereas ventral pectoral fins often characterize fish with less precise movements (Blake, 2004; Su et al., 2019). Second, we used the ratio of body length to body depth, which reflects fish hydrodynamics (Villéger et al., 2017; Su et al., 2019) (Table 1).

Parental care – We used the parental care variable from the "RepGuild1" column of the *species()* table of the "rfishbase" R package (Table 1). The parental care variable considered three categories: nonguarders corresponding to species which do not guard eggs, guarders corresponding to species which guard eggs, and bearers which are species that incubate eggs on or in the parental body.

Total length (TL) – To gather this information, we used the “TL” column of the *morphometrics()* table of the “rfishbase” R package. As a species can have several different total length, we took the median of all the given total length for each species.

Species taxonomy – We used FishBase as the taxonomic reference (Froese and Pauly, 2019). For each species, we completed the order using the *load_taxa()* table from the “rfishbase” R package. The number of species per order was heterogeneous, which can cause statistical issues due to class imbalances, especially for minority classes (*i.e.*, orders with only one or a few species). Therefore, we kept the main orders (*i.e.*, Characiformes, Cypriniformes, Cyprinodontiformes, Perciformes, and Siluriformes) in the models and grouped together the remaining orders in the “other” category.

Ecological characteristics

Main native bioregion – Freshwater fish have evolved in isolated biogeographical regions for the past 10-20 million years (Leroy et al., 2019). Consequently, each bioregion has distinct characteristics pertaining to its environmental conditions, faunistic composition, and associated interactions. In addition, biogeographical regions broadly cover the main geopolitical regions of the world, with distinct intra-region and inter-region properties in terms of species displacement and propagule pressure. Hence, the region of origin of a species is a proxy of several characteristics: environmental conditions, diversity of interactions during evolutionary history, and chances of introduction to non-native ecosystems (Table 1). We defined two variables based on the biogeographical regions of Leroy et al (2019): the number of native bioregions (defined as bioregions where the species has native occurrences) and the main bioregion, defined as the bioregion with the highest number of native basins where the species is found. It is important to note that 85% of the species considered here have only one bioregion. We excluded species that did not occur within the limits of the bioregions. A total of 2 species equally occurred in two native bioregions. For these species, we selected one region at random and verified whether this choice had an impact on the model results using sensitivity analysis.

Temperature amplitude, minimum and maximum temperature in the native basins – We used the minimum temperature of the coldest month and the maximum temperature of the warmest month from Worldclim (Fick and Hijmans, 2017) to derive two variables: annual maximum temperature and temperature amplitude (Table 1). We excluded the annual minimum temperature, as this variable was correlated to temperature amplitude. We only took into account the 0.95 quantile of the maximum temperature of the warmest month and the 0.05 quantile of the minimum temperature of the coldest month across the native basins for each species to avoid extreme outlier values.

Socioeconomic drivers

Introduction pathways – Using the *introduction()* table from the "rfishbase" R package, we considered each pathway as an independent variable (Table 1). Therefore, species could have several introduction pathways. We filtered out pathways containing only a few species. We thus reclassified pathways documented in FishBase into the seven following categories: aquaculture, sport/angling, species control, diffusion, accidental, fisheries, and ornamental trade (Appendix 1).

Use by humans – Four columns of the *species*() table in the "rfishbase" R package indicate the human use of species through fisheries ("Importance" column), bait ("Usedasbait" column), sport ("GameFish" column), or aquariums ("Aquarium" column). If a species is used in at least one of these four sectors (*i.e.*, belonging to a category other than "never/rarely," "of no interest," "of potential interest," or "potential"), we considered this species to be used by humans.

Table 1: Variable descriptions.

Variable type	Variable	Variable modalities	Hypothesis / Justification
Response variable	Number of countries where the species: (i) is introduced (ii) is established (iii) has ecological impacts (for all species and the ornamental and aquaculture pathways)	Quantitative variables	/
Species characteristics	Main diet	▪ Detritus ▪ Nekton ▪ Plants ▪ Zoobenthos ▪ Zooplankton	Broad food spectrum, piscivorous diet, as well as some specialized diets facilitate establishment (Ruesink, 2005; Tonella et al., 2018). A nekton diet can be associated with species having an impact (Moyle and Light, 1996; Howeth et al., 2016).
	Number of diets	Quantitative variable	
	Hydrodynamics	Quantitative variable	Good swimming ability enables fish to colonize new regions, spread, establish, and have wide impacts (Carvajal-Quintero et al., 2019).
	Pectoral fin vertical position	Quantitative variable	
	Parental care	Ordered categorical variable ▪ Non-guarder ▪ Guarder ▪ Bearer	A high level of parental care facilitates establishment (Marchetti et al., 2004b; Lawson and Hill, 2021).
	Total length	Quantitative variable	At the introduction step, the body length of successful species is linked to the introduction pathway (Wonham et al., 2000; Su et al., 2020). At the establishment step, body length depends on the environmental conditions (Vila-Gispert et al., 2005). At the impact step, small species can have greater impacts (Marchetti et al., 2004).
	Taxonomy	▪ Cypriniformes ▪ Cyprinodontiformes ▪ Siluriformes ▪ Characiformes ▪ Other	Order is a surrogate for missing characteristics that could influence species success at different stages of the invasion.
Ecological characteristics	Temperature amplitude in the native basins	Quantitative variable	Temperature amplitude in native basins can be a proxy of temperature tolerance. Temperature tolerance influences the establishment and spread of invasive species (Kolar and Lodge, 2002; Marchetti et al., 2004b; Snyder et al., 2014).
	Maximum temperature in the native basins	Quantitative variable	

	Main native bioregion	▪ Nearctic ▪ Palearctic ▪ Sino-Oriental ▪ Neotropical ▪ Ethiopian ▪ Madagascan	Native bioregions reflect socioeconomic characteristics, propagule pressure, and environmental conditions.
Socioeconomic characteristics	Aquaculture	1/0 Quantitative variable	Introduction pathways constrain the characteristics of introduced species (Wonham et al., 2000; Su et al., 2020). The number of introduction pathways is linked to high propagule pressure.
	Sport/Angling		
	Accidental		
	Ornamental		
	Fisheries		
	Diffusion		
	Species control		
	Number of introduction pathways		
	Use by humans	Yes/No	Species used by humans have greater chances of being introduced than those not used by humans.

Response variables

In this study, we considered three steps of the invasion: introduction, establishment, and impact. We gathered data on three variables that reflect these three steps: the number of countries where species are introduced, the number of countries where introduced species are established, and finally, the number of countries where the established species have impacts. To obtain information about these variables for each species, we used the *introductions()* function of the “rfishbase” R package. This table describes the introduction events of fish species, giving the location of the introduction, the species concerned, as well as the establishment and impact status of the species.

Number of countries where species are introduced, established, and have impacts

We used the locations found in the “TO” column of the *introduction()* table of the “rfishbase” R package. It should be noted that some species were simply transported to the new location without being introduced to the wild. These species were impossible to separate from others, although they remain scarce because most alive imported species are introduced (intentionally or accidentally) to the natural environment (Nicolas Bailly pers. com.). Thus, we assumed that all species were introduced to the wild. The locations listed in FishBase were not standardized at a specific spatial scale (names ranged from the names of cities to entire continents), so we manually harmonized names to the country scale as follows : We excluded all records above the country scale. Then we grouped islands located far from their country by archipelago or considered them separately when they did not belong to an archipelago. As some of the introductions were old, the listed countries no longer exist and could not be grouped or assimilated with the new country. This was the case for the USSR and Korea. We therefore considered these countries independently. When the spatial grain was the river or lake, we considered all the riparian countries independently. We listed as "Unknown" any locations given at a larger scale than a country (*e.g.*, "Europe") or locations that could not be identified. The list of 208 countries considered in this study is available in Appendix 2.

For each species, we counted the number of countries where the species were introduced, established, or had impacts. Concerning the establishment step, all the species noted as "Yes," "Probably Yes," "Established," or "Probably established" in the "Estabwild" column of the *introduction()* table were taken as species established in the wild in the considered locations. We removed from the analysis the species that were listed as established but not introduced beforehand, as we could not access the establishment location of these so-called non-introduced species. We took as established any species that had an impact but were not established (*i.e.*, "No" or "Probably no" in the "Estabwild" column) or had an unknown establishment status. Concerning the impact step, we considered that all the species noted as "Yes," "Probably some," or "Some" in the "EcolEff" column of the *introduction()* table had ecological impacts in the considered locations.

We obtained 840 species with an introduction status (307 species filled as introduced species, and 533 as non-introduced species). For the 307 introduced species, the number of countries where the species were introduced was provided. Among these 307 introduced species, 217 species were established in at least one country and 117 had ecological impacts in at least one country.

Statistical analysis

To determine the characteristics of the species at each step of the invasion process, we used generalized linear models (GLM) to analyze the influence of species, ecological, and socioeconomic characteristics on the number of countries where the species are introduced, established, or have impacts. First, we assessed the correlations between all the 20 explanatory variables. We used the *ggcorr()* R function of the GGally package (Schloerke et al., 2020) to explore the Spearman correlations between quantitative variables. We also used the *model.matrix()* from the stats package (R Core Team, 2020) to separate each modality of the numerical variables into binary variables. We then used the *cor()* function (stats package; R Core Team, 2020) to explore the Pearson correlations between the new binary variables and between the binary and quantitative variables. To avoid multicollinearity, we centered the variables “total length,” “temperature amplitude in the native region,” and “number of diets.”

We performed GLMs considering all the species, regardless of their introduction pathway, to explain the number of countries where the species (i) were introduced, (ii) were established, and (iii) had impacts (Appendix 3). We used the 20 explanatory variables and six interactions between the variables: the interactions between total length and temperature amplitude, between total length and order, between total length and ornamental pathway, between total length and sport/angling pathway, between total length and aquaculture pathway, and between number of diets and order (Appendix 3). We also conducted the same analyses while considering only the species introduced through the aquaculture pathway or through the ornamental trade pathway (*i.e.*, 11 variables and 3 interactions; see Appendix 3).

As our data were count data, we computed these GLMs with Poisson distributions or negative binomial distributions when our response variables were overdispersed. To check for overdispersion, we used the dispersiontest() function from the "AER" R package (Kleiber and Zeileis, 2008). Then we used the stepAIC() function from the "MASS" R package (Venables and Ripley, 2002) and a stepwise selection to choose the best model based on the Akaike information criterion. For each model, a pseudo-r2 was estimated using the following formula: 1 – Model Deviance / Model Null Deviance. We identified the significant variables of each model using the Anova() function from the "car" R package (Fox and Weisberg, 2019). The variable importance of each variable in the models (*i.e.*, absolute value of the t-statistic of each model variable) was calculated using the varImp() function from the "caret" R package (Kuhn, 2008).

To take into account the potential fluctuations due to the randomly chosen main diet and main regions for some species, we performed sensitivity analysis. For the species with several main diets or several main native regions, we randomly selected the main diet and the main native region. Then we performed the above GLMs on the new dataset. We repeated the process 100 times to observe the variation in the results due to the random choices. The results of these analyses are presented in Appendix 4.

Results

All species

Considering the 307 introduced species, species introduced in a high number of countries were associated with a high number of different introduction pathways (variable importance [VI] = 10), a high level of parental care (VI = 5.3 for the linear relation), had aquaculture (VI = 4.5) or fisheries (VI = 2.7) as one of their introduction pathways, and had a high number of diets (VI = 2.4) (Fig. 1a., Fig. 4). Siluriformes with a high number of diets also tend to be introduced in many countries (VI = 2.3). The establishment step model showed similar results to the introduction model for selected variables (Fig.1b., Fig. 4), except that the species established in a high number of countries were not significantly more introduced through the aquaculture pathway. Finally, species with impacts in a high number of countries were associated with most of the pathways (except for species control, accidental, and aquaculture), a high level of parental care, and a high number of diets when species were from the Siluriformes order (Fig. 1c., Fig. 4). Nonetheless, parental care was only significant in 22% of models in sensitivity analysis, thus reducing its robustness (Appendix 4C).

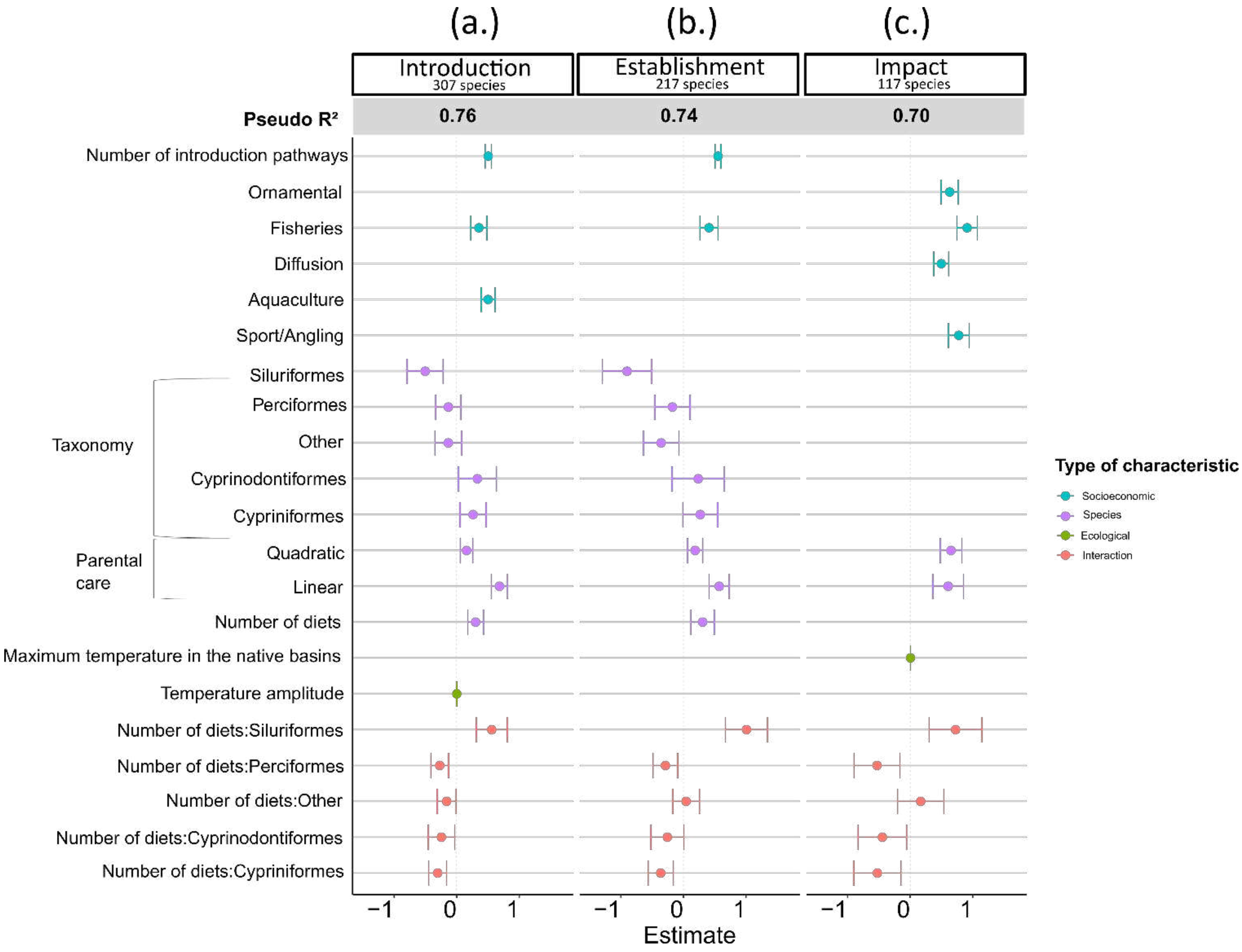

Figure 1: Estimates (with standard errors) of significant variables resulting from the generalized linear model for all the introduced species (Global) and for each step of the invasion. The sign of the coefficient depends on the category of reference for the Taxonomy and Major native bioregion variables. For taxonomy, the reference is the Characiformes order. Introduction step intercept: 0.676 (SE = 0.209). Establishment step intercept: 0.249 (SE = 0.305). Impact step intercept: -3.813 (SE = 1.036).

Species introduced through the aquaculture pathway

Species introduced through aquaculture (Fig. 2a.) in a high number of countries were associated with a high number of diets (VI = 2.9) and more often belonged to the Cypriniformes order (VI = 1.6). They were also more often associated with high parental care (significant variable in 57% of models in sensitivity analysis) (Fig. 2a., Appendix 4A). In terms of establishment, species established in many countries by aquaculture had a high number of diets (VI = 3.8) and belonged to all orders except for Characiformes, even though this tendency was less robust for the Cyprinodontiformes order (Fig. 2b , Appendix 4). They were also often associated with high parental care (significant variable in 76% of models; Fig. 2b., Appendix 4B).

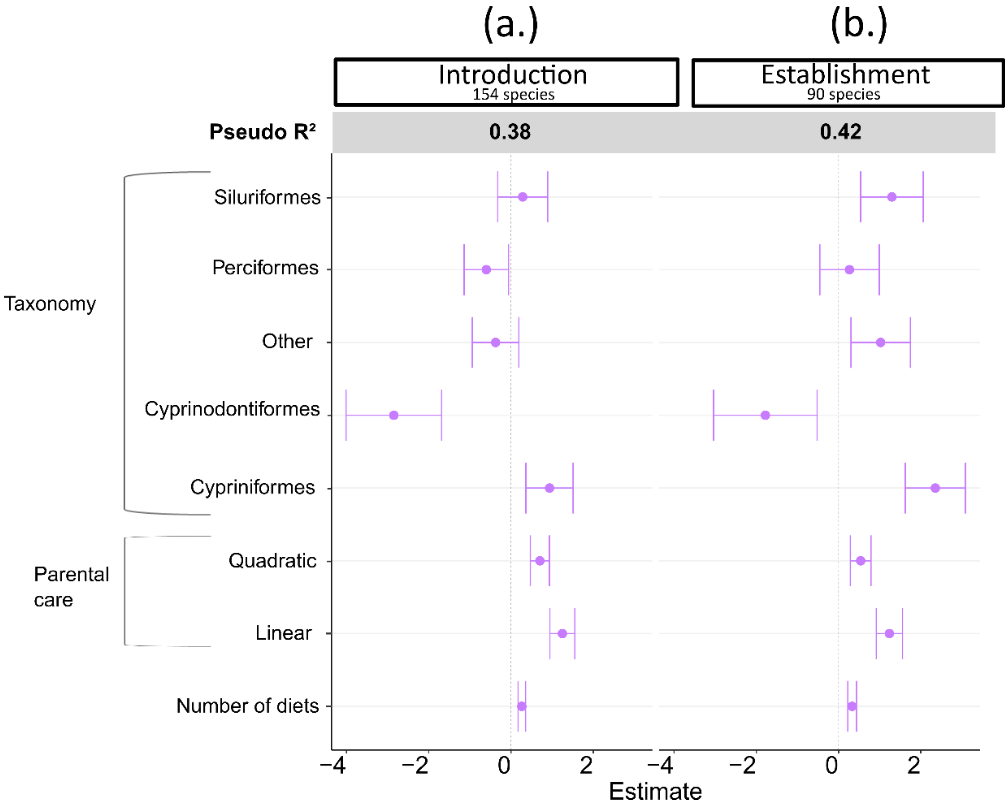

Figure 2: Estimates (with their standard errors) of significant variables resulting from the generalized linear model for the established species introduced through the aquaculture pathway and for the introduction and establishment steps. The sign of the coefficient depends on the category of reference for the Taxonomy, Main diet, and Major native bioregion variables. For taxonomy, the reference is the Characiformes order. For diet, it is the detritus diet. Introduction step intercept: 2.367 (SE = 0.538). Establishment step intercept: -0.95 (SE = 1.227).

Species introduced through the ornamental trade pathway

We analyzed the characteristics of 126 species introduced through ornamental trade (Fig. 3a.). Species introduced to many countries were not hydrodynamic (VI = 5.5), were native to the

Neotropical (VI = 2.5) or Sino-Oriental regions (VI = 2.3), and had a high number of diets (VI = 1.6).

Concerning the establishment step (Fig. 3b.), we considered a subset of 70 established species among those introduced through the ornamental trade pathway. Species established in many countries were not hydrodynamic (VI = 4.9), were from the Cyprinodontiformes (VI = 4.3) or Cypriniformes (VI = 2.4) orders, and mainly came from the Ethiopian (VI = 1.2) or Neotropical (VI = 1.1) regions.

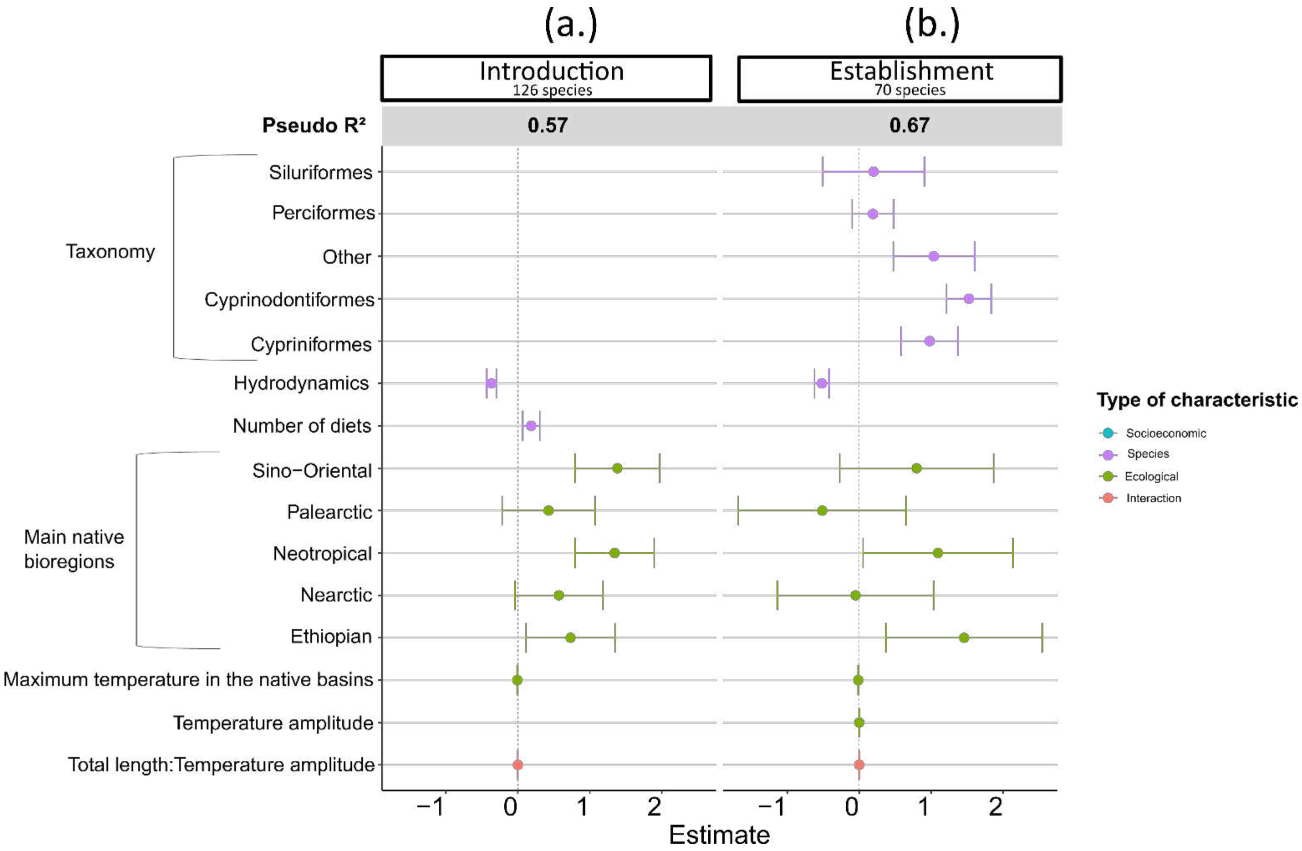

Figure 3: Estimates (with their standard errors) of significant variables resulting from the generalized linear model for the species introduced through the Ornamental pathway. The sign of the coefficient depends on the category of reference for the Taxonomy and Major native bioregion variables. For the order, the reference is the Characiformes order. For the major native bioregion, the reference is the Australian region. Introduction step intercept: 1.752 (SE = 1.31). Establishment step intercept: 4.6 (SE = 1.9).

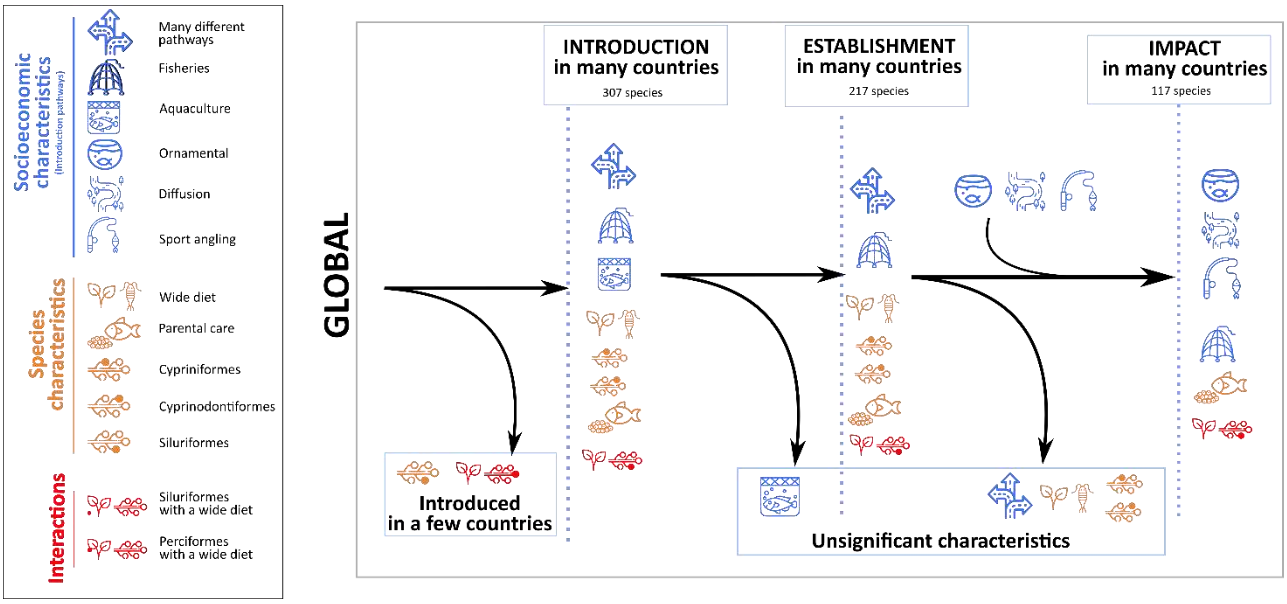

Figure 4: Main important characteristics favoring the success of each step of the invasion process.

Discussion

Using the socioeconomic, ecological, and species characteristics of 307 freshwater fish species, we were able to identify a profile of successful invasions for each step of the invasion process (Fig. 4, Appendix 5). As we hypothesized, we found that species characterized by a broad diet and high parental care as well as multiple socioeconomic pathways of introductions, including fisheries and aquaculture, were particularly successful at being introduced and established in multiple countries. By contrast, socioeconomic characteristics seem highly important to explain the impact of freshwater fish in many countries, and contrary to our hypothesis, diet did not have a significant effect on the success of this step.

Introduction step

We found that species introduced to many countries have specific characteristics. As hypothesized, multiple introduction pathways favored widespread introductions, with different entry routes increasing the chances of being transported and introduced in many locations. For example, the common carp is introduced through six of the seven pathways considered here, but some of the pathways are specific to certain countries. This is the case with the common carp introduced to several countries via aquaculture (*e.g.*, Australia, Shearer and Mulley, 1978; Varadi and Gorda, 2021), to New Zealand and South Africa for ornamental purposes (De Moor and Bruton, 1988; Hanchet, 1990, Froese and Pauly, 2019; Varadi and Gorda, 2021), and to Finland for angling (Froese and Pauly, 2019). Species introduced to a high number of countries also tend to have a high level of parental care and a high number of diets: for example, *Oreochromis mossambicus* and *Oreochromis niloticus*, respectively introduced to 97 and 94 countries, are bearers and have at least four diets (Froese and Pauly, 2019). This result confirms our initial hypothesis, as these two characteristics have already been highlighted in previous studies, although only at the state or country scale and for the establishment step (Marchetti et al., 2004a in California; Tonella et al., 2018 in Brazil; Chan et al., 2021 in Singapore; Lawson and Hill, 2022 in Peninsular Florida). Nonetheless, the role played by parental care in the introduction step of the invasion process has not yet been reported, and the underlying mechanisms remain to be clarified (*e.g.*, Marchetti et al., 2004a). One possible explanation could be that species with high parental care tend to be more introduced, because their reproduction is easier in captivity. For instance, several species of Poecilids (*e.g.*, guppies, *Poecilia reticulata*) and Cichlids (*e.g.* *Haplochromis* sp. or *Cichlasoma* sp.) are popular aquarium fish known to be highly prolific and easy to rear (Bianchi, 1993).

Establishment step

For species established in many countries, we found characteristics similar to the introduction step: high number of pathways, high parental care, and high number of diets. The high number of introduction pathways is linked to the high propagule pressure, which is known to be one of the main characteristics of invasion success (Jeschke and Strayer, 2006). High parental care maximizes offspring survival in the presence of competitors, thus providing an advantage that can favor establishment (Levine and D’Antonio, 1999). Moreover, generalist diets allow introduced species to adapt in different environments and thus provide the opportunity to establish in a wide range of environments (Tonella et al., 2018).

Despite this common overall pattern of introduction and establishment characteristics, we found several noteworthy differences. For example, although species introduced through the aquaculture pathway are introduced in many countries, their establishment success remains limited. This result is counterintuitive, as aquaculture is recognized as the most important introduction pathway of non-native freshwater fish (Gozlan et al., 2010). Our results suggest that even though aquaculture allows the establishment of many different species, it does not result in these species establishing in many different countries. This trend can be explained by the concentration of aquaculture production in Asia, especially in China, which produces a higher diversity of species (Metian et al., 2020). The way in which the species are cultured in each country also affects the probabilities of establishment. For example, species reared in and escaping from natural ponds are more likely to establish, because the individuals often escape in high numbers (Gu et al., 2022). This trend could also reflect the efficiency of management methods set by governments to limit or avoid fish escapes (Kolar et al., 2010). We can also hypothesize that some species introduced through aquaculture are not able to survive and reproduce in recipent environments (*e.g.*, East Asian carp in North Europe; Lehtonen, 2002).

Ecological impact

The variables influencing the number of countries where species have ecological impacts are distinct from those influencing the introduction and establishment steps. Contrary to our hypothesis, diet did not have a significant impact on the impact step. Fisheries, ornamental trade, and angling along with the diffusion of already established species were the major pathways favouring non-native species impacts. Surprisingly, the aquaculture pathway did not stand out as an important variable despite the substantial impact of some cultured fish. In fact, the impacts of fish introduced through aquaculture may be understudied due to their economic benefits (Gozlan, 2008; Haubrock et al., 2022), which explains why aquaculture does not stand out as an important variable. For example, the channel catfish (*Ictalurus punctatus)* is known to be responsible for the decline of native species outside its native range (Townsend and Winterbourn, 1992). Though widely introduced in Brazil for aquaculture, no ecological impact has been recorded in FishBase for the species in this country (Vitule et al., 2009; Froese and Pauly, 2019). At the global scale, data on freshwater fish impacts are incomplete, which hinders the identification of important characteristics for this invasion step (Vitule et al., 2009). Introduction pathways are not the only important variables for the impact step. Indeed, Siluriformes are introduced, established, and have impacts in many countries, but only if they have a broad diet. This tendency seems to be driven by a few species that have a broad diet and are present in a high number of countries (*i.e.*, *Clarias angilaris*, *Ictalurus punctatus, Ameiurus melas, Ameiurus nebulosus, Silurus glanis).*

Importance of interactions between pathways and species characteristics

In this study, we highlighted differences in the species characteristics according to the introduction pathways. Preliminary analysis comparing introduced and non-introduced species highlighted the influence of introduction pathways on invasion success (Appendix 6). Considering all the species, the overrepresentation of species native to the Palearctic and Sino-Oriental regions among the introduced species could be due to the influence of the two most important pathways: aquaculture and ornamental trade. Indeed, these regions are economically well developed, making them more prone to export fish species for the aquaculture (FAO, 2012). This may also be linked to the early development of aquaculture in these regions, in particular in the Palearctic region (Balon, 1995). With the development of aquaculture in tropical countries (Garlock et al., 2020), this trend is likely to spread throughout developing regions of the globe. Considering the models per pathway, the species introduced and established in many countries through aquaculture are similar to those of the global pool (*i.e.*, high number of diets, high parental care). They also tend to be from the Cypriniformes order. This can be explained by human selection. Fish from the Cypriniformes order such as carp have been cultured for centuries (Balon, 2004) and thus constitute the main species produced in global aquaculture (FAO, 2020).

However, species introduced and established in many countries through the ornamental trade are not hydrodynamic and are more often native to the Neotropical and Sino-Oriental regions. These characteristics correspond to the description of the most popular aquarium fish such as *Poeciliids* and *tetras* (Duggan et al., 2006; Gertzen et al., 2008), thus pointing to the strong influence of propagule pressure.

Limitations and recommendations for future studies

It is important to note that the similarity between the introduction and establishment steps can be partially explained by a detection bias: introductions that fail to establish have less chance of being reported than successful introductions (Drake, 2007). Nonetheless, a non-negligible number of failed introductions were reported here (90 out of 307). We used the number of countries where species are introduced, established, and have impacts as an indicator of alien success, although the size of the countries is highly variable, which implies possible biases. Species established in many small countries are considered to be more established than species established in a limited number of large countries, even though they may both cover the same area. This bias could be corrected by using the number of basins, but we only have this information for the establishment step (Tedesco et al., 2017). Nonetheless, the number of countries where species have become established is significantly and positively correlated to the number of basins, thus minimizing the importance of the bias (Appendix 8). Moreover, some of our results can vary at the local scale, because the characteristics of the recipient environment can significantly influence the outcome of an introduction (Vila-Gispert et al., 2005). To improve future studies, more data should to be collected in relation to the impact step as well as certain characteristics such as fecundity, which has been shown to influence the establishment of species at the local scale (Vila-Gispert et al., 2005).

Conclusion

This study provides a comprehensive understanding of the characteristics that allow for the success of the whole invasion process. It highlights the importance of considering different invasion steps separately to account for the wide variety of extrinsic and intrinsic factors involved in invasion models and disentangle the effects of introduction pathways. These results can be useful in order to improve screening tools. For example, the invasiveness tool of FishBase only takes into account the introduction pathway and the climate adequacy between the native and recipient environment to determine the potential invasiveness of a species (Froese and Pauly, 2019). By contrast, our results stress the importance of considering a wider variety of characteristics. The findings also show the importance of determining not only the invasive status of a species but also the profile of species with the potential to invade large areas. Ultimately, this approach considering the different steps and pathways of invasion could be helpful to better identify the determinants of invasion success in other taxa (Capellini et al., 2015).

Data availability statement:

All the R code necessary to generate the data and the results present in the paper will be available on GitHub after the acceptance of the paper. Used data also include open access data : (i) FishBase (Froese and Pauly, 2019, version 19.04, accessed with the “rfishbase” R package; Boettiger et al., 2012); (ii) the FISHMORPH morphological database (Brosse et al., 2021); (iii) the database on freshwater fish occurrences complied by Tedesco et al. (2017); (iv) the global biogeographical regions of freshwater fish (Leroy et al., 2019); and (v) the world climate database WorldClim (Fick and Hijmans, 2017).

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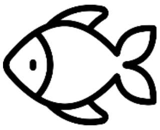
Conclusion : Cette étude nous a permis de souligner que l'importance des différentes caractéristiques varie selon les étapes de l'invasion et la voie d'introduction des espèces exotiques. Par exemple, nous avons déterminé que les poissons d'eau douce exotiques ayant un régime alimentaire varié, qui prodiguent des soins parentaux et qui sont introduits par de multiples voies sont les plus largement introduits et établis dans le monde. De plus, les espèces introduites via l'aquaculture font majoritairement partie de la famille des Cypriniformes et ont un régime alimentaire varié. Au contraire, les espèces introduites via le commerce ornemental sont quant à elles principalement originaires des régions tropicales. Cette étude nous permet aussi d'avoir un premier aperçu du lien entre caractéristiques et impact. Ainsi, certaines voies d'introduction, telles que les pêcheries ou le commerce ornemental, semblent être associées à un impact dans un grand nombre de pays. Cependant, le manque de données – tant en terme de quantité que de qualité – pour estimer l'impact diminue notre capacité à déterminer précisément les caractéristiques écologiques des poissons associés à ces impacts.

En effet, les étapes d'introduction et d'impact ne bénéficient que de peu d'attention dans la littérature par rapport à l'étape d'établissement, qui est l'étape la mieux renseignée (García-Berthou 2007). Toutefois, l'étape d'établissement est souvent étudiée de façon binaire : soit l'espèce est établie dans un milieu exotique, soit elle ne l'est pas (*e.g.*, Kolar and Lodge, 2002 ; Ruesink, 2005 ; Ribeiro et al., 2008). Or, toutes les espèces ne parviennent pas à s'établir de la même façon. Par exemple, certaines espèces s'établissent dans de nombreuses régions partout dans le monde. C'est le cas de la carpe commune (*Cyprinus carpio*) qui est établie dans 730 bassins à travers le monde. Au contraire, certaines espèces ne s'établissent que dans peu d'endroits, proches de leur milieu natif. Par exemple, la perche du Nil n'est établie que dans 14 bassins, et seulement dans la biorégion Ethiopienne, sa biorégion native. Nous pouvons ainsi identifier différentes dimensions à l'établissement, qui pourraient être déterminées par des caractéristiques liées à l'espèce exotique. De plus, certaines études avancent le fait que l'impact des espèces exotiques envahissantes dépend de l'étendue de leur aire géographique, leur abondance, et leur effet unitaire (Latombe et al. 2022; Parker et al. 1999; Sofaer et al. 2018). Ainsi, l'étude de différentes dimensions de l'établissement, dont l'étendue de l'aire géographique établies via le nombre de bassins établis, pourraient aider à mieux caractériser l'impact des espèces exotiques de poissons d'eau douce.



Chapitre 4 : Importance relative des caractéristiques des espèces exotiques le long d'un gradient d'établissement : l'exemple des poissons d'eau douce

Title

Relative importance of ecological traits along a gradient of establishment: the example of exotic freshwater fishes

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Abstract

Understanding the factors responsible for the success of exotic species has been a prevalent question in invasion biology. Ecological traits of exotic species are known to play a major role, but whether those traits are responsible for different degrees of invasiveness is still an open question for vertebrates. Here, we assessed the ecological, morphological and behavioral profile of 222 exotic freshwater fish along a gradient of establishment, described by the number of basins and the location of establishment, and their ecological profile. We found that fish with low establishment abilities were clustered in the trait space, showing traits related to low temperature amplitude, no parental care, and zoobenthic-based diet. In contrast, super-established fish encompassed a broader range of functional strategies, with a high proportion of species with multiple diets and a high level of parental care. Overall, fish with low establishment abilities showed low values of functional overlap with other fish along the gradient of establishment. Our findings highlight the importance of considering the trait variability among a gradient of established species for a more accurate anticipation of their ability to spread.

Teaser

Super-established fish have a broad range of functional strategies, and the majority of them have multiple diets and a high level of parental care.

Keywords

Exotic fish, establishment success, exotic range, traits, vertebrates

Introduction

To date, the overwhelming majority of countries in the world are recipients of exotic species (Dawson et al. 2017). The current rise of new exotic species introductions promises an amplification of biological invasion phenomenon in the future (Seebens et al. 2021). Understanding why some exotic species become established into a new location while others fail to do so remains a challenging question (Enders et al. 2020). Studies showed that the success of exotic species results from a combination of factors involving propagule pressure, biotic characteristics of the recipient ecosystem and exotic species traits (Blackburn et al. 2009, Capellini et al. 2015, Allen et al. 2017, Novoa et al. 2020, Bernery et al. 2022a, Marino and Bellard 2022). For instance, reptiles and amphibians established in exotic environments have larger or more frequent clutches compared to species failing at establishment (Allen et al. 2017). Exotic birds successful at establishment present mostly slow life history traits (*e.g.*, large body mass and low brood value, (Sol et al. 2012)) while those with high ecological impacts have large clutch sizes (Marino and Bellard 2022). In addition, exotic freshwater fish with a broad food spectrum have more chances to establish than species with more specialized diets (Ruesink 2005), but this varies with the stage of invasion (Bernery et al. 2022b). Species' traits, among other factors, thus play an undeniable role in the abilities of exotic species to become established.

Yet, not all exotic species succeed in the same way to invade new ecosystems. Some species will establish in many locations and spread widely (*e.g.*, the black rat *Rattus rattus* has established populations in 417 islands around the world ("Threatened Island Biodiversity Database Partners" 2018), the common carp *Cyprinus carpio* has established populations in 730 basins worldwide (Tedesco et al. 2017)) while others will remain restricted to a specific location (*e.g.*, the lesser ricefield rat *Rattus losea* established in only four islands in the Taiwan Strait; ("Threatened Island Biodiversity Database Partners" 2018). As widespread and impactful exotic species are at the core of management strategies, it is crucial to consider the different dimensions of species' invasiveness (Catford et al. 2016). Recent studies showed that exotic range size, exotic species abundance, or the impact on native fauna, all represent dimensions of invasiveness (Catford et al. 2019, Liao et al. 2021). When applied to exotic plants, these dimensions were found to be independent, and differentially related with exotic plant traits. For instance, leaf nitrogen content and leaf area were more strongly associated with exotic range size while leaf dry weight correlated more with local abundance of exotic plants (Liao et al. 2021). However, how traits-association vary along a gradient of invasiveness remains unaddressed in animal taxa. By ignoring apparent distinction among the dimensions of invasiveness, one can draw inconsistent conclusions about the factors responsible for establishment success (Liao et al. 2021). Here, we propose to fill this gap by studying the traits of exotic freshwater fish as an animal model system, considering the invasiveness dimensions that are specific to a gradient of establishment.

Freshwater fish are one of the most introduced taxa worldwide and are known for their important impacts on native faunas (Cucherousset and Olden 2011). For instance, the sole introduction of the Nile perch in Lake Victoria has caused the disappearance of more than 200 endemic fish (Aloo et al. 2017). Yet this taxon remains understudied regarding the factor influencing their invasion success (Pyšek et al. 2020), but see (Su et al. 2020, Bernery et al. 2022a). In this study, we aimed to disentangle the ecological, morphological and behavior factors associated with two dimensions of exotic freshwater fish's establishment: the number of basins where exotic species established and the location of the establishment (*i.e.*, inside or outside the native bioregion). Taken together, those dimensions form a gradient of establishment, ranging from species established in a handful basins within their native bioregion (*i.e.*, species with low establishment abilities) to exotic species widespread over several basins including some outside their native bioregion (*i.e.*, super established species). We distinguish four groups of exotic species along the establishment gradient (see Fig. 1 for details). After documenting 13 morphological and ecological traits of 222 freshwater fish species with at least one exotic established population, we built a trait-based multidimensional space, to synthesize the complexity of fish functional diversity (Mouillot et al. 2021). We evaluated (dis)similarities between groups of exotic fish on the establishment gradient using density distributions along axes of the functional space, further completed with a probabilistic hypervolume approach (Mammola and Cardoso 2020, Mammola et al. 2021). Then, we performed trait-by-trait comparisons between the four groups to depict more precisely the profile of exotic fish along the gradient. Altogether, those complementary methods represent a first attempt to classify exotic vertebrates along a gradient of establishment using species' traits.

Methods

Species data

Using a global database on freshwater fish species distribution (Tedesco et al. 2017), we compiled a list of freshwater fish that were defined as exotic in at least one drainage basin (n = 551). Exotic species are introduced species that have established and complete all their life cycle with a self-sustainable population in a given basin outside their native range. We then collected information on the exotic fish related to their establishment abilities, as well as their life-history traits (Froese and Pauly 2019, Brosse et al. 2021). All the analyses were performed on a set of 222 established exotic freshwater fish for which we had complete data regarding these variables (see the "species trait" section below).

Species exotic distributions

We gathered information on the two dimensions of the establishment gradient for each exotic fish: (i) the number of basins where established and (ii) the location of the establishment. For the number of basins, we counted the number of drainage basins where the species have an exotic status using the (Tedesco et al. 2017) database. We further separated fish species into two categories: species established in four basins or less, and species established in more than four basins. The cutoff at four corresponds to the median of the number of basins among the 222 species. Regarding the location of establishment, we also distinguished two groups: species that have been introduced and established only in their native bioregion, and species introduced outside their native bioregion(s), (even if they can also be introduced inside) following the classification of bioregions of (Leroy et al. 2019). Among the 222 exotic species, 120 were established in four basins or less while 102 were in more than four basins, and 118 were established only inside their native bioregion while 104 had an established population outside. Based on those two dimensions of establishment gradient, we constituted four groups of fish that are represented in Fig. 1. The gradient ranged from species with low establishment abilities that had low values on both dimensions (number of basins and location of establishment) to super-established fish that had high values on both dimensions. We defined two intermediary groups that had a low value on one dimension but a high value on the other.

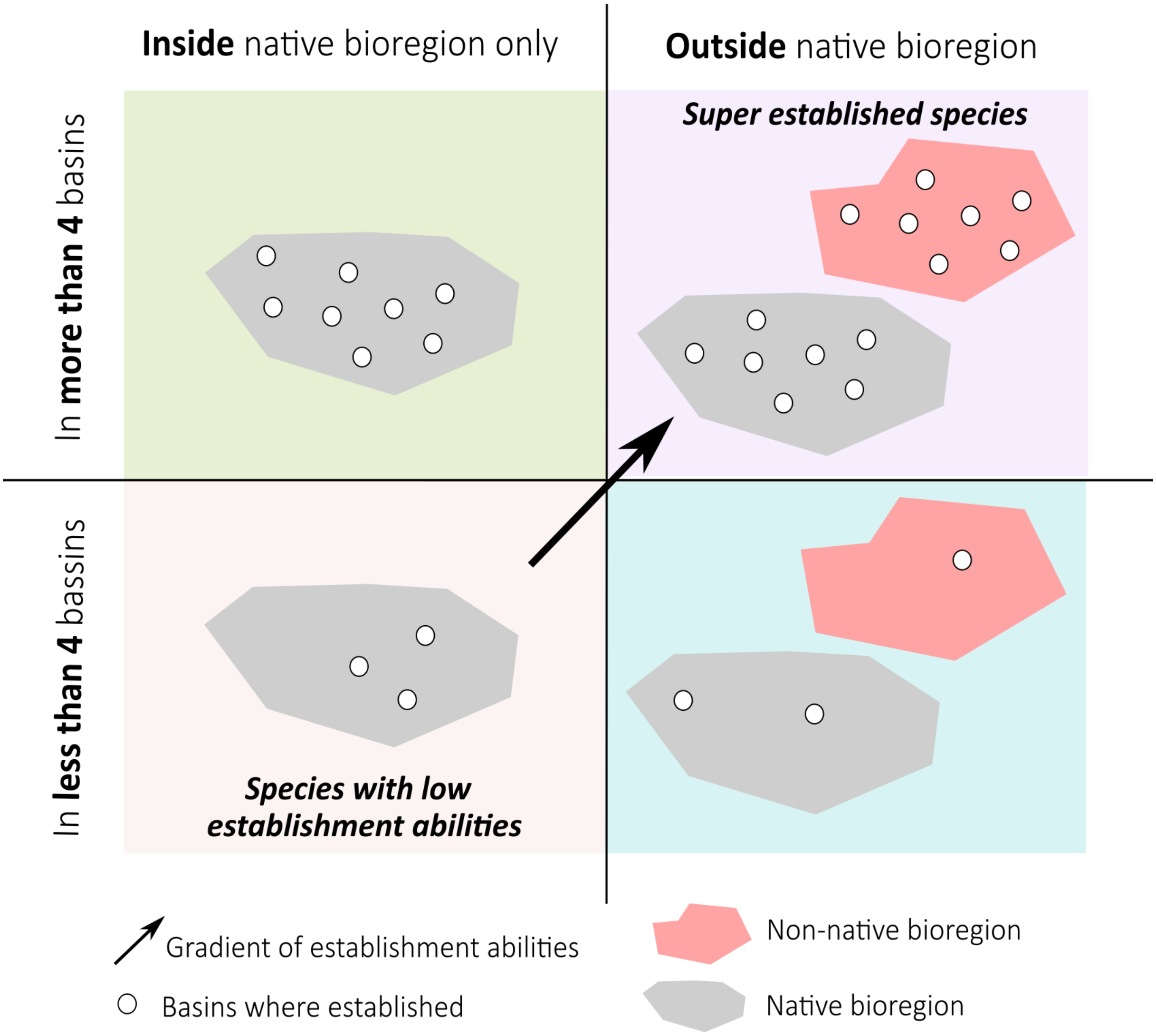

Figure 1. Schematic representation of the different fish groups according to their establishment abilities. The white circles represent the drainage basins where the species are established. Gray areas represent fish's native bioregion, and red areas the non-native bioregion.

Species traits

We collected information on 13 ecological, behavioral and morphological species traits that were likely to influence freshwater fish establishment in exotic basins according to previous studies. For instance, good swimming abilities, broad temperature tolerance, high level of parental care and generalist diet facilitate fish establishment in exotic basins (Ruesink 2005, Snyder et al. 2014, Tonella et al. 2018, Carvajal-Quintero et al. 2019, Su et al. 2020, Bernery et al. 2022b, Lawson and Hill 2022). Regarding the ecological traits, we collected diet data using the “FoodI" column of the *fooditems()* table of the *rfishbase* package (Boettiger et al. 2012, Froese and Pauly 2019). Each species can have one or several diets belonging to five categories: detritus, nekton, plants, zoobenthos and zooplankton, so we transformed the “FoodI” variable into five binary variables following the five diet categories. We also counted the number of diet categories for each species to determine their diet breadth. Then, we calculated the temperature amplitude of each species. For this purpose, we retrieved the minimum temperature of the coldest month and the maximum temperature of the warmest month in the species’ native basins from Worldclim (Fick and Hijmans 2017). We only considered the 0.95 quantile of the maximum temperature of the warmest month and the 0.05 quantile of the minimum temperature of the coldest month to avoid extreme outlier values. We obtained information on behavioral traits such as the fish parental care thanks to the “RepGuild1” column of the *species()* table of the *rfishbase* package (Boettiger et al. 2012, Froese and Pauly 2019). The parental care variable was divided into three categories from the lowest level of parental care to the highest: nonguarder, guarder, and bearer. Regarding morphological traits, we considered five variables from the FISHMORPH database (Brosse et al. 2021). First, we used the pectoral fin vertical position PFiBd (*i.e.*, ratio of Pectoral Fin position relative to Body depth), which reflects the swimming style. Pectoral fins which are placed laterally are rather used for propulsion and fine movements, whereas pectoral fins placed ventrally often characterize fish with less precise movements (Blake 2004, Su et al. 2019). Second, we used the ratio of body length to body depth BlBd, reflecting fish hydrodynamics (Villéger et al. 2017, Su et al. 2019). Third, we used the ratio between the eye position and the body depth EhBd, which reflects the “Position of fish and/or of its prey in the water column” (Su et al. 2019). Fourth, we used the ratio between the oral gape position and the body depth

MoBd, indicating the feeding position of the species in the water column (Su et al. 2019). All ratios were unitless. Finally, we used the maximum body length of the species (in cm). We obtained those traits information for 222 exotic fish species.

Statistical analyses

Building trait space

To ensure that traits were not intercorrelated, we regressed each trait against all others using linear models and computed variance inflation factors (VIF) using the *vif()* function from the *car* package (Fox and Weisberg 2019). As the diet breadth was aliased with other diet variables, we did not consider this trait in the rest of the analyses and considered only 12 traits for which VIF values for all remaining variables were below three. We then used the 12 traits on the 222 fish species to build a multidimensional trait space. First, we calculated synthetic axes providing new species coordinates in a low-dimensional space using the *funct.dist()* and *quality.fspace()* functions from the *mFD* package (Magneville et al. 2021). The first function computes pairwise trait-based distances between species using the Gower dissimilarity index (Gower 1971). This method enables one to consider different types of traits (*i.e.*, continuous numeric, discrete numeric and categorical traits). We used mostly numeric traits (*i.e.*, continuous for all morphological traits and the amplitude of temperature; binary for the diet items), except for the parental care that was ordinal (categories were ordered as non-guarders < guarders < bearers). The second function calculates species coordinates in a multidimensional space by applying a PCoA, and measures the quality of spaces according to the number of dimensions. Based on the quality criteria of (Maire et al. 2015), we selected the 4D trait space to pursue our analyses (RMSD = 0.046, which is minimal for the 4D space).

Functional distinction of species along the dimensions of the establishment gradient

To assess the functional differences between the group of fish according to the number of establishment basins and the location of establishment, we compared the distribution between groups along the PC axes using Kolmogorov-Smirnov (KS) tests, which were run independently for the number of basins (four or less vs. more than four) and the location (inside native bioregion vs. outside native bioregion). To determine if the results were not sensitive to the group definition, we repeated the same analyses for different thresholds regarding the number of basins (cutoff = 2, 3, 5 and 6 basins). As the results obtained between the groups of small and large numbers of basins of establishment for the different cutoffs were in congruence with the cutoff at four (Supporting information), we kept the four or less vs. more than four groups for the rest of the analyses.

Hypervolume comparison along the establishment gradient

In order to assess the functional differences between the four groups along the establishment gradient, we proceeded to a dissimilarity analysis of the probabilistic hypervolumes encompassed by each group in the 4D trait space. All the following functions for computing hypervolumes and associated metrics came from the *BAT* package (Cardoso et al. 2022). We first built kernel density hypervolumes thanks to the *kernel.build()* function, using the first four axes of the PCoA as traits, and the four groups of fish as groups. We used the Gaussian kernel density method and kept the default parameters (Blonder et al. 2018). Second, we calculated the pairwise distances between hypervolume centroids (giving six 2-by-2 distances) with the *kernel.similarity()* function. Then, to estimate how the four groups are dissimilar in terms of trait space occupation, we computed pairwise hypervolume dissimilarities between the groups using the *kernel.beta()* function. The total beta dissimilarity was further decomposed into replacement (Beta replacement) and gain/ loss in richness (Beta richness), which respectively describe the shift in the functional space and the expansion/ contraction between two given groups. Finally, we tested whether the observed distances and dissimilarities between groups were significantly higher or lower than expected by chance. In this aim, we randomly attributed species to one of the four groups of the gradient and calculated each metric. We obtained null distributions of 999 simulated values, and calculated the deviation from random expectation by measuring effect sizes and associated p-values following (Marino et al. 2021). We considered an observed value as significantly different from random expectation when it was above 97.5% or below 2.5% of the simulated values (resulting in a level of significance of 5%).

Individual trait distinctions along the establishment gradient

We evaluated the trait modalities or values associated with the four studied groups. For each numeric trait, we compared the mean value of the groups using wilcoxon and post-hoc tests. For binary and categorical traits, we performed non-parametric chi-squared tests of independence.

All analyses were performed with R software (version 4.1.0) (R Core Team 2021).

Results

Functional qualification of fish on the dimensions of the establishment gradient

The first four axes of the functional space represented 65% of the total variance among the traits described for the 222 exotic freshwater fish species (Fig. 2). The two first axes were essentially driven by diet traits: while PC1 was mostly associated with plant and detritus feeding strategies, PC2 was positively associated with nekton and zooplankton feeding strategies. PC3 was positively associated with a high level of parental care and negatively correlated to the amplitude of temperature. Finally, PC4 was also associated with diet traits (*i.e.*, negatively associated with zooplankton but positively associated with plant and nekton feeding strategies), in addition to fish swimming abilities (*i.e.*, pectoral fin vertical position).

We found that exotic fish were differently distributed along the first three axes of the functional space regarding both dimensions of establishment (Fig. 2). For instance, fish established in more than four basins are more likely to feed on zooplankton, plant and detritus compared to other exotic fish (Fig. 2, blue curves; see Supporting information for statistical tests). Our results also showed that exotic fish with established populations outside their native bioregion were distributed in a part of the functional space correlated with high parental care compared to exotic species established only inside their native range (Fig. 2, pink curves; Supporting information).

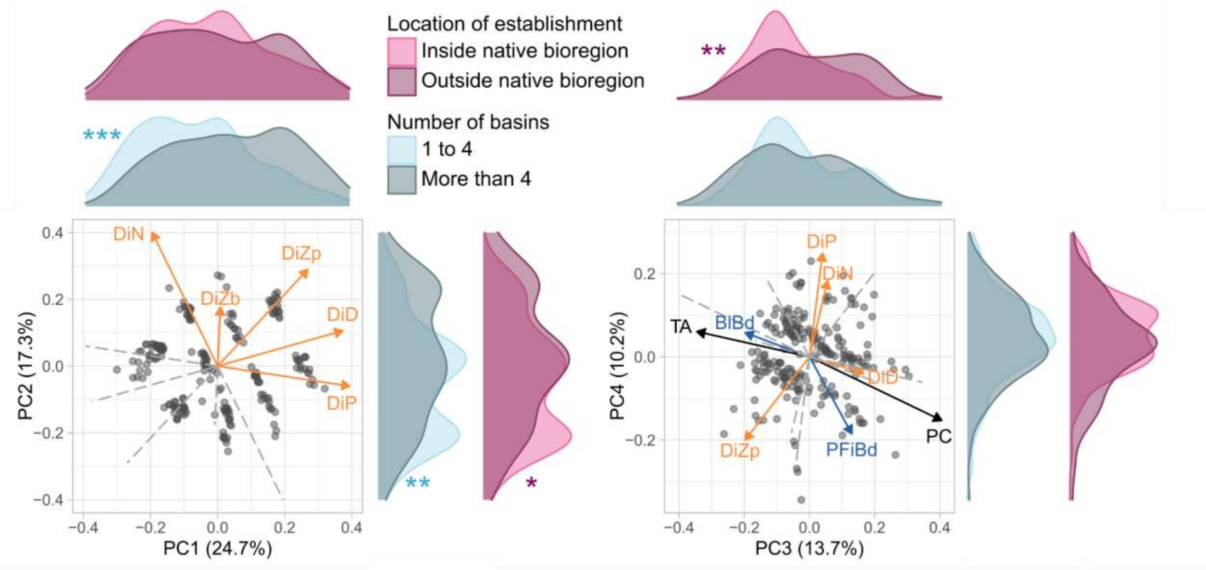

Figure 2. Functional space of introduced fish and repartition according to the location and number of introductions. The biplots represent the distribution of fish on the first four axes of the PCA. Each point depicts a species (n = 222) and arrows represent the traits that contribute mostly (r>0.3) to the different axes (BlBd: body elongation, DiD: diet detritus, DiN: diet nekton, DiP: diet plant, DiZb: diet zoobenthos, DiZp: diet zooplankton, PC: parental care, PFiBd: pectoral fin vertical position, TA: temperature amplitude). Correlation coefficients and associated p-values are detailed in Supporting information. Arrow colors correspond to the trait categories: diet (orange), morphology (blue), parental care and temperature amplitude (black) as depicted in Fig. 4. Distributions on the right and above the plot illustrate the density of species along the PC axes according to their location of establishment (pink curves) and the number of establishment basins (blue curves). Stars indicate that distributions are significantly different between groups following Kolmogorov-Smirnov tests (*: $0.01 < p < 0.05$; **: $0.001 < p < 0.01$; ***: $p < 0.001$).

Fish with low establishment abilities are functionally distinct from other fish groups

We further explored whether the functional space may provide insights into the (dis-)similarities of exotic fish accounting for the gradient of establishment, from species with low establishment abilities to super-established species (Fig. 1). The centroids of the hypervolumes representing each group were rather close in the functional space (Fig. 3A). However, the observed distances in the 4D space were higher than expected under a null hypothesis. Specifically, fish with low establishment abilities were significantly distant from fish established outside their native bioregion (Supporting information). We also found that a large part of the functional space was shared between some groups along the gradient (Fig. 3B). Both groups of exotic fish established in more than four basins showed a high overlap (Jaccard index = 0.61), as well as both groups of exotic fish established outside their native bioregions (Jaccard index = 0.62). Conversely, fish with low establishment abilities showed a Jaccard index of 0.35 with super-established fish. In fact, the group of fish with low establishment abilities systematically differed from the other groups due to a high beta richness. This group contained more species (n = 77) but encompassed a smaller part of the functional space than any other group (Fig. 1, 3).

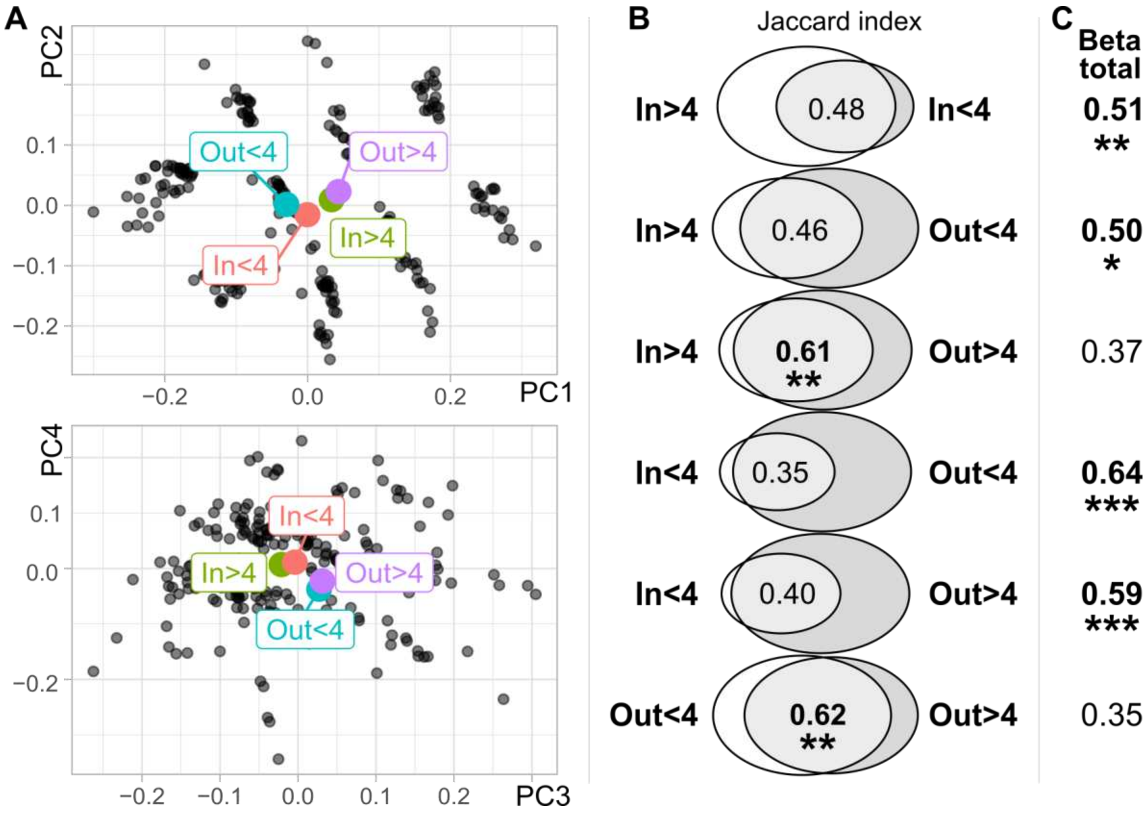

Figure 3. Distance, overlap and functional turnover between the four groups of introduced fish. The four groups correspond to the establishment gradient: species introduced inside their native bioregion in four basins or less (In<4), inside their native bioregion in more than four basins (In>4), outside their native bioregion in in four basins or less (Out<4), and outside their native bioregion in more than four basins (Out>4). The biplots (A) represent the functional space as in Fig. 2 and coloured points indicate the centroid of the hypervolume encompassed by each of the four groups. Venn diagrams (B) represent the functional overlap between hypervolumes (light gray) and the unique portions of the left (white) and right (dark gray) group. Jaccard similarity index is specified in each intersection between groups. The table (C) indicates the differentiation (Beta total) between the two hypervolumes on the diagrams. Stars and bold values indicate significant positive deviation from the null hypothesis, *i.e.* the observed value is higher than expected by chance (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

Trait profile of exotic fish along the establishment gradient

Ultimately, we explored the differences trait-by-trait between the four groups of exotic fish along the establishment gradient (Fig. 4). We found that the traits were differently associated to the two dimensions of the establishment gradient. The ability of species to spread into a high number of basins was mostly associated with the diet types and the temperature amplitude, while parental care was more associated with the location of establishment. In contrast, morphological traits were important to explain both the number of basins where established and the location of establishments.

More specifically, we found that super-established species had a higher feeding position in the water column, a longer body length, had rather a lateral pectoral fin and were less hydrodynamic compared to species at the other side of the gradient, with low establishment abilities. Moreover, the super-established species consumed more diverse diet items than species established in four basins or less, eating more detritus and zooplankton. Overall, species established in a large number of basins consumed in proportion more diet items (plants, zooplankton, detritus) had a higher temperature amplitude in their native basins than species established in a small number of basins. In contrast, species established outside their native bioregion had rather a lateral pectoral fin and were more caring to their offspring compared to species inside their native bioregion, which had a ventral pectoral fin and a non-guarder behavior.

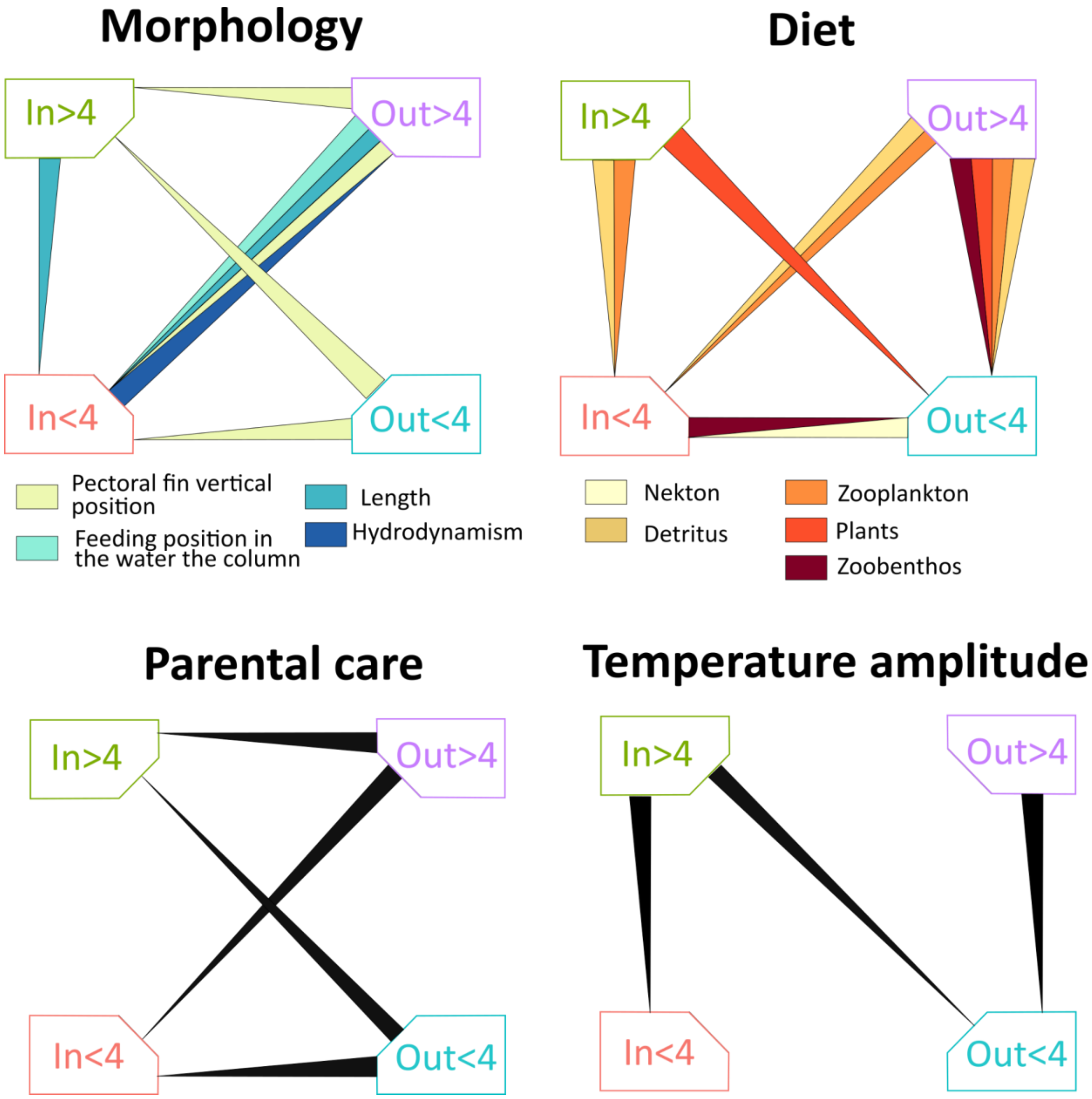

Figure 4. Trait comparison between the four groups of fish. The four groups correspond to the establishment gradient: species introduced inside their native bioregion in four basins or less (In<4), inside their native bioregion in more than four basins (In>4), outside their native bioregion in in four basins or less (Out<4), and outside their native bioregion in more than four basins (Out>4). Only significant differences are represented ($p < 0.05$). The group on the wide side of the triangle represents the group that has the higher values or which is more represented in the considered trait, compared to the others. Concerning the parental care panel, the group on the wide side of the triangle corresponds to the group with significantly more bearer and guarder than the group on the narrow side of the triangle.

Discussion

Our work demonstrated that various traits are responsible for differences within established species along the two dimensions of establishment (*i.e.*, the exotic range size and the exotic location), as previously shown for plants (Catford et al. 2016, Liao et al. 2021). Using freshwater fish as an animal model, we were able to disentangle the characteristics of exotic species along a gradient of establishment. The gradient ranged from species with low establishment abilities that were zoobenthos eaters, feeding in a low position in the water column to super-established species, which were large generalist species with a broad temperature amplitude and a high level of parental care. The multidimensional and the trait-by-trait analyses we performed showed concordant results, highlighting the importance of diet and temperature amplitude in explaining the number of establishment basins (a proxy for exotic range size) while parental care had a larger effect on exotic location (Fig. 2, 4).

The importance of traits to disentangle dimensions of establishment in exotic species

Interestingly, all the types of traits (ecological, morphological, behavioral) considered in our analyses played a role in characterizing the establishment abilities of exotic fish, underlying the importance of accounting for all these variables when studying several dimensions of establishment success. However, some traits were more important to disentangle the species ability to establish. For instance, the high level of parental care stood out as the main feature associated with exotic fish established outside their native bioregion. This result corroborates previous studies that found a higher establishment success for exotic fish with a high level of parental care (Marchetti et al. 2004, Bernery et al. 2022a, Lawson and Hill 2022), although they did not demonstrate a link specifically between the location of establishment and parental care. Within terrestrial vertebrates, parental care is often associated with slow life history, and (Sol et al. 2012) showed that exotic birds with a slow life history (and more care invested in the next generation) were more successful at establishment than fast-living ones. By increasing offspring's survival rate, parental care proves to be a critical trait in explaining establishment success and demography (Marchetti et al. 2004, Bernery et al. 2022a).

Even though expected, we did not find any effect of temperature amplitude (a proxy of the temperature tolerance) for explaining the abilities of fish to establish outside their native bioregion. Most terrestrial exotic species from islands experience a niche shift after invasion, suggesting that their native climatic conditions are not a constraint for establishing outside their native realm (Stroud 2021). As freshwater bodies are island-like systems (Itescu 2019), fish might not be at their niche equilibrium in their native range and thus the climatic conditions they experience are narrower than the one they can cope with (Lauzeral et al. 2011). Nevertheless, we found that high temperature amplitude of fish in native basins correlated positively with the number of establishment basins, as highlighted in several previous studies (Kolar and Lodge 2002, Marchetti et al. 2004, Snyder et al. 2014). This is easily explained by the ability of species to adapt to different, and thus numerous, environments.

More surprisingly, we found that the number of basins also correlated with detritus and zooplankton diets. As detritus are not limited in the environment, detritivorous species can easily find food resources without having to compete with native species (Tonella et al. 2018). In previous studies, nekton diet, associated with predatory behavior on fish, was strongly linked with invasiveness (Moyle and Light 1996, Tonella et al. 2018), but we did not find any effect of this diet in our study.

Taking the two establishment dimensions together, the super-established fish differentiated from others regarding previously cited traits, but also regarding their morphology (Fig. 4). Specifically, we found that super-established fish were rather big fish with lateral pectoral fins (*i.e.*, fins used for propulsion and fine movements) and a superior mouth-type. Big fish, generally preferred by anglers and consumers, were widely introduced worldwide via the aquaculture and the fishery pathways, explaining their introduction and establishment in many basins all around the world (Bernery et al. 2022b). Moreover, the propulsion use of lateral pectoral fins could be a good advantage in order to disperse and easily colonize new environments, especially anthropized ones where the water flow is potentially disturbed by canals or dams (Dumay et al., 2004). Finally, the mouth position of the super-established fish probably denotes a high trophic position, and thus a diet based on other fish with a predatory behavior (Brosse et al. 2021). Like demonstrated in other vertebrate taxa, predators are undoubtedly the most impacting species in exotic environments, especially on isolated systems such as islands or ponds (Doherty et al. 2016). As a consequence, we may expect that exotic fish with those characteristics are the most widely established species, taking advantage of naïve faunas or the lack of competitors in native ecosystems.

Beyond species traits, socio-economic factors potentially contribute to the establishment gradient

Despite the differences in traits highlighted between the groups of exotic fish along the establishment gradient, we found that all groups shared a large part of the functional space, at least 0.35 Jaccard index (Fig. 2, 3). As a consequence, other drivers unrelated to the morphological, ecological or behavioral traits that we tested here might contribute to explain the distribution of exotic fish along the gradient of establishment. For instance, the local context of invasions, including the native community invaded, is most likely a strong explanatory driver of the success of establishment, due both to the functional and the phylogenetic distances between exotic and native species (Xu et al. 2022).

Moreover, the wide exotic distribution of certain fish could also be explained by the propagule pressure and thus their introduction pathways (García-Berthou et al. 2005). Indeed, in aquatic systems, species introductions due to aquaculture and ornamental purposes have highly contributed to the current exotic fauna, facilitating the introduction and establishment of certain selected species worldwide (Padilla and Williams 2004). The selection of species through pathways has been also demonstrated for birds, and it strongly interacts with species traits for explaining establishment probabilities (Cassey et al. 2004). In a preliminary attempt, we separated the groups of fish along the establishment gradient by pathway, but we did not find significant results. Indeed, the fish introduced through aquaculture did not differ from the fish introduced for ornamental trade for any of the establishment groups. One possible explanation for this lack of contribution of the pathway could lie in the few number of fish species per pathway, strongly reducing the statistical power of our analyses. Moreover, several fish species in our database such as the common carp have been introduced and established through several pathways, blurring the possible distinction we expected between pathways.

Link between establishment abilities and potential impact

In this paper, we focused on the dimensions of invasiveness related to the establishment stage of invasions, thus disregarding the ecological impact of the species. However, impact is at the core of management strategies because it will determine which response should be implemented to counter current or future invasion effects (McGeoch et al. 2021), but the paucity of data make it difficult to study at large scales (Thomsen et al. 2011, Bernery et al. 2022b). Moreover, it is very challenging to quantify the impact in a standardized way (but see the EICAT framework: (Blackburn et al. 2014, Hawkins et al. 2015)) due to the time lag of the impacts. Ecological changes due to invasions, and thus impacts, can be unnoticed for years or decades, then hardly associated with invasions as a cause (Courchamp et al. 2017). However, theoretical frameworks propose that the impact of an exotic species depends on three components: its exotic geographic range size, its abundance and its effect per capita (Parker et al. 1999, Sofaer et al. 2018, Latombe et al. 2022). Using the number of basins and the location of establishments as indicators of exotic geographic range size, we assume that widely established exotic species are more likely to have a higher potential impact compared to species established in a small number of basins and restricted to their native bioregion. This has been recently demonstrated by (Evans et al. 2018) for birds, in which birds with large exotic range sizes tend to have more severe impacts than species with small exotic ranges. We tested this association (Supporting information) and found a significant correlation between the super-established exotic species that showed high ecological impacts (*i.e.*, 76% of them), while species with low establishment abilities included only a low proportion of species with ecological impacts (*i.e.*, 17%).

Limits of the study

Although our results contribute to better understanding invasion dynamics, it is crucial to consider the context in which they were obtained, specifically regarding the data on which they are based in order to acknowledge the limits of interpretations. We focus our analyses on the most comprehensive database of fish traits, which includes 222 traits with complete data (Froese and Pauly 2019, Brosse et al. 2021), but over 300 exotic fish species had incomplete trait data, preventing us from considering them in our analysis. We could have partially reduced those taxonomic biases using imputation techniques based on phylogenetic information (Kim et al. 2018). However, the current phylogeny of Actinopterygii has undergone many changes and is not complete yet (Mirande 2017). In addition, the rate of missing values in species traits was high (*e.g.*, 127 species upon 551 do not have any parental care level filled, and 146 species do not have the diet filled), preventing us from using those imputation techniques (Johnson et al. 2021). Global databases are often taxonomically and spatially biased toward developed countries, especially regarding the distribution of exotic species (Bellard and Jeschke 2016, Bernery et al. 2022b, Seebens and Kaplan 2022).

Concerning the dimensions of establishment following the definition of (Catford et al. 2016), we focused on two of them without exploring the demography of exotic species (*e.g.*, spread rate or abundance). We recognize that those dimensions can also be determinant at assessing invasiveness of exotic species because they represent fundamental indicators for supporting invasive exotic species management policies (McGeoch et al. 2021). However, abundance data at global scale are really scarce for vertebrates and come from confusing sources ((Kissling et al. 2018) but see recent estimates for global bird abundances (Callaghan et al. 2021)). Although new techniques of data collection are developing (*e.g.*, citizen sciences or eDNA sampling), a large effort of standardized data acquisition is indispensable before applying abundance information to global exotic populations, and especially to fish populations.

Conclusion

When assessing the species' traits responsible for establishment success of exotic vertebrates, previous studies considered establishment as a binary response, with successful species opposed to failing ones (Ruesink 2005, Sol et al. 2012, Capellini et al. 2015, Allen et al. 2017). Our present study emphasizes the importance of considering the differences in species characteristics among established exotic vertebrates using fish as a model for better understanding their invasion dynamics, as previously shown for plants (Catford et al. 2016, 2019, Liao et al. 2021). Ultimately, being able to identify the traits that promote high establishment abilities would help at identifying the most problematic invasive species, and thus prevent their potential introduction and impacts.

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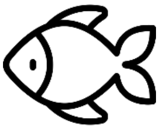
Conclusion : Cette étude a mis en avant l'importance de considérer simultanément différentes dimensions de l'établissement, tels que le nombre de bassins envahis et la zone géographique d'établissement (au sein ou en dehors de la région native) afin de comprendre et d'anticiper les dynamiques d'invasions. Nous avons montré que les espèces considérées comme super-établies présentent des caractéristiques propres par rapport aux espèces avec de faibles capacités d'établissement. Cette étude est la première à déterminer des profils différents d'espèces exotiques suivant plusieurs dimensions de l'établissement pour les vertébrés, et pourrait servir d'étude modèle pour d'autres taxons, tels que les vertébrés sur les îles. Nous avons aussi mis en avant dans cette étude une corrélation significative entre ces différentes dimensions de l'établissement et la probabilité que l'espèce exotique ait un impact écologique. Il s'agit probablement d'une question qui nécessite d'avantage d'efforts, mais elle permet de donner un premier aperçu des liens qui existent entre l'établissement (à travers sa dimension démographique) et l'impact écologique des poissons exotiques envahissants. Dans les Chapitres 1 et 3 de cette thèse, nous avons identifié l'impact écologique comme étant une variable assez mal renseignée dans les bases de données, et dont une classification standardisée manquait. Les dimensions de l'établissement pourraient, à terme, être utilisées comme un indicateur d'impact des espèces exotiques envahissantes.



6. DISCUSSION GÉNÉRALE

6.1. Synthèse des avancées majeures sur les connaissances et remise en contexte

Les travaux de synthèse (Chapitres 1 et 2) menés dans le cadre de cette thèse ont mis en évidence l'étendue des connaissances à l'échelle globale de chaque étape des invasions biologiques de poissons d'eau douce, mais ont aussi permis une évaluation des biais géographiques et des manques de littérature sur certaines questions clefs du succès des invasions biologiques, comme par exemple celles liées à l'étape d'impact (Chapitre 1 - Fig. 3). Nous avons aussi pu évaluer, par dire d'experts, le niveau de confiance des informations et des tendances de chaque aspect des invasions présents dans la littérature sur le sujet des invasions de poissons d'eau douce (Chapitre 1 - Fig. 3). Plus spécifiquement, les deux travaux de synthèse menés (Chapitres 1 et 2) complètent les synthèses présentes dans la littérature (*e.g.*, Cucherousset & Olden (2011) sur les impacts écologiques ; Gozlan et al. (2010) sur les voies d'introduction, les impacts et la gestion), et sont des sources essentielles pour dresser l'état de l'art des connaissances sur la problématique des invasions de poissons d'eau douce. Par exemple, la revue de la littérature (Chapitre 1) permet de comprendre que les invasions de poissons d'eau douce sont influencées par plusieurs facteurs qui peuvent agir en synergie, tels que les traits des espèces exotiques, les caractéristiques du milieu, ou encore les voies d'introduction, et qu'il est primordial de considérer l'ensemble de ces différents facteurs plutôt que de les étudier indépendamment des autres. Cette synthèse de la littérature apporte également une vision quantitative des principales voies d'introduction empruntées par les poissons d'eau douce exotiques, de leurs impacts écologiques, des mécanismes d'impacts les plus fréquents, ainsi que des méthodes de gestions mises en place. Nous avons par exemple montré que l'aquaculture et le commerce ornemental sont les principales voies d'introduction des poissons d'eau douce, représentant respectivement 42% et 17% des établissement répertoriés dans FishBase (Froese & Pauly 2019). À l'échelle mondiale, le principal impact écologique des poissons exotiques envahissants est la réduction de la biodiversité des écosystèmes natifs, au travers de la compétition et de la prédation qui représentent respectivement 53% et 30% des cas d'impact décrits dans GISD (ISSG 2015). Enfin, les principales méthodes de gestion mises en place pour les invasions de poissons d'eau douce s'avèrent être des mesures de contrôle, même si cette tendance est incertaine car les données sur la gestion sont rares.

En outre, les Chapitres 3 et 4 complètent les travaux précédents en mettant en évidence l'effet relatif des principaux facteurs d'invasion, qui peuvent différer suivant les voies d'introduction ou être similaires au sein des différentes étapes de l'invasion. Par exemple, les variables socio-économiques associées aux voies d'introduction sont importantes pour déterminer la réussite de toutes les étapes de l'invasion (introduction, établissement et impact) (Chapitre 3). De même pour les soins parentaux, qui est une caractéristique spécifique importante à chaque étape de l'invasion, que ce soit pour l'ensemble des poissons considérés ou seulement pour ceux provenant de l'aquaculture (Chapitre 3). De plus, les soins parentaux permettent de distinguer les espèces établies seulement dans leur biorégion native des espèces établies en dehors de leur biorégion native (Chapitre 4). Les traits morphologiques, tels que les traits liés à la nage et à l'hydrodynamisme, permettent quant à eux de différencier les espèces établies avec une faible capacité d'établissement (présentes dans moins de 4 bassins et seulement dans la biorégion native) des espèces super-établies (présentes dans plus de 4 bassins et en dehors de leur biorégion native) (Chapitre 4). Les facteurs peuvent aussi agir en synergie, d'où l'importance de les considérer simultanément dans les analyses. Par exemple, la région native est une variable importante pour déterminer le succès d'introduction et d'établissement des espèces introduites via le commerce ornemental (Chapitre 3). Finalement, cette thèse a aussi permis de mettre en avant les facteurs de succès des invasions à l'échelle globale, une échelle qui était jusque-là peu utilisée pour les invasions de poissons d'eau douce. Pourtant, la considération de différentes échelles pour étudier les tendances écologiques est importante (Pyšek et al. 2020b). Les analyses à l'échelle globale permettent de mettre en place de conventions et d'objectifs de gestion internationaux (*e.g.*, établissement de listes d'espèces à risque ; Copp 2013). Elles permettent aussi de mettre en avant les grandes tendances dans les systèmes écologiques sans que des aspects locaux spécifiques ne soient les principaux facteurs de variations mis en évidence (Capellini et al. 2015; Latombe et al. 2017; Pyšek et al. 2020b).

6.1.1. Importance de mettre en avant les tendances des facteurs de succès à l'échelle globale

L'échelle locale est l'échelle la plus souvent utilisée pour caractériser les facteurs influençant le succès des poissons d'eau douce (*e.g.,* la Californie, Marchetti et al. 2004 ; les grands lacs Nord-Américains, Howeth et al. 2016 ; la région méditerranéenne, Vila-Gispert et al. 2005, le fleuve Paraná, Tonella et al. 2018), ce qui permet notamment d'étudier en détail l'influence de l'environnement récepteur sur le profil des poissons exotiques envahissantes. Seuls Ruesink (2005) et Su et al. (2020) ont étudié les facteurs d'invasion de poissons d'eau douce à l'échelle globale auparavant. En comparaison, d'autres taxons comme les oiseaux (*e.g.*, Blackburn & Duncan 2001; Blackburn et al. 2009; Sol et al. 2012), ou les amphibiens et reptiles (*e.g.*, Allen et al. 2017; Ferreira et al. 2012) bénéficient tous d'une plus grande attention à l'échelle globale sur ce même sujet (Pyšek et al. 2020a). Pourtant, il est essentiel d'étudier les invasions à différentes échelles pour en identifier toutes les tendances (Pyšek et al. 2020b). En effet, Vila-Gispert et al. (2005) ont montré que les profils des espèces de poissons exotiques s'établissant dans les cours d'eau présentant une variation du débit fluvial au cours de l'année étaient opposés à ceux présents dans les cours d'eau sans variation de débit concernant les variables de taille et de fécondité. Ainsi, bien que le contexte local mette en évidence les facteurs associés au succès d'invasion, il ne permet pas de dégager les tendances à grande échelle liées aux voies d'introduction ou aux étapes de l'invasion. Nos études permettent ainsi de confirmer l'importance de facteurs observés à l'échelle locale (*e.g.*, une grande tolérance physiologique est importante pour l'établissement, Kolar & Lodge 2002; Marchetti et al. 2004), mais aussi et surtout une prise de recul sur des tendances contradictoires à l'échelle locale. Par exemple, alors que Ribeiro et al. (2008) montrent que le niveau de soins parentaux est plutôt associé négativement au succès d'invasion dans les bassins versants ibériques, Marchetti et al. (2004) montrent l'inverse en Californie. Notre étude s'est intéressé à l'influence à large échelle des soins parentaux, et a démontré son effet positif globalement sur le succès d'invasion (Chapitre 3 et 4). Enfin, nos résultats démontrent l'influence des facteurs morphologiques qui sont très peu mis en avant à l'échelle locale, mis à part pour la taille, en partie grâce à la très récente base de données FISHMORPH rassemblant de nombreuses données morphologiques (Brosse et al. 2021b)

6.1.2. Similitudes et dissimilitudes des caractéristiques des poissons exotiques envahissants avec d'autres taxons

Nos résultats portant sur les principaux facteurs influençant le succès des invasions de poissons d'eau douce comportent des similitudes avec les travaux menés sur d'autres taxons. Ainsi, nous avons démontré dans cette thèse l'importance des soins parentaux pour envahir chez les poissons d'eau douce. Cette tendance se retrouve chez les oiseaux, ceux présentant des traits d'histoire de vie lents, c'est-à-dire faisant des petites couvées et investissant plutôt de l'énergie pour la survie des petits, ayant un meilleur succès d'invasion (Sol et al. 2012). Au contraire, cette tendance ne se retrouve pas chez les autres vertébrés –*i.e.*, les amphibiens, reptiles ou mammifères (Allen et al. 2017; Capellini et al. 2015). Une explication de cette tendance pour les oiseaux est que leurs traits d'histoire de vie lents sont aussi liés à des meilleures performances d'exploration et d'apprentissage pour s'adapter à leur nouvel environnement (Maspons et al. 2019). On peut émettre l'hypothèse que le même phénomène peut se produire pour les poissons, ceux présentant des soins parentaux tirant alors meilleur parti de leur nouvel environnement exotique. Cette explication pourrait être aussi en accord avec le fait que la position de la nageoire pectorale chez les poissons d'eau douce est importante pour s'établir, notamment en dehors de leur milieu natif (Chapitre 3 et 4). En effet, des nageoires pectorales placées latéralement (et non ventralement) permettent une grande manœuvrabilité du corps conduisant potentiellement à une meilleure exploration du milieu. Par ailleurs, Soares et al. (2021) ont montré que les oiseaux exotiques sur les îles océaniques étaient plus gros et plus représentés par des espèces omnivores que les natives. Ces résultats sont similaires à ceux que l'on a pu mettre en avant durant cette thèse, une grande taille caractérisant les poissons établis dans un grand nombre de bassins (Chapitre 4), et un régime alimentaire large étant associé aux poissons introduits et établis dans un grand nombre de pays (Chapitre 3). Toutefois, il est difficile de comparer les profils des autres taxons avec les profils de poissons d'eau douce exotiques, les traits utilisés étant différents. Ainsi, nous avons utilisé des traits morphologiques, alors que ce type de traits n'est pas disponible à l'échelle mondiale pour les autres vertébrés, mise à part la taille et la masse corporelle. Seuls les oiseaux disposent d'une base de traits morphologiques spécifiques depuis très récemment (Tobias et al. 2022), mais qui n'a pas encore été utilisée pour déterminer les profils d'espèces exotiques envahissantes d'oiseaux à grande échelle. Les traits les plus utilisés pour les vertébrés à l'échelle globale (*i.e.*, les traits les plus complets dans les bases de données, voir Etard et al. 2020) sont par exemple les traits liés à la période d'activité (diurne/nocturne), au type et à l'étendue de l'habitat, à la masse corporelle ou encore au régime alimentaire, qui sont des données qui ne sont pas nécessairement utilisées pour les poissons. Par ailleurs, il existe potentiellement des similitudes dans les milieux envahis par les poissons et ceux envahis par les oiseaux. En effet, Dawson et al. (2017) ont étudié les corrélations entre la richesse d'espèces exotiques établies dans le monde de différents taxons (plantes, oiseaux, reptiles, amphibiens, araignées, mammifères, et poissons). La corrélation la plus forte pour la richesse des poissons établies s'avère être avec celle des oiseaux (coefficient de corrélation = 0.34), même si elle reste bien plus faible que pour d'autres couples (*e.g.*, plantes et araignées, ou amphibiens et oiseaux). Ces résultats pourraient refléter que les caractéristiques biotiques et abiotiques des écosystèmes envahis par les poissons sont différentes de celles de l'ensemble des autres groupes.

De même, les variables socio-économiques liées aux voies d'introduction sont apparues comme étant des variables importantes pour l'étape d'impact. Ces résultats sont en adéquation avec les travaux de Pergl et al. (2017) qui lient certaines voies d'introduction et le nombre de voies d'introduction avec l'impact pour les plantes, les mammifères et les invertébrés terrestres.

L’utilisation humaine des espèces est aussi un facteur d’invasion qui se retrouve chez d’autres taxons, tels que les oiseaux et les mammifères (Jeschke & Strayer 2006). Toutefois, des analyses des facteurs influençant les invasions par voies d’introduction n’ont encore jamais été menées à l’échelle globale sur les autres taxons, ce qui limite les possibilités de comparaisons. De la même façon, l’influence des différentes dimensions d’une même étape sur les caractéristiques liées aux espèces n’avait jamais été explorée pour les vertébrés, mais seulement pour les plantes, en utilisant des traits liés au feuilles (Buckley & Catford 2016; Catford et al. 2016; Liao et al. 2021). Par exemple, Liao et al. (2021) ont montré que la teneur en azote des feuilles et la surface foliaire étaient positivement associées avec l’abondance et négativement avec la taille de l’aire de répartition des plantes exotiques. Ainsi, les questions et approches utilisées dans cette thèse pourraient être transposées à d’autres taxons, en particulier chez les tétrapodes.

6.1.3. Implication de l’identification des profils d’espèces de poissons exotiques comme indicateurs des profils des espèces natives et menacées

Déterminer le profil des poissons exotiques envahissants pourrait aussi indirectement donner des informations sur les espèces les plus sensibles aux invasions. Plusieurs études menées sur les poissons d’eau douce ont ainsi démontré que les espèces natives avaient des caractéristiques qui se différenciaient des caractéristiques des espèces exotiques (Liang et al. 2020; Vila-Gispert et al. 2005; Xiang et al. 2021). Ainsi, une étude à grande échelle en Chine de Xiang et al. (2021) a mis en avant que les caractéristiques liées à l’hydrodynamisme, à la nage, et au niveau trophique (caractéristiques mises en avant dans les Chapitres 3 et 4 de cette thèse pour les poissons exotiques) permettaient de différencier les espèces de poissons exotiques des espèces de poissons natives. Ces différences peuvent indiquer que les espèces exotiques ont des utilisations de l’habitat différentes des espèces natives, leur permettant de s’établir plus facilement. Cette différenciation entre espèces natives et exotiques se retrouve notamment pour les oiseaux sur les îles océaniques : Soares et al. (2021) ont démontré que les oiseaux natifs et exotiques sur les îles se différenciaient par leur régime alimentaire, leur taille et l’utilisation de l’habitat. Ainsi, connaître les caractéristiques des espèces exotiques susceptibles de s’établir dans de nombreux endroits pourrait permettre d’aider à déterminer les caractéristiques des espèces natives sensibles à cette menace (Marino & Bellard 2022). Ces informations pourraient aussi être utilisées pour aiguiller plus généralement la détermination des caractéristiques des espèces menacées d’extinction. En effet, Liu et al. (2017) ont démontré que les espèces de poissons exotiques en Chine avaient des profils opposés à ceux des espèces menacées d'extinction (par n'importe quelle menace) concernant des traits liés à la fécondité et à la taille.

6.1.4. Influence des changements climatiques sur les futures invasions de poissons d'eau douce.

Dans la revue de la littérature (Chapitre 1), nous avons mis en avant le fait que le développement des activités humaines pourrait influencer les voies et lieux d'introduction des poissons d'eau douce exotiques et ainsi le succès des invasions. Cette évolution dans les lieux d'introduction des espèces exotiques envahissantes et leurs profils associés au cours du temps a déjà été démontré pour les oiseaux par Dyer et al. (2017). En effet, les voies, lieux d'introduction et espèces d'oiseaux exotiques introduites ont évolué au cours des 500 dernières années, passant d'oiseaux Européens appartenant aux Anatidés, Phasianidés et Colombidés et introduits par les sociétés d'acclimatation à des oiseaux provenant plutôt d'Asie et d'Afrique, appartenant aux Psittacidés, Estrildidés et Sturnidés, introduits via le commerce d'animaux de compagnie (Dyer et al. 2017). Les oiseaux sont un taxon très différent des poissons, tant par les caractéristiques étudiées que par les voies d'introduction par exemple, mais à notre connaissance aucun taxon aquatique plus proche des poissons (*e.g.*, invertébrés aquatiques) n'a été étudié à large échelle concernant les profils d'espèces exotiques (Pyšek et al. 2020a). Cependant, les tendances concernant les oiseaux peuvent tout de même informer sur l'influence des futurs changements anthropiques sur les résultats de cette thèse. De même, les changements futurs pourraient favoriser des caractéristiques d'espèces différentes de celles mises en avant dans cette thèse. Toutefois, aucune étude ne s'intéresse pour le moment au possible changement de profils des espèces envahissantes dans le futur, que ce soit pour les poissons d'eau douce ou pour d'autres taxons de vertébrés. Nous pouvons tout de même émettre des hypothèses quant aux profils qui pourraient être les plus favorisés dans le futur. Ainsi, on peut émettre l'hypothèse que comme les espèces de poissons exotiques super-établies sont caractérisées par une large tolérance aux températures, alors elles ont un avantage par rapport aux espèces natives qui seront plus susceptibles aux changements. Ainsi, les changements climatiques pourraient encore faciliter les invasions futures de ces espèces (Havel et al. 2015). Cette hypothèse est soutenue par les résultats de Liu et al. (2019), qui démontrent que le changement climatique augmentera le risque d'invasion en Chine notamment en relâchant les contraintes thermiques limitant l'aire de distribution actuelle des espèces de poissons exotiques. Concernant les poissons d'aquarium plus particulièrement, leurs invasions pourraient être facilitées dans des zones où les conditions climatiques actuelles sont trop froides pour leur établissement, comme en Amérique du Nord (*e.g.*, Herborg et al. 2007). Avec le développement des échanges internationaux pour des régions encore peu connectées aujourd'hui, certaines zones vont potentiellement voir leur risque d'invasion augmenter. Ainsi, le développement de l'aquaculture et du commerce ornemental en Amérique du Sud pourrait entrainer de nouvelles invasions de poissons d'eau douce (Brosse et al. 2021a). L'Arctique est aussi une région qui va voir ses échanges internationaux augmenter, notamment à cause de la fonte glaciaire permettant de développement d'activités humaines telles que les pêcheries (Ricciardi et al. 2017). Les changements climatiques pourraient aussi rendre l'Arctique compatible thermiquement aux optimums de certaines espèces qui ne pourraient pas y survivre actuellement. Ces changements pourront potentiellement mener à de nouvelles invasions de poissons dans la région Arctique, impliquant des espèces ayant des profils différents des profils actuellement présents.

6.2. Implication pour la gestion

Dans le but de limiter les invasions de poissons d'eau douce dans le futur, la mise en place d'une gestion efficace de ces espèces est indispensable. Les résultats de cette thèse pourraient contribuer à améliorer les outils de gestion.

6.2.1 Utilisation des modèles pour la gestion des invasions

En dépit du fait que les méthodes de prévention soient considérées comme les méthodes les plus efficaces et les moins coûteuses pour gérer les invasions biologiques (Ahmed et al. 2022), ces dernières ne sont pas reportées comme étant les plus utilisées pour les invasions de poissons d'eau douce (Bernery et al. 2022a). Mon travail de revue de la littérature a permis de mettre en lumière un déficit de documentation des méthodes de gestion des invasions biologiques de poissons. Spécifiquement, la prévention des invasions de poissons se décline en plusieurs axes d'action, tels que la mise en place de lois et de restrictions (*e.g.*, restrictions sur les eaux de ballast, Robertson et al. (2020) ; Werschkun et al. (2014)), l'éducation du grand public et des gestionnaires (Novacek 2008), ou bien l'évaluation des risques des espèces pouvant potentiellement être introduites (*e.g.*, Pheloung et al. (1999)). Nos résultats pourraient notamment aider à l'amélioration de ces outils d'évaluation, en améliorant la pertinence des caractéristiques prises en compte pour déterminer le potentiel envahissant des espèces exotiques.

Par exemple, l'outil « *invasiveness* » de FishBase (Froese & Pauly 2019) permet d'évaluer avec des critères simples le potentiel envahissant des poissons (Fig 8). Cet outil prend en compte notamment les voies d'introduction liées au commerce ornemental et à l'aquaculture, que nous avons identifiées comme étant les principales voies d'espèces établies dans le Chapitre 1. Toutefois, cet outil pourrait prendre en compte d'autres variables enregistrées dans FishBase et facilement utilisables, comme la variété du régime alimentaire, le type de soins parentaux, et le nombre de voies d'introduction, que nous avons identifiées comme étant des variables importantes pour l'étape d'établissement dans le Chapitre 3.

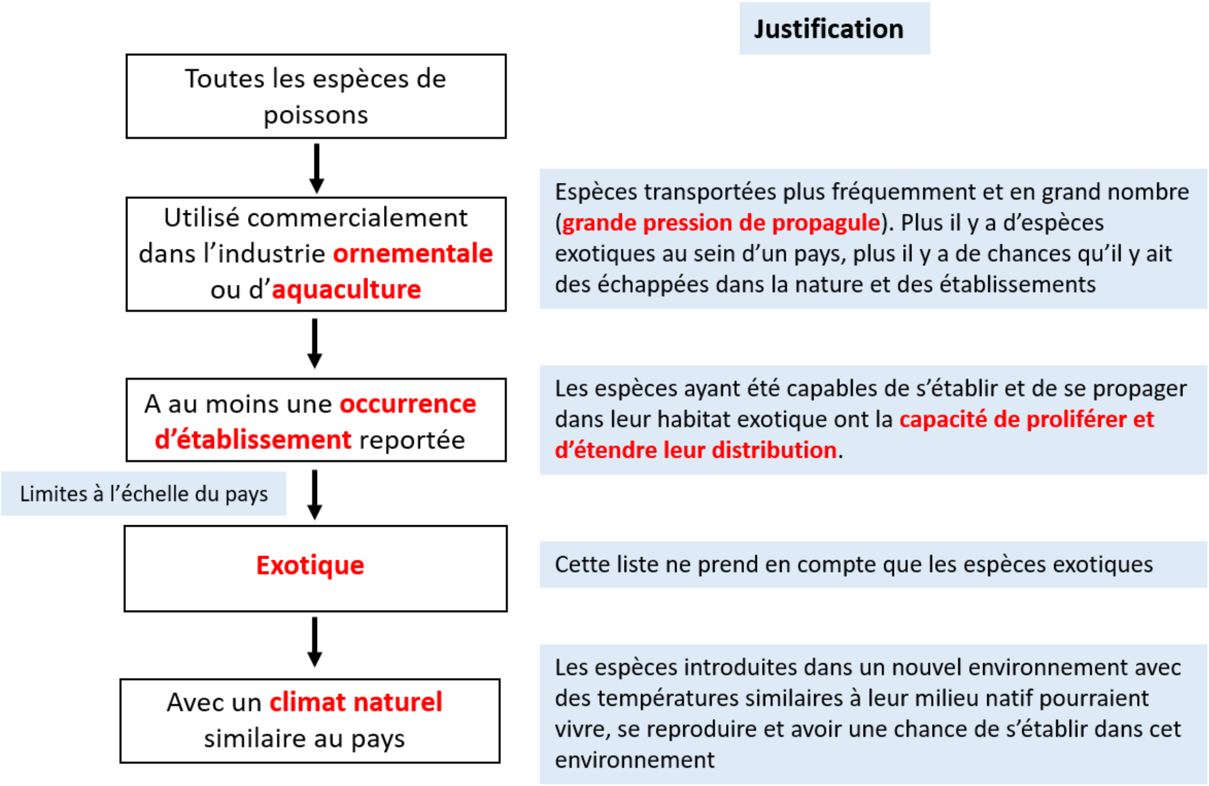


Figure 8 : Description des différents filtres de l'outil « invasiveness » de FishBase. Traduit depuis Casal (2014).

D'autres outils plus complexes et prenant en compte plus de critères existent également pour évaluer et classer les espèces suivant leur risque d'invasion. Ainsi, le WRA (*Weed Risk Assessment*) permet la classification d'espèces de plantes d'Australie et de Nouvelle Zélande pour évaluer leurs impacts potentiels si introduites, en leur attribuant des scores au travers de questions portant sur leurs caractéristiques concernant leur biogéograhie (*e.g.*, préférences climatiques, statut envahissant ailleurs), leurs attributs indésirables (*e.g.*, fruits toxiques), et leur biologie/écologie (*e.g.*, capacité à se reproduire, à se disperser) (Pheloung et al. 1999). Plusieurs autres outils d'évaluation des risques ont été développés sur la base du WRA, dont des outils permettant l'évaluation du caractère envahissant de plusieurs taxons aquatiques tels que les amphibiens (Amph-ISK, Kopecký et al. 2016), les invertébrés (FI-ISK, Tricarico et al. 2010), les poissons marins (MFISK, Copp et al. 2013) et les poissons d'eau douce (FISK, Copp et al.

2008). Le FISK a déjà été appliqué 1973 fois, sur 372 espèces différentes pour 45 pays différents, en faisant un outil d'évaluation majeur pour les invasions de poissons d'eau douce (Vilizzi et al. 2019). Dans cette thèse, nos études ont été menées à l'échelle mondiale, permettant de mettre en évidence les grandes tendances régissant l'influence des facteurs des invasions à l'échelle globale. Nos résultats pourraient ainsi aider à compléter les critères pris en compte, mais aussi à évaluer leur importance relative. En effet, plusieurs des questions d'évaluation présentes dans le FISK sont en adéquation avec les résultats que nous avons trouvé dans le Chapitre 3 de cette thèse. Ainsi, le FISK comporte des questions portant sur les soins parentaux, l'utilisation humaine, les différents climats rencontrés et les attributs physiques (*e.g.*, taille), le régime alimentaire, ainsi que le nombre de voies d'introduction potentiellement utilisées par l'espèce. Plusieurs questions se penchent également sur la détermination du potentiel d'impact des espèces. Or, comme nous l'avons vu grâce au Chapitre 1 et 3, les facteurs associés aux impacts sont encore mal connus, et les données sur ces mêmes impacts restent assez rares. Le protocole EICAT (Hawkins et al. 2015), permettant de répertorier et standardiser les impacts écologiques des espèces exotiques, n'est pas encore appliqué aux poissons d'eau douce. Dans ce contexte, une solution à moyen terme serait d'utiliser un indicateur de l'impact des poissons exotiques envahissants, comme, par exemple, le potentiel d'établissement des espèces, décrit par le nombre bassins envahis et la localisation d'établissement (dans ou en dehors de la biorégion native). En effet, nous avons montré dans le Chapitre 4 qu'un fort potentiel d'établissement est corrélé à la probabilité pour une espèce d'avoir un impact écologique. Les facteurs régissant l'établissement étant mieux connus que ceux régissant l'impact, peut-être vaudrait-il mieux axer les questions sur cette étape, et appliquer ensuite le principe de précaution concernant les espèces ayant un fort potentiel d'établissement (D'hondt et al. 2015).

Certaines questions pourraient aussi porter sur la morphologie de l'espèce puisque la position des nageoires pectorales est par exemple fortement associée à l'établissement, comme nous l'avons démontré dans le Chapitre 4. La question portant sur le nombre de voies d'introduction possibles pourrait prendre en importance au vu de nos résultats. Nous pourrions aussi imaginer avoir des questions différentes suivant la voie d'introduction, puisque les espèces sont susceptibles d'avoir des caractéristiques différentes suivant les voies d'introduction, comme montré dans le Chapitre 3. Il a aussi été récemment montré que l'utilisation de certaines voies d'introduction par les espèces pourraient augmenter leur score de potentiel d'invasion. En effet, Turbelin et al. (2022) (Annexe 6), dans un article auquel j'ai participé, a étudié 478 espèces tous taxons confondus, et a mis en avant que les voies d'introduction involontaires étaient à l'origine d'invasions d'espèces plus coûteuses que les voies volontaires, les deux voies les plus coûteuses étant les contaminations (*i.e.*, introduction involontaire avec une marchandise spécifique) et les « passagers clandestins » (*i.e.*, introduction involontaire grâce à un vecteur de transport). Dans le Chapitre 3, nous mettons en évidence que certaines voies d'introduction pourraient être plus liés aux impacts que d'autres pour les poissons d'eau douce, tels que le commerce ornemental ou les pêcheries. Se concentrer sur ce type de voies d'introduction pourrait aider à la gestion et à la prévention des invasions de poissons d'eau douce. Enfin, ces outils d'évaluation se basent essentiellement sur les caractéristiques liées aux espèces considérées. Toutefois, on pourrait imaginer le même type de procédé mais sur les régions réceptrices, en évaluant leur capacité à être envahi. En effet, comme nous le développeront brièvement dans la partie « Perspectives », des résultats préliminaires montrent qu'une grande anthropisation peut, par exemple, augmenter le potentiel d'invasion.

6.2.2 Importance de la vision du grand public et influence du charisme pour la recherche et la gestion

Les invasions biologiques sont une menace importante pour la biodiversité, mais elles restent mal connues et mal considérées du grand public, et parfois des gestionnaires, qui sous-estiment leur importance (Courchamp et al. 2017). La perception du grand public des espèces exotiques envahissantes peut alors influencer la bonne gestion de ces espèces. Par exemple, la mauvaise perception et connaissance du grand public concernant les invasions biologiques peut limiter la disponibilité des données, et ainsi biaiser les études sur le sujet, dont les études présentes dans cette thèse, mais aussi la gestion mise en place pour limiter leurs impacts. Le travail de vulgarisation est un outil important afin d'introduire clairement au grand public l'importance des invasions biologiques et leurs conséquences. Ainsi, parce qu'il s'agit d'un outil important, j'ai tenu à participer à des actions de vulgarisation tout au long de ma thèse.

6.2.2.1 Les invasions biologiques restent moins connues que les autres composantes des changements globaux

Plusieurs classements des menaces en fonction de leur impacts relatifs sur la perte de biodiversité sont disponibles dans la littérature. Ces classements sont différents suivant l'organisme les publiant (*e.g.*, *the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, IPBES ; ou *the International Union for Conservation of Nature,* IUCN), mais aussi suivant la métrique ou le groupe taxonomique pris en compte (Bellard et al. 2022). Ainsi, les invasions biologiques représentent le premier facteur responsable des extinctions insulaires à l'échelle globale (Leclerc et al. 2018), mais sont classées dernière menace à l'échelle globale par l'IPBES (Bellard et al. 2022). De même, les invasions biologiques sont classées deuxième menace (sur cinq menaces considérées) après la perte d'habitat concernant les amphibiens, mais première pour les oiseaux (Bellard et al. 2022). Les classifications considèrent aussi les menaces indépendamment les unes des autres, ignorant souvent leurs effets synergiques, et peuvent ainsi sous-estimer leurs possibles effets (Bellard et al. 2022; Novacek 2008). De plus, cette tendance à la classification ne permet pas de prodiguer un message clair, que ce soit aux décideurs ou au grand public : toutes les menaces sur la biodiversité doivent être prises en compte pour gérer la crise environnementale, et ces classements supposent que certaines menaces sont moins importantes que d'autres à gérer pour la sauvegarde de la biodiversité. L'absence de message clair peut être particulièrement délétère à la prise de conscience de l'importance des invasions biologiques, car elles sont une menace particulièrement mal connue du grand public. Mon expérience au palais de la découverte m'a permis d'être témoin de cette méconnaissance. Durant mes exposés, j'interagissais souvent avec le public, et je leur demandais notamment de me lister les cinq menaces pesant sur la biodiversité. Alors que le changement climatique, la pollution et la perte d'habitat étaient systématiquement citées, les invasions biologiques n'étaient pas connues dans la majorité des cas, bien qu'elles figuraient dans le titre de l'exposition.

En effet, même si la crise de la biodiversité est une préoccupation grandissante du grand public, la préoccupation principale est aujourd'hui centrée sur le changement climatique, au détriment d'autres menaces, particulièrement des invasions biologiques (Jarić et al. 2020a; Novacek 2008). Alors que le changement climatique est vu comme une menace globale avec des impacts à large échelle, les invasions biologiques sont plutôt vues comme une menace plus localisée, à laquelle on ne serait pas directement confrontés et dont les impacts sont plus difficiles à démontrer (Courchamp et al. 2017 ; Jarić et al. 2020a). De plus, le concept d'invasion biologique est une notion compliquée, impliquant un vocabulaire spécifique (*e.g.*, espèces natives, non-natives, exotiques, envahissantes, établies) (Courchamp et al. 2017) et dont la définition n'est pas arrêtée même dans la sphère scientifique (*e.g.*, présence ou non d'impacts ; Blackburn et al. 2011 ; Lewis et al. 2016). Dans des cas extrêmes, la mauvaise compréhension des menaces pesant sur la biodiversité, notamment des invasions biologiques, peut mener au déni et à penser par exemple que les invasions sont un phénomène naturel (Stratton et al. 2022).

S'en suit une sous-estimation du danger que les invasions représentent pour la biodiversité. Ce déni, en plus de toucher le grand public, peut aussi toucher les gestionnaires et politiques. C'est pourquoi il est important de véhiculer des informations claires concernant cette menace (Stratton et al. 2022).

En outre, la menace des invasions biologiques pose des considérations éthiques importantes par rapport aux autres menaces, étant donné qu'éradiquer des populations d'espèces exotiques pour préserver la biodiversité native peut être grandement contre-intuitif, rendant d'autant plus difficile sa gestion et le soutien du grand public (Courchamp et al. 2017). De même, empêcher le public de relâcher des espèces dans la nature, qui est pourtant souvent vu comme un acte bénéfique (Kilian et al. 2012), tant pour l'espèce relâchée que pour l'écosystème receveur, est aussi contre-intuitif. Les espèces envahissantes peuvent aussi bénéficier d'un capital sympathie élevé du public : certaines espèces envahissantes font partie intégrante de l'économie des pays concernés (*e.g.*, la perche du Nil, Aloo et al. 2017) ou sont vues comme charismatiques, ce qui peut entraver la mise en place de plans de gestion (Jarić et al. 2020b). J'en ai là aussi fait l'expérience lors de mes exposés au Palais de la Découverte. Un exemple que j'abordais était l'invasion des chats en Australie, espèce avec un capital sympathie très élevé. Certaines personnes étaient choquées alors d'apprendre les méthodes d'éradication mises en place, faisant le parallèle avec leurs propres chats de compagnie.

6.2.2.2 Charisme des poissons et implications pour la recherche

Le charisme est un élément important à prendre en compte, car il influence grandement les connaissances et la perception du public, mais aussi de la recherche en général (Jarić et al. 2020b). Certains poissons bénéficient d'un charisme particulier, charisme qui influe sur la probabilité d'introduction par des voies intentionnelles. Ainsi, les poissons d'aquarium, appréciés par le public pour leurs couleurs, sont des poissons populaires et sont souvent relâchés dans la nature (Padilla & Williams 2004). De même, les gros poissons souvent recherchés par les pêcheurs, sont introduits par ces derniers pour augmenter l'attractivité de leurs prises (*e.g.*, l'achigan à grande bouche *Micropterus salmoides* que l'on retrouve notamment dans les eaux françaises, Nentwig 2007). Ce charisme peut être une aide à la récolte de données pour la recherche, encourageant l'investissement du public dans des programmes de sciences participatives (Jarić et al. 2020b). Par exemple, un projet de science participatives visant à identifier des lieux d'établissement des guppies (*Poecilia reticulata*) en Allemagne a permis d'identifier deux nouveaux lieux d'établissement pour cette espèce (Lukas et al. 2017). De même, l'introduction en Amérique du Nord de poissons appartenant au genre *Ictobius* a été détectée grâce à des photos postées par des pêcheurs sur internet (Jarić et al. 2021). Dans le Chapitre 3, nous avions identifié que les données d'introduction étaient difficiles à récupérer, notamment parce que les espèces exotiques n'étaient souvent repérées qu'une fois établies. L'intérêt du grand public pour les poissons pourrait ici être un atout pour une meilleure récolte de données utilisables pour des recherches sur le sujet des invasions biologiques.

6.2.2.3. Pistes de remédiations

Afin d'améliorer l'intérêt du public pour les invasions de poissons d'eau douce, plusieurs solutions pourraient être mises en place, dont des solutions visant à communiquer avec le grand public. La place prise par les sujets de biodiversité dans les médias, au travers de documentaires ou de journaux scientifiques, peut avoir un impact important sur la vision du public (Novacek 2008). Ainsi, Jarić et al. (2021) ont montré, au travers d'analyses de sentiments sur Twitter, que les sentiments du grand public envers le poisson à tête de serpent (*Channa argus*) envahissant étaient plus négatifs durant la période où l'espèce avait reçu beaucoup d'attention de la part des médias, que durant les six mois précédents. Toutefois, les médias se centrent encore beaucoup sur les sujets du changement climatique au détriment des autres menaces, auxquelles il faudrait accorder plus d'importance qu'actuellement (Novacek 2008), comme les invasions biologiques. Lors de ma thèse, j'ai pu participer à cet effort de mise en avant des invasions biologiques dans les médias notamment avec un article dans le journal en ligne *The Conversation* (https://theconversation.com/1-288-milliards-de-dollars-chiffrer-les-degats-causes-par-les-invasions-biologiques-pour-enfin-agir-158204), qui a ensuite été repris par plusieurs journaux (*e.g.*, Ouest France). Les musées sont aussi un bon moyen de rendre accessible la science au grand public, et ont l'atout de bénéficier d'un haut taux de crédibilité (Novacek 2008). Ainsi, durant ma thèse, j'ai aussi essayé de rendre accessible le sujet des invasions biologiques au grand public lors d'exposés au Palais de la découverte à Paris. Enfin, le développement d'outils de science participative pour les invasions biologiques peut avoir le double avantage de fournir des données possiblement exploitables par les scientifiques, mais aussi d'être un bon moyen d'améliorer les connaissances du grand public sur ces sujets (Novacek 2008). Pour les invasions biologiques, des applications existent telles que « *Find a pest* » en Nouvelle Zélande, « *Wild Spotter* » pour les zones de nature sauvage Américaines, ou « EEE en Europe » pour l'Europe, et qui mériteraient d'être plus développées pour d'autres régions. Toutefois, le développement d'outils de science participative demande beaucoup d'investissement de la part de la communauté scientifique, et gagne à être développé en collaboration avec des éducateurs scientifiques (Novacek 2008).

6.2.3 Paradoxes des invasions et influence sur la gestion

Au-delà des problèmes de méthodes de gestion, d'éthique et d'influence du grand public, les invasions biologiques mettent en avant des paradoxes de conservation et de gestion. Deux questions peuvent ainsi se poser : (i) Comment gérer les invasions d'espèces nécessitant d'être conservées dans leur régions natives ? (ii) Comment mettre en œuvre une gestion des espèces envahissantes ayant des impacts économiques positifs dans leurs régions d'introduction ?

La première question a déjà été abordée pour plusieurs espèces dans la littérature, mettant en avant leur statut envahissant dans certaines régions, et leur statut menacé dans d'autres (Gillard et al. 2017 ; Marchetti & Engstrom 2016). Par exemple, l'Arapaïma (*Arapaima gigas*) est un poisson d'eau douce en danger d'extinction dans son milieu natif au Brésil, mais envahissant en Bolivie (Marchetti & Engstrom 2016; Miranda-Chumacero et al. 2012). La perche de Sacramento (*Archoplites interruptus*) est quant à elle éteinte dans son milieu natif mais envahissante à l'Ouest des États-Unis (Crain & Moyle 2011; Marchetti & Engstrom 2016). Au cours de cette thèse, j'ai pu m'impliquer dans une étude visant à identifier ces paradoxes de conservation chez des espèces exotiques envahissantes (mammifères, oiseaux et plantes) ayant un impact économique, en analysant leur statut de menace, leur originalité phylogénétique et fonctionnelle (Robuchon et al., soumis ; Annexe 7). Nous avons ainsi démontré que parmi les 397 espèces de plantes, mammifères et oiseaux documentés comme ayant des coûts économiques, sept espèces de mammifères et deux espèces de plantes envahissantes sont également en danger d'extinction dans leur milieu natif. Ces situations doivent alors être gérées au cas par cas, impliquant par exemple de ne pas intervenir malgré les impacts de l'espèce exotique, de relocaliser l'espèce, ou de la retirer du milieu d'introduction (Marchetti & Engstrom 2016). Ces situations n'étant pas si rares, il serait intéressant de les quantifier pour d'autres taxons à l'échelle globale y compris les poissons.

Si cette première question implique des problèmes pour la conservation des espèces, la deuxième est plutôt d'ordre sociétal, mais complique aussi la gestion de ces espèces. En effet, certaines espèces envahissantes peuvent avoir des impacts économiques positifs et bénéficier aux économies locales, et ceci est particulièrement vrai pour les poissons d'eau douce envahissants qui bénéficient aux pêcheries (Gozlan 2008). Ainsi, la question de l'éradication des espèces envahissantes peut se poser. De mon point de vue, la meilleure documentation des impacts économiques positifs permettrait de mieux comprendre certains manques de données d'impacts écologiques ou manques de gestion, ces espèces pouvant être délaissées par les politiques de gestions de par leurs avantages économiques. Cette documentation pourrait aussi permettre de mettre en place de meilleures priorisations de gestion sur les espèces envahissantes. Pour répondre à ce besoin, la base SEICAT+, calquée sur la base SEICAT répertoriant les impacts socio-économiques des espèces envahissantes (Bacher et al. 2018), est en développement afin de répertorier ces impacts économiques positifs (Bacher et al. 2018). Toutefois, le danger de cette documentation réside dans le fait de donner des arguments à la conservation d'espèces envahissantes ayant de forts impacts écologiques. Ainsi, la perche du Nil (*Lates niloticus*) permet à plus de 1.2 million de personnes de vivre au travers des pêcheries dans le la Victoria (Matsuishi et al. 2006). Toutefois, la perche du Nil est aussi à l'origine de la plus grande extinction de vertébrés jamais observée (Witte et al. 1992) et a mené à la précarisation des pêcheurs locaux qui n'ont pas le matériel nécessaire pour la pêcher (Onyango & Jentoft 2010). Il semblerait aussi que la pêche à la perche du Nil ne soit pas durable au vu du déclin de l'espèce avec la pêche intensive (Matsuishi et al. 2006). Encore une fois, les décisions devraient être prises au cas par cas, en utilisant toutes les connaissances à disposition.

Dans cette partie, j'ai ainsi synthétisé les principaux résultats découlant de mon travail de thèse, et discuté de leur application sur les aspects fondamentaux de la recherche et sur les aspects plus appliqués au travers des prises de décisions en gestion. D'autres aspects des invasions de poissons d'eau douce pourraient être étudiés pour faire suite à cette thèse, dont certaines sont abordées dans la partie suivante.

6.3. Perspectives

Suite aux travaux de thèse que j'ai mené au cours des dernières années, j'ai identifié trois pistes d'amélioration et de perspectives qui pourraient être mises en œuvre pour approfondir l'étude des facteurs des invasions de poissons d'eau douce. Ces perspectives portent à la fois sur l'approfondissement de travaux que j'ai effectué, sur des développements théoriques liés à la théorie de la biogéographie insulaire et sur l'exploration des facteurs de succès de l'étape d'impact grâce à la classification des impacts écologiques des poissons exotiques envahissants. Ces perspectives ne sont que des exemples de la multitude de travaux qui pourraient faire suite à cette thèse.

6.3.1. Approfondissement des travaux de cette thèse : profils des bassins envahis et futures tendances d'invasions dans les bassins.

Dans cette thèse, nous avons déterminé les principales caractéristiques des espèces de poissons d'eau douce exotiques envahissantes associées à leur succès. Toutefois, les caractéristiques des espèces ne suffisent pas pour expliquer complètement le succès d'invasion. Les caractéristiques du milieu receveur sont aussi un élément essentiel à prendre en compte. Par exemple, l'anthropisation peut perturber le milieu et faciliter l'établissement d'espèces exotiques (Clavero et al. 2013) ou bien rendre certains lieux plus accessibles et faciliter ainsi l'introduction d'espèces exotiques (Johnson et al. 2008). Les caractéristiques du milieu envahi et le contexte local jouent un rôle prépondérant dans le processus d'invasion. Pour les poissons, plusieurs facteurs du milieu, qu'ils soient biotiques, abiotiques ou anthropiques, ont ainsi été identifiés comme expliquant en partie la vulnérabilité des bassins versants aux invasions (Clavero et al. 2013 ; Jeschke & Heger 2018 ; Liu et al. 2019 ; Su et al. 2021). Toutefois, les études portant sur le sujet se sont concentrées sur des échelles locales et/ou sur un faible nombre d'espèces (Californie, Marchetti et al. 2004 ; Japon, Yonekura et al. 2004 ; région ibérique, Clavero et al. 2013 ; Malaisie, Vythalingam et al. 2021). Une perspective de nos travaux serait de déterminer les caractéristiques des bassins envahis à l'échelle globale. Nous avons déjà entamé en partie ce travail grâce à des analyses préliminaires. Ainsi, nous avons souhaité explorer les caractéristiques de 991 bassins versants à travers le monde. Nous avons utilisé sept facteurs du milieu liés aux pressions anthropiques et aux conditions biotiques et abiotiques, afin de caractériser les différences entre les bassins comportant des espèces de poissons d'eau douce exotiques établies (n=411), et les bassins ne comportant pas d'espèces de poissons exotiques (n=580). Nous avons sélectionné des variables qui avaient déjà montré un effet dans la littérature (sur d'autres taxons ou à échelle locale) ou pour lesquelles nous avions des hypothèses à tester (Annexe 8 – Table S1). Ces facteurs sont le nombre d'espèces de poissons d'eau douce natives, le nombre de barrages, l'amplitude des valeurs d'élévation, l'amplitude de températures et de précipitations, le *human footprint index* médian et l'aire des bassins. L'objectif de ces analyses était de déterminer les caractéristiques des bassins envahis à l'échelle mondiale en utilisant des variables anthropiques, biotiques et abiotiques. Les méthodes utilisées sont disponibles en Annexe 8. Les premiers résultats montrent que six variables (le nombre d'espèces de poissons d'eau douce natives, le nombre de barrages, l'amplitude des valeurs d'élévation et de précipitation, le *human footprint index* médian, et l'aire des bassins) montrent des différences significatives entre les bassins envahis et les bassins non-envahis. L'ensemble de ces variables, à l'exception de l'amplitude des précipitations, montrent des valeurs significativement plus élevées pour les bassins envahis par rapport aux les bassins non-envahis (Fig 9, Annexe 8 - Table S2). La seule variable testée où il n'existe pas de différence significative entre bassins envahis et non-envahis est l'amplitude de température. Les premiers résultats concernant l'anthropisation, ici représentée par le nombre de barrages et le *human footprint index*, sont donc en adéquation avec la littérature (Clavero et al. 2013 ; Su et al. 2021). Une grande amplitude climatique semble aussi faciliter les invasions, mais cette tendance ne ressort que pour les précipitations et non pour la température. Concernant le nombre d'espèces natives, ces premiers résultats préliminaires ne semblent pas vérifier l'hypothèse de résistance biotique. Ces résultats seraient donc plutôt en adéquation avec l'hypothèse *rich-get-richer* (Jeschke 2014). Les résultats préliminaires issus de cette partie pourraient à terme faire l'objet d'une publication.

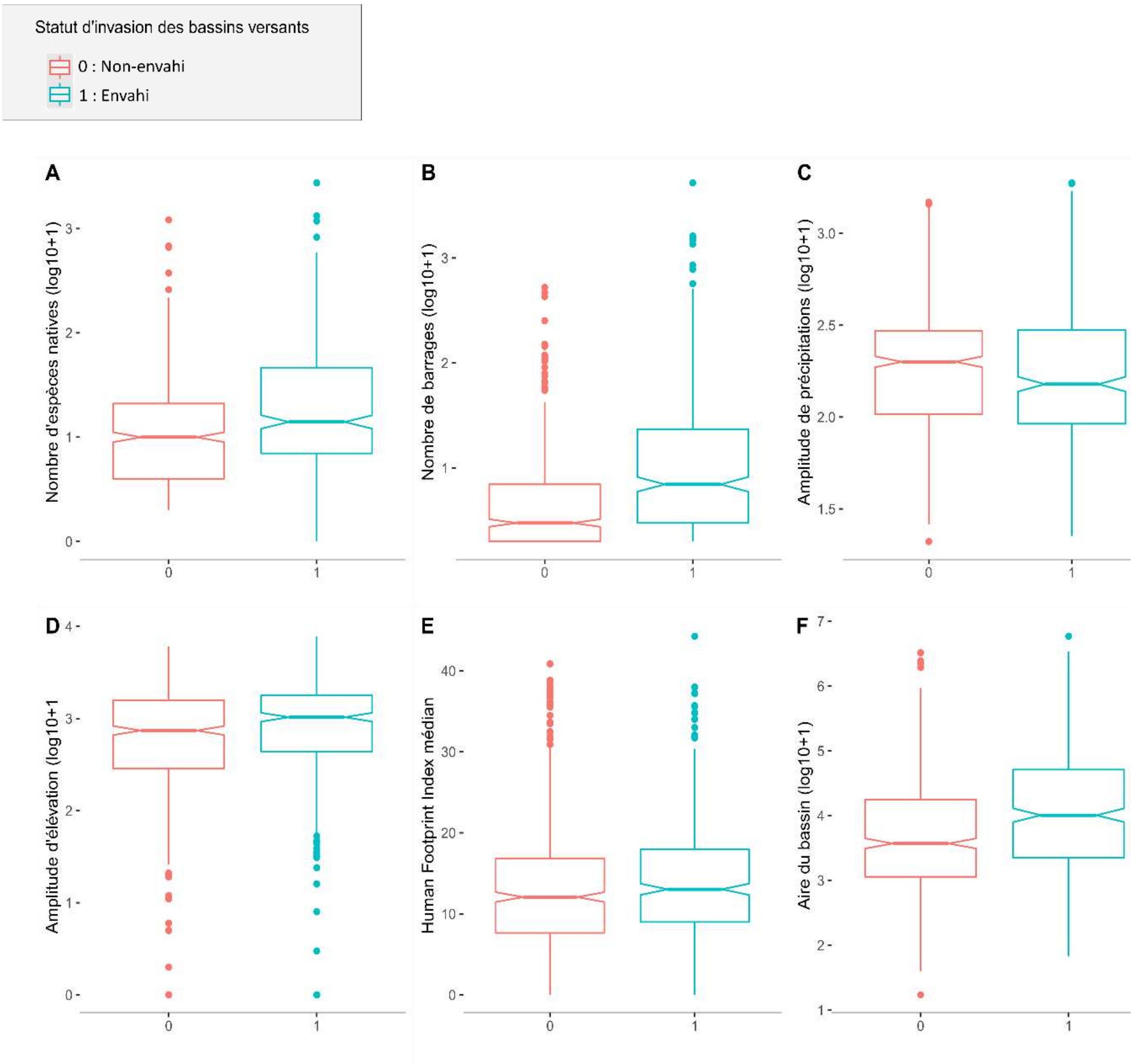


Figure 9 : Comparaison des données entre les bassins envahis et les bassins non-envahis. Seules les comparaisons présentant une différence significative sont représentées.

Nous avons ensuite analysé ces données à l'aide d'un modèle linéaire généralisé (GLM). Pour se faire, nous n'avons considéré que les bassins envahis (n=411), et nous avons considéré en variable à expliquer le nombre d'espèces établies dans chaque bassin. Cependant, cette analyse n'a pas donné les résultats escomptés, le modèle n'ayant un R^2 de seulement 0,16. Pour améliorer ce modèle, il serait intéressant d'incorporer des variables économiques, telles que l'intensité de l'aquaculture, qui est une des voies principales d'introduction de poissons d'eau douce, augmentant ainsi les chances pour que des espèces exotiques soient introduites. La présence d'aquaculture peut aussi être liée à une forte pression de propagule pour certaines espèces, augmentant ainsi les chances d'établissement. La distance au bassin le plus proche pourrait aussi être une variable intéressante à explorer, une distance courte pouvant faciliter les échanges d'espèces entre les bassins par les pêcheurs par exemple. La proximité avec une grande ville peut aussi faciliter l'introduction de poisson d'aquarium et serait intéressante à prendre en compte. Enfin, des études précédentes ont montré que les caractéristiques biotiques des assemblages natifs, telles que la diversité fonctionnelle, pouvaient aussi influencer le devenir des introductions d'espèces exotiques (Habit et al. 2012; Tingley et al. 2011). Ces résultats préliminaires montrent tout de même l'intérêt d'explorer les profils de bassin versant à l'échelle mondiale.

En outre, les caractéristiques des espèces exotiques et les caractéristiques du milieu d'introduction sont connues pour agir en synergie et influencer ensemble le succès d'invasion des espèces (Pyšek et al. 2020a). Par exemple, l'adéquation entre les conditions dans la zone d'introduction et les caractéristiques physiologiques de l'espèce, de même que l'accessibilité de la zone par l'espèce (il faut que l'espèce puisse y être introduite) sont des facteurs importants. Un développement des travaux que j'ai mené pourrait viser à combiner les variables importantes mises en avant dans les Chapitres 3 et 4 cherchant à déterminer les caractéristiques des espèces les plus établies, avec les variables importantes des bassins les plus envahis. Par exemple, nous pourrions explorer les questions suivantes : 1) Parmi les espèces ayant des fortes capacités d'établissement (Chapitre 4), certaines pourraient-elles rencontrer des conditions climatiques favorables leur permettant de s'établir dans plus de bassins ? 2) Parmi les bassins versants pouvant être envahis en raison d'une compatibilité climatique avec des espèces à fortes capacités d'établissement, certains possèdent-ils des caractéristiques typiques des bassins envahis (*e.g.*, forte densité de barrages, forte densité de population humaine) ? 3) En outre, est-ce que les bassins susceptibles d'être envahis en raison des conditions climatiques favorables aux espèces exotiques envahissantes ayant des caractéristiques intrinsèques de bassins envahis sont accessibles à ces espèces (*e.g.*, présence de voies d'introduction telles que l'aquaculture ou la pêche) ?

6.3.2. Comparaison entre îles et bassins versants

Les bassins versants peuvent être considérés à bien des égards comme des systèmes insulaires. Plusieurs études dans la littérature ont mis en avant les similitudes entre les bassins versants et les îles concernant leur niveau d'endémisme et leur isolement (Hugueny et al. 2010; Leroy et al. 2019; Olden et al. 2010). Toutefois, aucune étude ne s'est encore intéressée à la comparaison entre les invasions dans les îles et au sein des bassins versants en termes de richesse en espèces exotiques.

Sur les îles, la richesse des espèces natives est régie par des facteurs différents de la richesse des espèces exotiques. Ainsi, la richesse en espèces natives est déterminée par des facteurs biogéographiques tels que l'aire des îles agissant positivement sur la richesse en native (Blackburn et al. 2016), et la distance au continent agissant négativement (Moser et al. 2018). La richesse en espèces exotiques est, quant à elle, plutôt régie par l'aire des îles (Blackburn et al. 2016), par la pression de propagule, des facteurs humains (*e.g.*, densité de population) (Dawson et al. 2017), par l'élévation et aussi par la distance au continent (Moser et al. 2018), qui sont toutes des variables agissant positivement sur la richesse en espèces exotiques. Des variables similaires à celles utilisées pour les îles pourraient ainsi être utilisées pour décrire les richesses en espèces dans les bassins versants à l'échelle globale, telles que la distance entre les bassins, la distance à la ville la plus proche, l'aire des bassins, ou bien encore l'amplitude de profondeur des bassins considérés. Ces mêmes variables pourraient être utilisées pour décrire non seulement la richesse en espèce, mais aussi la richesse fonctionnelle et phylogénétique des assemblages exotiques, qui sont pour le moment peu étudiés même pour les autres taxons de vertébrés.

6.3.3. Classification EICAT pour identifier les profils des poissons d'eau douce exotiques envahissants

Dans le premier axe de cette thèse, nous avons mis en avant le manque de données d'impact des invasions de poissons d'eau douce. En effet, à l'heure actuelle, il n'existe aucune classification standardisée des impacts des poissons d'eau douce envahissants, qu'ils soient écologiques ou socio-économiques. La standardisation des impacts écologiques au travers du protocole EICAT, ou socio-économiques au travers de SEICAT, a permis la classification d'informations telles que la sévérité, les mécanismes et la région d'impact pour les espèces exotiques. La classification EICAT a ainsi permis la classification des impacts des oiseaux (Evans et al. 2016), des amphibiens (Kumschick et al. 2017), de certains gastéropodes (Kesner & Kumschick 2018), des bambous (Canavan et al. 2019), des mammifères (Hagen & Kumschick 2018) et des poissons marins méditerranéens envahissants (Galanidi et al. 2018). Néanmoins, les impacts des poissons d'eau douce envahissants n'ont pas encore été classés, alors que ces espèces sont connues pour avoir des impacts écologiques conséquents (Cucherousset & Olden 2011). En outre, les données d'impacts de FishBase ne permettent pas de connaître les mécanismes ni l'intensité des impacts. Une perspective des travaux menés dans le cadre de cette thèse serait de classifier les impacts écologiques des poissons d'eau douce envahissants dans la base EICAT, afin de disposer d'une base de données complète pour étudier les profils d'espèces ayant des impacts écologiques à l'échelle mondiale. J'ai ainsi encadré Julie Larcheron, une stagiaire de M1, durant quatre mois pour mener un premier travail préliminaire de classification des impacts écologiques des poissons d'eau douce au travers du protocole EICAT. Ce travail a permis la classification de 52 espèces de poissons d'eau douce. Toutefois, cette base de données nécessite encore de nombreuses vérifications et il faudrait intensifier l'échantillonnage des poissons en faveur des espèces les moins renseignées, afin de diminuer les biais taxonomique potentiels. La classification EICAT des poissons d'eau douce permettrait à terme de déterminer les profils en fonction du mécanisme d'impact mis en œuvre et de déterminer par exemple si les espèces ayant des impacts par compétition ont des caractéristiques différentes des espèces ayant des impacts par prédation. De même, à l'image du Chapitre 4 avec l'établissement, nous pourrions étudier les changements de profils des espèces le long d'un gradient d'impact décrit par la sévérité d'impact.

6.4. Limites des études : Biais et manques de données

Plusieurs limites peuvent être identifiées dans ce travail de thèse, que ce soit au niveau des méthodes, du modèle d'étude, des bases de données ou des définitions utilisées. Dans la suite de cette partie, nous allons nous focaliser essentiellement sur les biais présents dans les données que nous avons utilisées.

6.4.1. Biais spatial

Comme identifié dans la revue de la littérature (Chapitre 1), les données et les études portant sur les invasions biologiques de poissons d'eau douce sont biaisées envers les régions développées qui peuvent investir de l'argent dans la recherche, tel que l'Amérique du Nord (Bellard & Jeschke 2016; Pyšek et al. 2008). Même si les régions développées sont probablement celles qui ont aussi les plus hautes probabilités d'être envahies (*e.g.*, plus d'échanges internationaux) (Vilà & Pujadas 2001), les données sur lesquelles nous avons travaillé durant cette thèse ne sont pas l'exact reflet des localisations des invasions, mais sont biaisées de par l'effort de recherche. Ainsi, les données portant sur les invasions dans les pays en voie de développement sont souvent trouvées dans la littérature grise, ou alors ne sont pas disponibles en anglais (Angulo et al. 2021; Fazey et al. 2005; Nuñez & Pauchard 2010) et sont donc peu utilisées par les chercheurs. Nous pouvons par exemple être témoins de cette tendance grâce à la Figure 10. En effet, la majorité des espèces renseignées comme exotiques dans la base de données Tedesco et al. (2017) sont exotiques dans les région développées (Néarctique, Paléarctique, Sino-Oriental). Cette tendance se reflète aussi dans les espèces utilisées dans le Chapitre 4 (Fig 10). Certaines tendance d'invasion, comme le nombre de pays ou de basins envahis (Chapitre 3 et 4) sont potentiellement sous-estimées dans les pays en développement. De même, certaines espèces n'y sont pas répertoriées comme étant établies ou envahissantes, biaisant les profils d'espèces envers les pays développés. Ainsi, les caractéristiques influençant le succès d'invasion dans les pays en voie de développement ne sont pas connues, ne permettant pas de réellement dresser des profils d'espèces à l'échelle mondiale. Il se peut que l'importance de certaines de nos caractéristiques utilisées aient été sous ou sur-estimées.

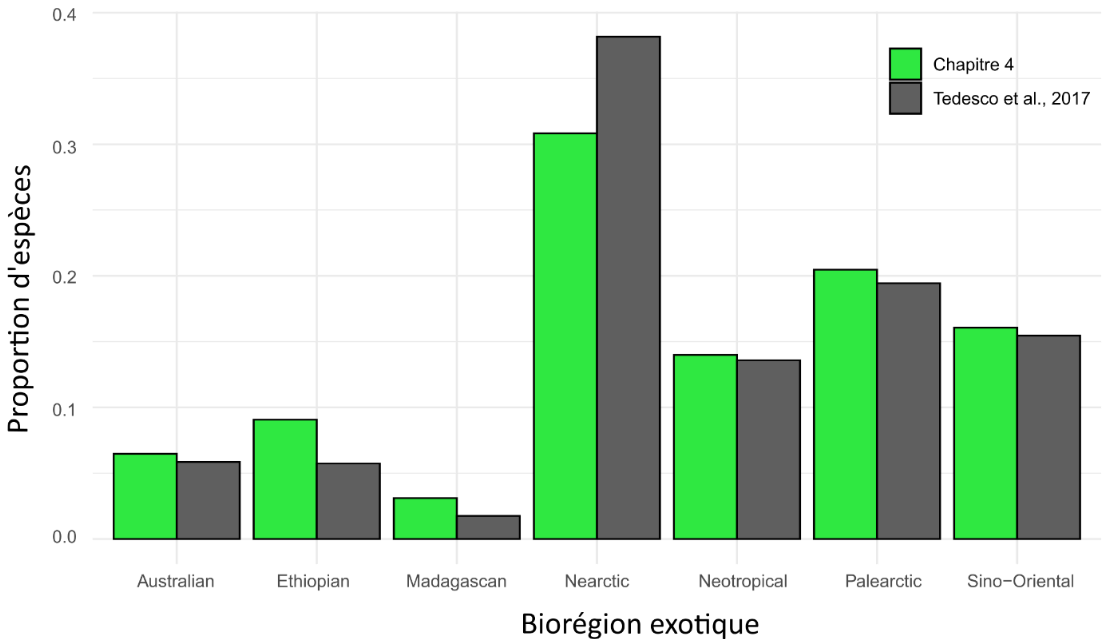


Figure 10 : Répartition des espèces exotiques entre les différentes biorégions dans la base de données de Tedesco et al. (2017) (Gris, N=605) et dans les analyses du Chapitre 4 (Vert, N=222).

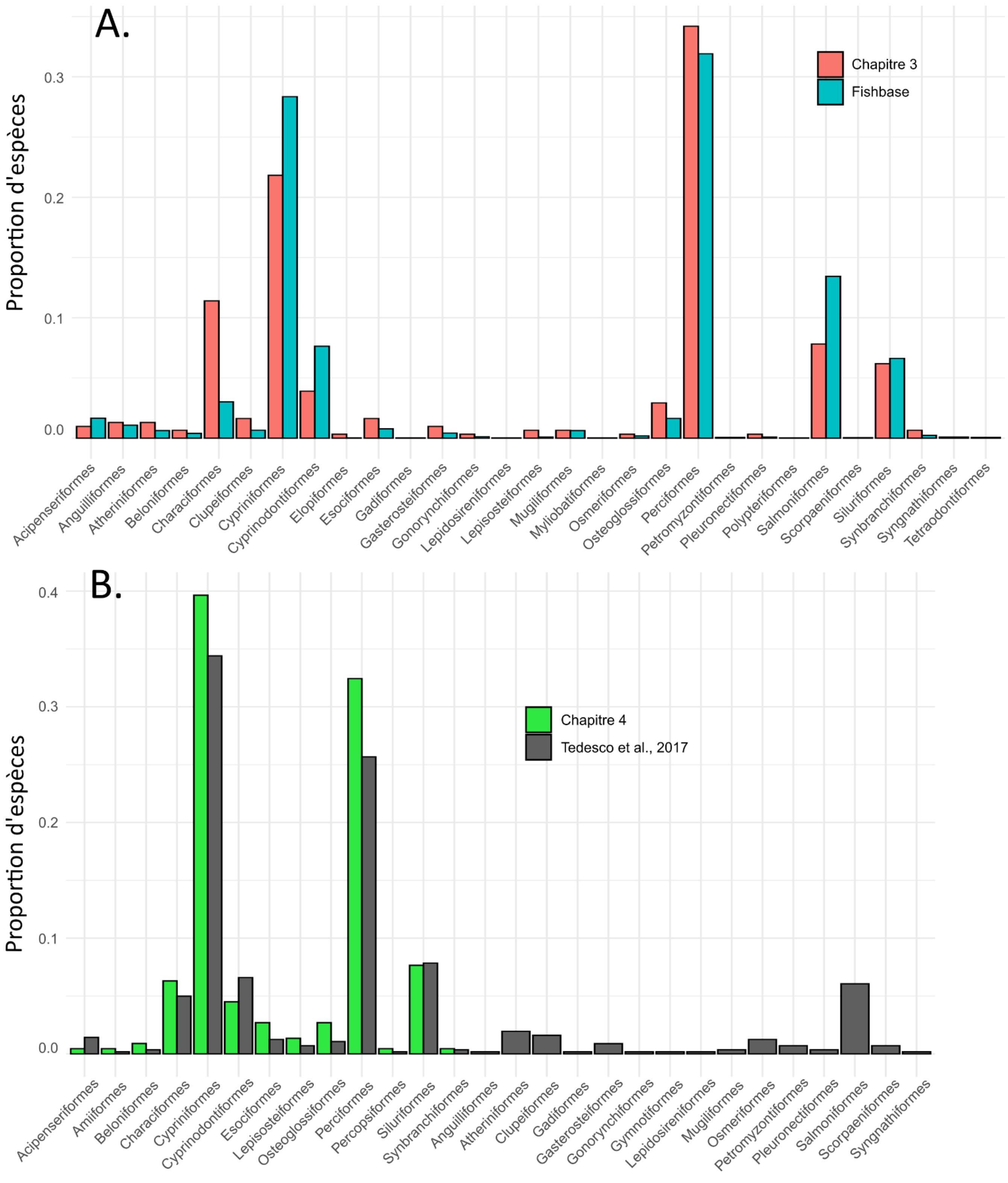


Figure 11 : Proportion de chaque ordre dans les espèces considérées A) dans les analyses du Chapitre 3 (rouge, N=307) et dans les espèces considérées comme introduites dans FishBase (Bleu, N=4238) (Froese & Pauly 2019) et B) dans la base de données de Tedesco et al. (2017) (gris, N=605) et dans les analyses du Chapitre 4 (vert, N=222).

6.4.2. Biais spécifiques

Les espèces ayant beaucoup d'impacts ont tendance à être plus étudiées, et à disposer d'un plus grand nombre de données disponibles (Pysek et al., 2008). En effet, nous pouvons remarquer dans la Figure 11 que les ordres composés d'espèces ayant beaucoup d'impacts (*i.e.*, les Perciformes et Cypriniformes, qui sont les ordres avec le plus d'impacts renseignés dans GISD, Annexe 9) sont les plus renseignés pour les caractéristiques que nous avons considérées dans les Chapitres 3 et 4. Ainsi, elles sont surreprésentées dans les analyses du Chapitre 4 par rapport aux espèces exotiques présentes dans la base de Tedesco et al. (2017). Il en est de même pour les Characiformes. Ceci peut être dû au fait que les Characiformes sont des poissons tropicaux d'aquarium charismatiques et sont donc mieux étudiés que d'autres espèces moins charismatiques. Au contraire, certains ordres sont sous-représentés dans nos études par rapport à leur présence dans les bases de données, et correspondent aux ordres des Cypriniformes, des Salmoniformes et des Siluriformes (Fig. 11). Ce déficit de données est potentiellement dû au fait que les habitats de ces espèces sont difficiles à échantillonner, comme c'est le cas par exemple pour les Siluriformes, qui vivent dans des canaux profonds et prairies flottantes (Miqueleiz et al. 2020). De plus, ces espèces ne font pas partie des espèces de poissons les plus charismatiques, ce qui influe aussi sur la disponibilité de leurs données (Jarić et al. 2020b). Par conséquent, les ordres considérés dans nos études ne sont pas le reflet exact des tendances d'établissement et d'introduction des espèces. Les caractéristiques des ordres surreprésentés (*e.g.*, Characiformes, Perciformes) risquent ainsi d'avoir plus d'importance dans nos modèles que si l'on considère un échantillon représentatif. Une solution pour éviter ce biais serait de rééchantillonner les espèces de manière aléatoire afin de correspondre à la distribution initiale, mais cette solution implique une perte de pouvoir statistique pour les analyses.

6.4.3. Biais liés aux caractéristiques considérées pour construire les profils d'espèces exotiques

Dans les Chapitres 3 et 4 nous utilisons la variation de la température et des précipitations dans le milieu natif comme approximation de la tolérance physiologique des espèces exotiques. Toutefois, nous sous-estimons surement grandement cette tolérance physiologique. En effet, il a été montré que la niche climatique réalisée dans l'aire native n'était pas le reflet de la niche fondamentale des espèces (Broennimann et al. 2007 ; Frederico et al. 2019). Par exemple, une espèce de poissons-chat (*Pterygoplichthys ambrosettii*) a vu sa niche climatique réalisée s'étendre de 27% dans son aire exotique (Frederico et al. 2019). Ainsi, l'influence des variables de variation de la température et des précipitations a probablement été sous-estimée dans nos modèles.

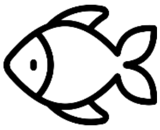
Dans cette thèse, nous considérons les caractéristiques à l'échelle spécifique, les caractéristiques morphologiques étant mesurées sur des individus adultes et considérées comme étant les mêmes pour toute l'espèce (Brosse et al. 2021b). Or, les caractéristiques des espèces peuvent différer au cours de leur développement, mais aussi entre les individus et les populations d'une même espèce (Cope et al. 2022). Une étude sur 97 mammifères introduits a montré que la variation intraspécifique des caractéristiques morphologiques, en particulier concernant la masse à l'âge adulte, était associée au succès d'établissement (González-Suárez et al. 2015). Chez les poissons, Zhao et al. (2019) ont aussi mis en avant l'importance de la variation intraspécifique pour caractériser la diversité fonctionnelle des communautés de poissons exotiques, car certaines différences intraspécifiques sont plus grandes que les différences entre espèces. En effet, la probabilité pour que certaines voies d'introduction soient empruntées par les poissons pourrait varier suivant leur stade de développement (Mandrak & Cudmore 2010; Wonham et al. 2000). Par exemple, les introductions par eaux de ballast et par contamination des espèces d'aquaculture sont surtout effectives pour des poissons de petites taille, donc dans leurs premiers stades de développement (Mandrak & Cudmore 2010; Wonham et al. 2000). Ainsi, pour certains traits tels que la taille, il serait intéressant de tenir compte de cette variabilité intraspécifique. Cependant, à grande échelle, il est extrêmement difficile d'obtenir de telles données, limitant les études possibles à mener sur ce plan.

6.5. Conclusion générale

Le but de cette thèse était de synthétiser les principaux aspects des invasions biologiques de poissons d'eau douce, et d'utiliser ce travail de synthèse pour déterminer les facteurs influençant le succès de ces invasions à l'échelle globale. Au final, cette thèse permet de souligner l'importance des travaux à larges échelles pour étudier les invasions biologiques. Nous avons ainsi synthétisé la littérature actuelle concernant les voies d'introduction, les facteurs influençant le succès des invasions, les impacts (avec une focalisation particulière sur les coûts économiques à l'échelle globale), et enfin les plans de gestions mis en place pour limiter ces impacts. La vision globale des invasions de poissons d'eau douce permise par ces synthèses a pu mettre en avant le fait que ces invasions, au vu de leur importance, sont un sujet nécessitant plus d'effort de recherche. Par exemple, il existe des biais spatiaux et des manques de données conséquents dans les bases de données utilisées et dans les études publiées, et certains aspects de ces invasions manquent d'exploration. Ainsi, au travers de recommandations fournies, cette thèse pourra permettre de guider les futures questions essentielles à traiter en recherche sur les invasions de poissons d'eau douce. En suivant ces recommandations, cette thèse s'est attachée à déterminer les caractéristiques influençant le succès d'invasion en prenant en compte un grand nombre d'espèces, de types de caractéristiques, et en explorant différentes étapes de l'invasion, le tout à l'échelle macro-écologique. Cette échelle globale est importante pour tenir compte de différents aspects des invasions, que ce soit les caractéristiques des espèces, socio-économiques ou écologiques, les étapes de l'invasion, ou même les différentes dimensions au sein même d'une étape d'invasion. Nous avons par exemple démontré que les profils des poissons exotiques sont différents suivant l'étape de l'invasion, mais aussi suivant la voie d'introduction utilisée. Ces profils peuvent aussi différer au sein même d'une étape. Ainsi, les poissons exotiques réussissant à s'établir ont des profils différents suivant différentes dimensions de l'établissement, telles que le nombre de bassins établis et leur localisation (en dehors ou dans la biorégion native). Les espèces étant établies dans un grand nombre de bassins et en dehors de leur région native, c'est-à-dire des espèces vraisemblablement avec de forte capacité d'établissement, ont des caractéristiques qui diffèrent des espèces avec de faibles capacités d'établissement. Ces méthodes à larges échelles et la considération simultanée d'un grand nombre d'espèces, de différentes voies d'introduction et étapes d'invasion, ainsi que de nombreux facteurs écologiques, spécifiques, et socio-économiques, permettent l'exploration des synergies entre les différents facteurs et l'identification de tendances qu'il n'aurait pas été possible de mettre en avant à l'échelle locale. Elles constituent une approche originale, encore jamais utilisée auparavant pour étudier les caractéristiques influençant les invasions de poissons d'eau douce, ni, à ma connaissance, pour aucun autre groupe taxonomique d'espèces envahissantes, ouvrant la voie à de nouvelles perspectives de recherche à explorer à l'échelle globale.

6.6. Conclusion personnelle

L'apport à la science de cette thèse est une chose, mais j'aimerais également m'étendre sur l'apport personnel que cette expérience a eu dans ma vie. La thèse est une expérience dont l'équivalent ne peut être retrouvé dans aucun autre domaine. Entre étudiant et salarié, elle est souvent mal comprise par mon entourage, et associée à une image négative de l'étudiant en *burn-out*. Pourtant, la thèse est une expérience de recherche exceptionnelle, avec une grande diversité de tâches à accomplir et de compétences à développer. J'ai ainsi pu travailler avec un réseau de collègues du monde entier, mener des équipes sur des projets, voyager dans des endroits que je n’avais jamais vu auparavant, partager mes connaissances mais aussi bénéficier de celle des autres, présenter mes travaux devant des centaines d’experts du sujet et m’en sentir fière, échanger avec des gens intéressants aussi bien sur le plan scientifique qu’humain, découvrir comment j’aimais travailler, contribuer aux connaissances scientifiques du monde entier, et j’en oublie sûrement. Afin de présenter tous ces aspects positifs, souvent oubliés en faveur des aspects négatifs, j’ai publié en première co-autrice un article mettant en avant les dimensions positives de la thèse (Bernery et al. 2022b; Annexe 10).



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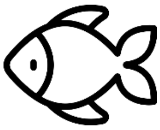

ANNEXES

Annexe 1

C. Bellard, **C. Bernery**, C. Leclerc (2021). Looming extinctions due to invasive species: Irreversible loss of ecological strategy and evolutionary history. *Global Change Biology*, 27(20), 4967-4979.

Implication dans le projet : J'ai procédé aux analyses statistiques et à l'interprétation de la partie du projet portant sur les comparaisons traits à traits entre les espèces menacées par les invasions biologiques, les espèces menacées par d'autres menaces, et l'ensemble des espèces.

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PRIMARY RESEARCH ARTICLE

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Looming extinctions due to invasive species: Irreversible loss of ecological strategy and evolutionary history

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Abstract

Biological invasions are one of the main drivers of biodiversity decline worldwide. However, many associated extinctions are yet to occur, meaning that the ecological debt caused by invasive species could be considerable for biodiversity. We explore extinction scenarios due to invasive species and investigate whether paying off the current extinction debt will shift the global composition of mammals and birds in terms of ecological strategy and evolutionary history. Current studies mostly focus on the number of species potentially at risk due to invasions without taking into account species characteristics in terms of ecological or phylogenetic properties. We found that 11% of phylogenetic diversity worldwide is represented by invasive-threatened species. Furthermore, 14% of worldwide trait diversity is hosted by invasive-threatened mammals and 40% by invasive-threatened birds, with Neotropical and Oceanian realms being primary risk hotspots. Projected extinctions of invasive-threatened species result in a smaller reduction in ecological strategy space and evolutionary history than expected under randomized extinction scenarios. This can be explained by the strong pattern in the clustering of ecological profiles and families impacted by invasive alien species (IAS). However, our results confirm that IAS are likely to cause the selective loss of species with unique evolutionary and ecological profiles. Our results also suggest a global shift in species composition away from those with large body mass, which mostly feed in the lower foraging strata and have an herbivorous diet (mammals). Our findings demonstrate the potential impact of biological invasions on phylogenetic and trait dimensions of diversity, especially in the Oceanian realm. We therefore call for a more systematic integration of all facets of diversity when investigating the consequences of biological invasions in future studies. This would help to establish spatial prioritizations regarding IAS threats worldwide and anticipate the consequences of losing specific ecological profiles in the invaded community.

KEYWORDS
extinction risk, invasive species, phylogenetic diversity, scenarios, trait diversity

1 | INTRODUCTION

Invasive alien species (IAS) are considered to be the second most important cause of worldwide extinctions (Bellard, Genovesi, et al., 2016; Gurevitch & Padilla, 2004; Maxwell et al., 2016). Invasive predators alone have contributed to 58% of modern extinctions (Doherty et al., 2016). Most of these extinctions occurred on islands, but mainland areas also suffer from the presence of IAS (Bellard, Cassey, et al., 2016; Clavero et al., 2009). The global threat of species invasions continues to increase with the spread of new emerging invaders (Seebens et al., 2017, 2018).

Over the past decades, several review articles and global analyses have investigated the ecological impact of IAS, ranging from local population declines to global extinctions (Lapiedra et al., 2015; McCreless et al., 2016). However, most studies focus on the number of species prone to extinctions without taking into account species characteristics in terms of ecological or phylogenetic properties, even though all three facets (taxonomic, phylogenetic, and trait) are advocated as essential for conservation (Mazel et al., 2014). Indeed, phylogenetic and trait diversity (TrD) provide a more direct link to ecosystem properties compared to species diversity (e.g., Cadotte et al., 2008; Sekercioglu, 2006). Extinctions and population declines are not random, and as a result, they are more likely to be associated with specific lineages or ecological profiles (i.e., combinations of morphological, phenological, or behavioral features; Cooke et al., 2019; Davis et al., 2018; Pavoine et al., 2019).

Previous assessments showed that climate change may lead to uncompensated phylogenetic or functional losses, causing further biotic homogenization (Buisson et al., 2013; Thuiller et al., 2011), although this has not yet been explored in the context of biological invasions. In other words, the manner in which species extinctions due to IAS affect the ecological and evolutionary dimensions of biodiversity mostly remains an open question (but see Lapiedra et al., 2015; Longman et al., 2018; Sunday et al., 2015). This issue is particularly important, as shown by the recent surge in interest among international experts of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), who advocated that including ecological and phylogenetic components of biodiversity is essential in biodiversity assessments (IPBES, 2019).

Moreover, taxonomic diversity often fails to capture phylogenetic and ecological diversity (Devictor et al., 2010; Leclerc et al., 2020; Mazel et al., 2014); it is thus highly important to consider multiple dimensions of diversity when providing recommendations on spatial conservation priorities (Brum et al., 2017; Pollock et al., 2017). Indeed, biodiversity is a multifaceted concept, and the emerging consensus is that a macro-ecological approach is needed to understand the impact of IAS worldwide. With increasing information about the phylogenetic and life-history traits of species, it is now possible to conduct such an assessment and provide a clear picture of the consequences of IAS on multiple dimensions of diversity.

A critical aspect of biodiversity assessments is thus to identify and characterize the diversity elements most likely to go extinct, thus inferring the future state of biodiversity. Here, we aim to provide such an assessment of at-risk biodiversity related to biological invasions with a focus on the trait and phylogenetic diversity (PD) of birds ($n = 8113$) and mammals ($n = 4804$). TrD represents how species are distributed in a multidimensional niche space and provides a way to assess the ecological strategy adopted by species. We measured the amount of trait space occupied by invasive-threatened species compared to the global pool worldwide following the methodology of Villéger et al. (2008) based on five ecological traits (Table 1). In other words, for TrD, we calculate how much of the total trait space is occupied by invasive-threatened mammals and birds. PD captures the evolutionary history of species (Pavoine et al., 2011) and potentially the species contribution to feature diversity (Faith, 1992). We measured the amount of evolutionary history represented by invasive-threatened species at a global scale for both birds and mammals. We expect that species losses due to IAS may result in the loss of ecosystem functions and/or adaptive features, which are indispensable in a changing environment. We also investigate the contribution of invasive-threatened birds and mammals to the total PD and TrD in different realms. Because all invasive-threatened species are unlikely to go extinct in the near future, we further investigate extinction scenarios related to IAS worldwide. We specifically explore the potential level of phylogenetic and ecological erosion in IAS extinction scenarios over the next 50 and 100 years as well as under randomized extinction scenarios. Finally, we determine the ecological profiles and species families most likely to be lost because of IAS.

2 | METHODS

2.1 | Species studied

We used the IUCN Red List of Species to identify the species considered to be the most threatened by IAS (Version 3, accessed in August 2019). We considered species classified as critically endangered (CR), endangered (EN), vulnerable (VU), near-threatened (NT), or least concern (LC) by the IUCN Red List. We focused on the threatened species defined by the IUCN (CR, EN, and VU) for which IAS are listed as a threat (hereafter, invasive-threatened) and excluded NT and LC species, which only represent "potentially threatened" species for two reasons. Therefore, we filtered out species for which IAS is listed as a future threat or when the threat is due to a problematic species/disease (including viral or prion) of unknown origin or native. First, we want to focus our analyses on the threatened species (CR, EN, and VU) facing imminent extinctions so as to be conservative in our study following the methodology of Toussaint et al. (2016). Second, IUCN only assigns a specific extinction probability to VU, EN, and CR. No quantitative analyses of the probability of extinction are required for NT or LC, while the latter category does not specify the major threat faced, which will add uncertainty to our analyses of the IAS threat (IUCN, 2012). Moreover, we focused our analysis on the most comprehensively assessed vertebrate groups by the IUCN: birds and mammals (Meiri & Chapple, 2016). This resulted in a total of 207 invasive-threatened mammals out of 5708 mammals assessed by the IUCN Red List and 499 invasive-threatened birds out of 10,965 birds (IUCN, 2017). Note that it is impossible to disentangle the effects of IAS from other threats. IAS threat is mostly associated with biological resource use and agriculture. In fact, the vast majority of species threatened by IAS are also likely to be threatened by other threats with an average of 3.9 threats co-occurring for IAS-threatened birds and mammals; thus, IAS-threatened species are species for which IAS is listed as a threat, although other threats might also occur. In fact,

TABLE 1 Description of the traits used to measure the trait diversity of birds and mammals as well as their modalities

Trait	Modality (Abbr.)	Taxa concerned
Main diet	Plant material and seeds (Plant-seeds)	B, M
	Fleshy fruits and nectar (Fruits-nect)	B, M
	Invertebrates (Invert)	B, M
	Vertebrate prey and carrion (Vert)	B, M
	Omnivore (Mixed)	B, M
	Mixed herbivore (Main veg)	B, M
	Mixed animal (Main ani)	B, M
Foraging strata	Water (W)	B
	Ground level (G)	B
	Understory (U)	B
	Mid-high (Mi)	B
	Canopy (Ca)	B
	Aerial (A)	B
	Multiple strata (Mult)	B
	Scansorial (S)	M
	Ground level (G)	M
	Marine (M)	M
	Arboreal (Ar)	M
	Aerial (A)	M
Period of activity	Crepuscular (C)	M
	Diurnal (D)	B, M
	Nocturnal (N)	B, M
	Crepuscular/Diurnal (CD)	M
	Crepuscular/Nocturnal (CN)	M
	Crepuscular/Diurnal/Nocturnal (CDN)	M
Habitat breadth	Number of habitats used	B, M
Body mass	Very small (Vsmall)	B, M
	Small	B, M
	Medium	B, M
	Large	B, M
	Very large (Vlarge)	B, M

837 mammals and 736 birds are threatened by other threats. We also used the mechanisms documented for each invasive-threatened species based on the IUCN information (e.g., competition, hybridization, reduced reproductive success, species mortality, and ecosystem degradation) to assess the contribution of each mechanism to the potential loss of PD and TrD. We considered the top three mechanisms for both birds and mammals, which represent more than 80% of all mechanisms documented for each taxon. We considered species mortality, competition, and ecosystem degradation for mammals and ecosystem degradation, species mortality, and reduction in reproductive success for birds. We considered each mechanism when cited alone or in association with another mechanism. Therefore, our indicator of mechanisms represents the documented occurrences of a given mechanism for each species. We also used the realm associated with each species extracted from the IUCN database to conduct analyses at the realm scale (i.e., Afrotropical, Australasian, Indomalayan, Neartic, Neotropical, Oceanian, and Paleartic).

2.2 | TrD analysis

To quantify TrD associated with invasive-threatened species, we used the five following traits: body size, habitat breadth, foraging strata, main diet, and period of activity (Table 1 for modalities), which are associated with the key ecological strategies of species (e.g., carcass removal, seed dispersal, soil fertility, and pollination; Sekercioglu, 2010; Hevia et al., 2017; see also Appendix S3). All traits were extracted from the Elton trait database (Wilman et al., 2014) except for habitat types, which were taken from the IUCN habitat classification scheme (version 3.1). Main diet category for mammals is based on the majority of diet consumed by each species, with a 50% threshold (following Wilman et al., 2014). For instance, the mixed herbivore category represents all species whose diet consists of more than 50% of plant material, seeds, fleshy fruits, and nectar. The omnivore (mixed) category includes all species that are 50% mixed herbivore and 50% mixed animal. Foraging strata category for birds is based on the location of the different items consumed by each species with a 50% threshold (following Wilman et al., 2014). If the foraging strata include several categories, we kept the foraging strata represented by more than 50% of the whole foraging strata; and if there is no main foraging stratum represented by more 50%, it is designated as "multiple." Body mass category for birds and mammals is based on their respective quantiles with the very large category representing the largest 20% of species. Overall, we extracted trait data for 4804 mammals, including 186 invasive-threatened mammals, and 8113 birds, including 360 invasive-threatened birds (Figure S2). The two continuous variables (i.e., main diet and body size) were categorized as discrete variables following the method of Leclerc et al. (2020; see also Table 1 for details).

To compute and investigate TrD for each invasive-threatened species assemblage, we followed different steps:

(i) First, we grouped species as ecological entities, which represent groups of species sharing the same trait values (Table 1), methodology that has been successfully applied in functional analyses (Keyel & Wiegand, 2016; Mouillot et al., 2014). This step allowed us to calculate trait vulnerability, which is related to the number of species included in each ecological entity. Trait vulnerability is high when ecological entities have a small number of species and low when ecological entities host a high number of species, which indicates high redundancy.

(ii) To build the trait space, we also calculated pairwise trait distances using the Gower metric, which allowed us to deal with data of mixed types (Pavoine et al., 2009). We then used principal coordinate analysis (PCoA) on the trait distance matrix to build a multidimensional trait space, where the position of ecological entities corresponds to their differences. We selected the best functional space by choosing the number of PCoA axes that provided the most faithful representation of the initial functional trait values. In other terms, we selected the number of axes that minimized the mean squared-deviation metric (i.e., average deviation between Euclidean distance and Gower distance; Maire et al., 2015), which allowed us to compute the indices in a reasonable timeframe. In this study, we selected five axes for mammals, which represent an average error of 3.6% (average deviation between original and transformation data) and three axes for birds, which had an average error of 5.6%, indicating functional spaces of high qualities.

(iii) Based on these trait spaces for birds and mammals, we calculated TrD (more commonly known as functional richness following the definition of Villéger et al., 2008), which represents the volume of trait space occupied by invasive-threatened species within the PCoA compared to the total pool of species. This metric is widely applied in functional studies (Leclerc et al., 2020; Mouillot et al., 2014; Toussaint et al., 2016). It has been demonstrated as the best performing index and is highly correlated to other functional diversity measures (Mouchet et al., 2010). This step was also conducted at the realm scale.

(iv) We also performed statistical analyses to compare the trait modalities associated with invasive-threatened species and those associated with either non-invasive-threatened species worldwide and species threatened by threats other than IAS (i.e., other-threatened species). Specifically, we compared the trait distributions of invasive-threatened species with a random sample (with replacement) of an equal number of species that are not invasive-threatened within the global pool (999 repetitions). We also compared the trait distributions of invasive-threatened species with a random sample of an equal number of other-threatened species within the global pool. These two comparisons allowed us to disentangle whether the trait modalities were specific to the invasive threat or whether there were related to threatened species (Table S1).

To test the significance of the results, we applied Chi-squared tests when the number of species in each modality was ≥5 for all the samples. Otherwise, a Fisher's exact test was used. If at least 95% of tests had a $p < 0.05$, the two distributions were considered to significantly differ. We repeated the same analyses for both mammals and birds.

2.3 | PD analyses

To compute PD hosted by invasive-threatened species, we used the PHYLACINE 1.2 complete phylogeny by Faurby et al. (2018) for mammals. This built phylogeny relies on the morphological and genetic data of 5831 known mammal species that have lived since the last interglacial period. It also contains 1000 trees that represent the uncertainties in topology and branch lengths. We also verified species synonyms using the rl_synonyms() functions in the rredList package (Chamberlain, 2019), and we pruned the original phylogenetic tree ($n = 5831$) to the species of the IUCN Red List included in the tree for mammals. In total, 5529 species, including 205 invasive-threatened species, were included in the phylogenetic trees (Figure S1 for the sample size of each analysis). For birds, we used the tree version (V2.iii, Ericson backbone) with the complete phylogeny of Jetz et al. (2014) and extracted 1000 trees. The built phylogeny combines the relaxed clock molecular trees of well-supported avian clades with a fossil-calibrated backbone with representatives from each clade. Similar to mammals, we also searched for synonyms and pruned the original phylogenetic tree to 8,113 birds, including 360 invasive-threatened species (Figure S1). Then, to measure PD associated with invasive-threatened species for both mammals and birds, we used the Faith Index (using the pd() function of the picante package; Kembel et al., 2010) and calculated the average PD across the 1000 trees. Ultimately, we calculated the percentage for the invasive-threatened species PD value compared to the total PD value of the sample to compare between taxa. We also conducted PD analysis for each realm.

2.4 | Null model analyses for both phylogenetic and TrD measures

For both mammals and birds, we tested whether the observed values of TrD were significantly different from the null hypothesis that species are randomly distributed into ecological entities. We used null models here to examine whether TrD values are related to the number of species or to the ecological profile of species. In each invasive-threatened sample, we simulated a random assignment of species to ecological entities while ensuring that each ecological entity has at least one species. We simulated 999 random assemblages while keeping the number of species and ecological entities constant.

We also randomized the phylogenetic information between the invasive-threatened species for both mammals and birds. For this purpose, we considered a constrained null model that randomizes the names of taxa to the phylogeny. Thus, it randomizes which species are most closely related to each other, although it does not alter the actual branch lengths or their distributions. The rationale for this null model is to investigate whether the species at risk of extinction due to IAS are more closely related than expected randomly given their number. The randomization was repeated 999 times over 1000 trees each time.

More specifically, we calculated the deviation from the null expectation by computing the standardized effect size (SES) and associated p value. SES represents the difference between the observed values of TrD or PD and the mean of predicted values by the null model divided by the standard deviation of predicted values. The significance of the difference between observed values and null expectations was tested using a bilateral test at a level of 5%. In short, an observed value is considered significantly different from null expectations if the observed value is in the top or bottom 2.5% of the null expectation distribution.

2.5 | Projected extinction scenarios

We considered two extinction scenarios based on the IUCN Red List categories over the next 50 and 100 years. The IUCN Red List designed probabilities of extinctions for the three threatened categories that are evaluated under criterion E: Prob(ext)CR = 0.5 in 10 years, Prob(ext)EN = 0.2 in 20 years, and Prob(ext)VU = 0.1 in 100 years (Mooers et al., 2008). Based on these probabilities of extinction, in the first scenario (50 years), we assigned a probability of extinction for all species (even if there are not evaluated under criterion E) of 97% for CR invasive-threatened species, 42% for EN, and 5% for VU following Cooke et al. (2019) and Mooers et al. (2008) Similarly, the probability of extinction under the second scenario (100 years) was 99% for CR invasive-threatened species, 66.7% for EN, and 10% for VU following Mooers et al. (2008). The randomized extinction scenario assigned an equivalent number of species that were predicted to go extinct (from the global pool) over the next 50 and 100 years but randomly with respect to species identity and traits (Cooke et al., 2019). All three extinction scenarios (100 years, 50 years, and random) were each repeated 999 times. Finally, we compared the potential level of phylogenetic and ecological erosion obtained under both scenarios with that obtained from a randomized extinction scenario.

We used R version 3.6.1 to conduct the analyses and the ggplot2 package to plot the figures (Wickham, 2016).

3 | RESULTS

3.1 | Trait and PD hosted by invasive-threatened species worldwide and within realms

Our results showed that invasive-threatened birds occupy 40% of the total trait space (TrD) for birds worldwide. By contrast, invasive-threatened mammals represented only 14% of the total trait space for mammals (Table 2). The contribution of invasive-threatened species to the total PD worldwide was 10.2% for mammals and 11.4% for birds. In all cases, the PD values for invasive-threatened mammals and birds were significantly lower than expected given the number of species (SES = –7.294 and $p > 0.99$ for mammals, and SES = −4.542 and $p > 0.99$ for birds). Similarly, TrD values were significantly lower than expected given the number of species (SES = −4.177 and $p > 0.99$ for mammals and SES = −3.672 and $p > 0.99$ for birds). Both diversity metrics were thus more clustered than expected under the null scenario.

We also calculated diversity measures for the top three mechanisms associated with invasive-threatened species (Figure 1). We found that the contribution of invasive-threatened birds worldwide to TrD and PD was largely driven by ecosystem degradation (36.8% for TrD and 11.1% for PD) and mortality induced by IAS. The reduction in reproduction success was also an important mechanism associated with the potential loss of TrD and PD in birds worldwide. Conversely, the contribution of invasive-threatened mammals to TrD and PD worldwide was mostly driven by mortality (12.05% for TrD and 8.8% for PD) induced by IAS, whereas competition and ecosystem degradation were less likely to lead to mammal TrD losses.

By analyzing the diversity represented by invasive-threatened birds and mammals for each realm, we found clear spatial differences (Figure 2). The contribution of invasive-threatened birds located in the Oceanian realm to the total bird TrD worldwide is nearly 30%. The contributions of invasive-threatened birds in the Afrotropical and Neotropical realms to total bird TrD was also high with 20% and 17%, respectively, whereas the contribution of invasive-threatened mammals in the Neotropical realm to total mammal TrD was only 4%. We found that all the realms showed low PD values for invasive-threatened mammals (0.7%–4.2%) and birds (0.93%–5.4%). In addition, we found an average of 1.4 invasive-threatened species for each ecological entity (groups of species sharing the same combinations of traits) for mammals and 1.2 for birds within realms, while we estimated 6.8 species per ecological entity in the rest of the species sample for mammals and 13.7 for birds.

3.2 | Extinction scenarios of invasive-threatened species compared to random scenarios

Because all the invasive-threatened species are unlikely to go extinct in the near future, we considered extinction scenarios following the methodology of Cooke et al. (2019). On average, 6.5%–7.7% of worldwide PD associated with invasive-threatened mammals is

TABLE 2 Trait and phylogenetic diversity observed in worldwide invasive-threatened mammals and birds with their standardized effect size (SES) and *p* value with significative figures are indicated with ***

Taxa	Type of diversity	Observed (%)	Expected under null scenario (%)	SES	*p* value
Mammals	Trait	14.0	37.9	−4.177	>0.999***
	Phylogenetic	10.2	14.6	–7.294	>0.999***
Birds	Trait	40.1	67.1	−3.672	>0.999***
	Phylogenetic	11.4	12.9	−4.057	>0.990***

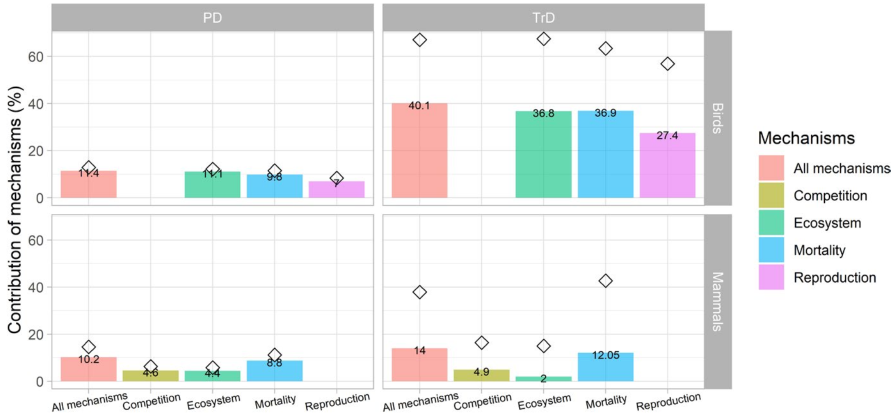

FIGURE 1 Contribution of the mechanisms (i.e., all mechanisms, competition, ecosystem degradation, mortality, and/or reduction in reproduction success) impacting invasive-threatened species to the total bird (or mammal) trait (TrD) and phylogenetic diversity (PD) in percentage. We only considered the top three mechanisms for each taxon. Bar plots represent the observed values of diversity, while the diamonds represent the null models (expected values when species identity is randomized)

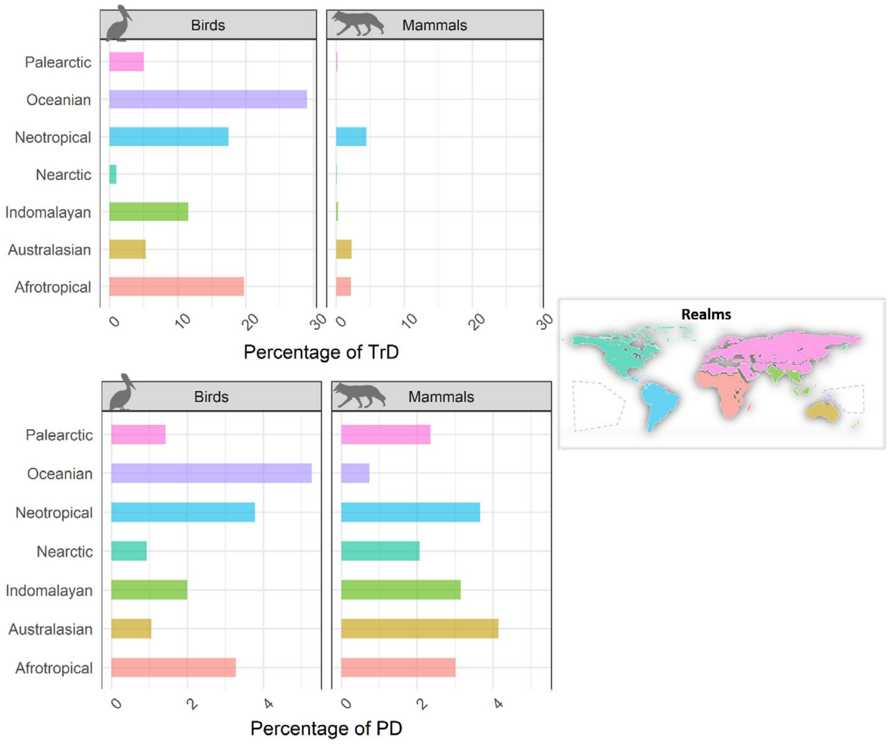

FIGURE 2 Contribution of invasive-threatened species located in each realm to the total bird (or mammal) diversity for both trait (TrD) and phylogenetic diversity (PD)

expected to be lost over the next 50–100 years, while the percentage is slightly higher under the randomized extinction scenarios for mammals (7.7%–9.3%). Loss of PD worldwide for birds is projected to be of a similar order of magnitude with 6.1%–7.2%, which is also slightly lower compared to randomized extinction scenarios (6.5%–7.8%). The potential loss is more pronounced for TrD, which may reach 5.8%–7.8% for mammals (11.3%–15.0% under the randomized extinction scenarios) and 27.4%–30.6% for birds worldwide (32.5%–36.3% under the randomized extinction scenarios) over the next 50–100 years due to IAS. In all cases, the potential loss of both facets of diversity (PD and TrD) induced by IAS is lower than expected given the species richness under the random extinction scenarios (Figure 3).

3.3 | Profile of species at risk of extinctions

We further analyzed the phylogenetic and ecological properties of invasive-threatened species for both mammals and birds and compared them to the characteristics of the pool of non-invasive-threatened species (hereafter, global pool) and species threatened by threats other than IAS. We found that the 186 invasive-threatened mammals represent 109 ecological entities (groups of species sharing the same combinations of traits, with 14 ecological entities exclusively represented by invasive-threatened mammals and not found in the global pool; Table S1). Four families were comprised exclusively of species threatened by IAS, although other threats may also be involved: Solenodontidae, Myrmecobiidae, Phascolarctidae, and Thylacomyidae. Muridae and Cricetidae were the most represented families among invasive-threatened mammals as well as among the global pool of mammals. Similarly, the 360 invasive-threatened birds represented 149 ecological entities (including 10 ecological entities exclusively hosted by invasive-threatened birds), which belong to 92 families, including five families (i.e., Balaenicipitidae, Strigopidae, Rhynochetidae, Notiomystidae, and Pedionomidae) that were exclusively found in the invasive-threatened pool. The two most represented families within invasive-threatened birds were Procellariidae and Psittacidae, although they were, respectively, ranked 59th and fourth when considering the global pool of birds.

A closer investigation of the ecological profile of invasive-threatened species revealed that mammals were represented by mostly large to very large species (68%), specialists with only one or two habitats (65%), only nocturnal species (61%), those feeding on the ground (76%), and those with a primarily or exclusively herbivorous diet (62%; Figure 4; see also Table S2). We observed some significant differences with the global pool of mammals regarding foraging strata (i.e., species were mostly aerial in the global pool), diet regime (species mostly feed on invertebrates) and body size (species have a very small body size; Figure 4; see also Table S4) while significant differences were also detected for the period of activity and habitat breadth when compared to other-threatened species (see Figure 4 and Table S4). We found a significantly higher percentage of ground-foraging species within invasive-threatened mammals compared to both the global pool and the other-threatened species pool (Figure 4). By contrast, invasive-threatened mammals were significantly less represented in the arboreal foraging strata compared to the global pool and the other-threatened pool of mammals. Our results also revealed that invasive-threatened species were less likely to be diurnal and less likely to be specialized to one habitat compared to other-threatened species. In addition, it appears that invasive-threatened mammals were significantly more represented among very large species and significantly less among very small species in comparison with the global pool, although these characteristics were not specific to invasive-threatened species, as other-threatened species were also very large species. Finally, our results also revealed that invertebrate diets were less represented among invasive-threatened mammals compared to the global pool (Figure 4). This was also the case with other-threatened species, although the difference was not statistically significant.

Invasive-threatened birds were mostly large to very large species (63%) and habitat specialists with three or less habitats (81%); the majority foraged in multiple strata (57%) were active during the day (97%), and mostly fed on animals (41%; Figure 5; see also Table S3). Again, invasive-threatened species had similar ecological characteristics compared to the rest of the species pool but with a few notable exceptions (Figure 5; see also Tables S6 and S7). For instance, a significantly higher percentage of invasive-threatened birds forages below the water surface compared to both the global pool and the other-threatened species pool while a significantly lower percentage forages in multiple strata compared to the other samples (Figure 5). Invasive-threatened species were also significantly less represented among very small species compared to both the global pool and the other-threatened species pool (Figure 4). Moreover, we also observed that invasive-threatened species mostly feed on animals. We also found that invasive-threatened birds were less likely to be habitat specialists compared to other-threatened species and more likely to live in three or four habitats, although we did not detect such differences when comparing these results to the global pool (Table S6 and S7).

4 | DISCUSSION

Our results highlight the global contribution of invasive-threatened species to biodiversity worldwide and illustrate the magnitude of the extinction debt related to biological invasions. As such, our results reveal that biological invasion is potentially a major threat to both the phylogenetic and TrD of birds and mammals worldwide. The contribution of invasive-threatened birds and mammals to the total PD reaches 11%. Moreover, invasive-threatened birds represent 40% of the total trait space for birds, which is considerable given the number of invasive-threatened birds worldwide (~4.5% of all known birds). Our results confirm that birds are more vulnerable to biological invasions compared to mammals (Bellard, Cassey, et al., 2016; Bellard, Genovesi, et al., 2016), not only in terms of the number of species at risk of extinction but also in terms of ecological and evolutionary diversity. Given the role of birds for ecosystem services such as pollination, seed dispersal, predation, and/or food-web structure (Sekercioglu, 2010; Sekercioglu et al., 2008), we expect that these losses will have important implications in the near future. Our results contrast with the recent assessment of the IPBES, which ranks IAS as one of the last drivers of change among global change components in the global state of nature (IPBES, 2019). We demonstrate that it is crucial not to overlook biological invasions as a top driver of biodiversity loss given the potential extinction debt. Note that on average, 3.9 threats were associated with invasive-threatened species (Appendix S1). We observed that biological resource use or agriculture and aquaculture are often associated with IAS threats for both birds and mammals (see also Leclerc et al., 2018, 2020 for insular ecosystems). In this context, our results suggest that IAS associated with these two threats may lead to an important ecological and evolutionary debt worldwide.

Because all the species threatened by IAS are unlikely to disappear, we also conducted 50- and 100-year extinction scenarios to provide an initial approximation of the potential cost of the current extinction debt due to biological invasions while considering only the imminent extinctions. The potential losses might be tremendous with around 7% of PD worldwide for both mammals and birds as well as

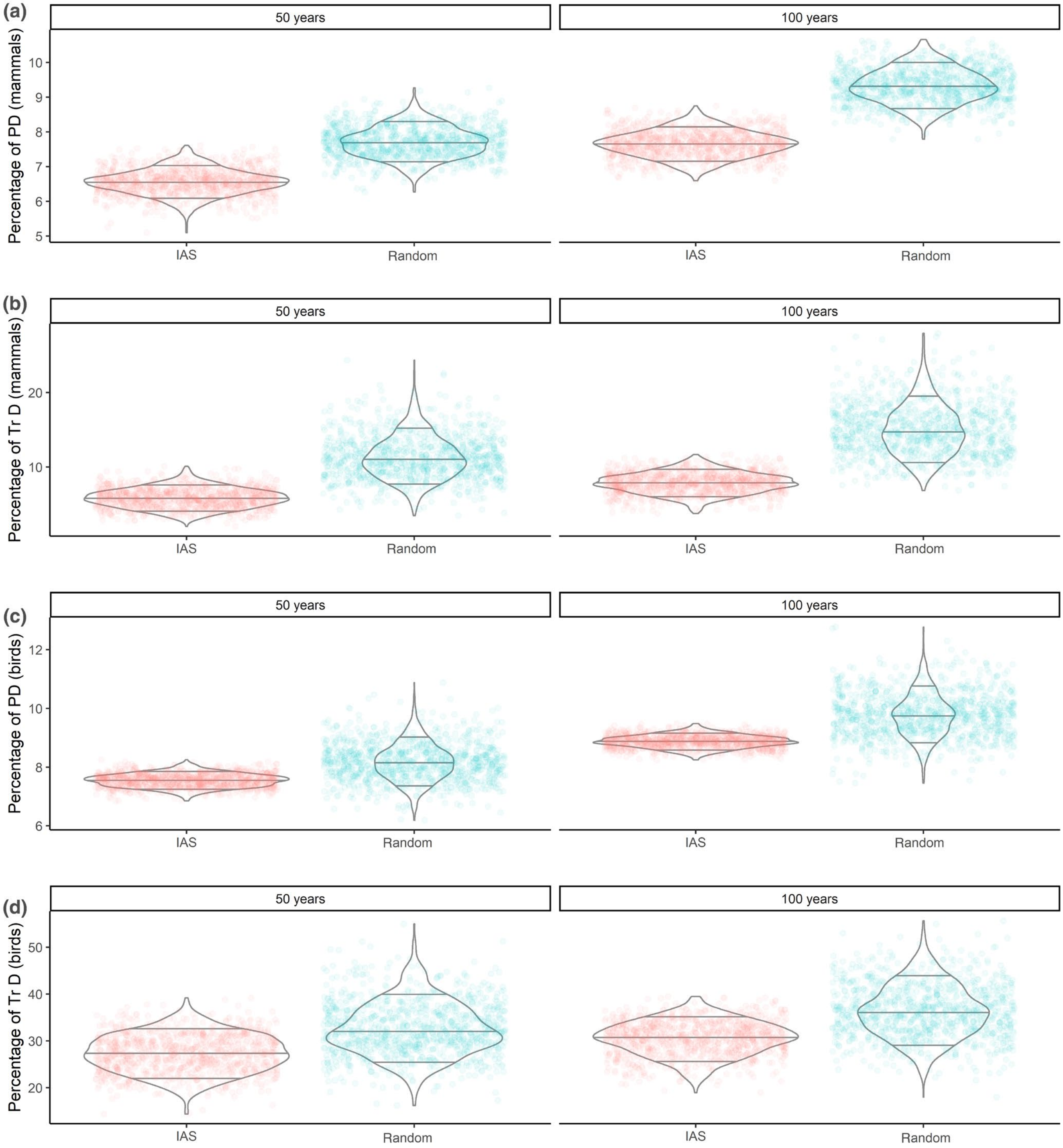

FIGURE 3 Contribution of mammals and birds to the total phylogenetic (PD) and trait diversity (TrD) expressed in percentages under 50- and 100-year extinction scenarios. These values represent potential losses of PD and TrD under different extinctions scenarios. We considered two samples of species: invasive-threatened species and random species (species taken from the total pool of mammal and bird species worldwide that are not invasive-threatened species). We included jittered points for each of the 999 repetitions; the median and quantiles (0.10 and 0.90) are also shown

6% (mammals) and up to 27% (birds) of TrD worldwide. It is worth noting that we only considered species that are facing imminent extinction according to the IUCN Red List criteria, thus ignoring NT, LC, or data-deficient species that might be at risk of extinctions in the near future due to IAS such as the Reunion Bulbul (BirdLife International, 2021). For instance, data-deficient species represent 15% of the entire mammal dataset. Consequently, we potentially underestimated the extinction debt due to IAS in this regard. On the contrary, the potential percentage of diversity predicted to become extinct due to IAS is significantly lower than expected under the projected randomized

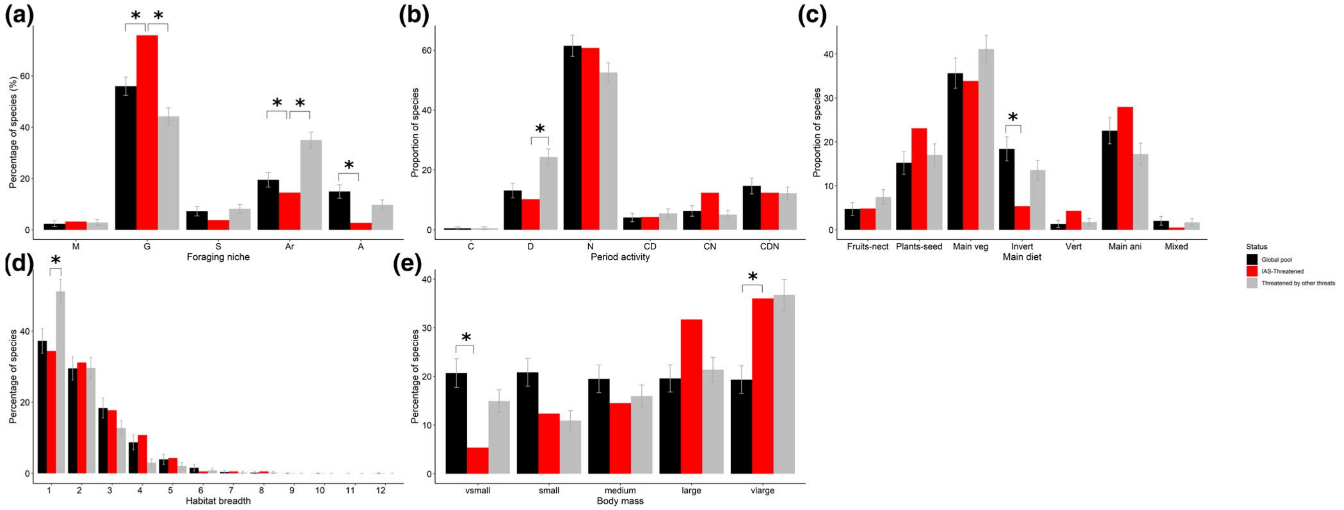

FIGURE 4 Percentage of invasive-threatened mammals (in red) for the five traits considered: (a) Foraging strata (with A, aerial, Ar, arboreal, G, ground level, M, marine, S, scansorial); (b) period of activity (with C, crepuscular; CD, crepuscular–diurnal; CDN, crepuscular–diurnal–nocturnal; CN, crepuscular–nocturnal; D, diurnal; N, nocturnal); (c) main diet; (d) habitat breadth; (e) body size. Their associated modalities are compared to the global pool (black bars with standard deviation errors bars) and other-threatened species (gray bars). See Table 1 for the modality descriptions and abbreviations. * indicates the percentage of trait modalities that are significantly different between invasive-threatened and other mammal species. A difference is significant when 95% of tests have a $p < 0.05$ (see Tables S4 and S5 for value details)

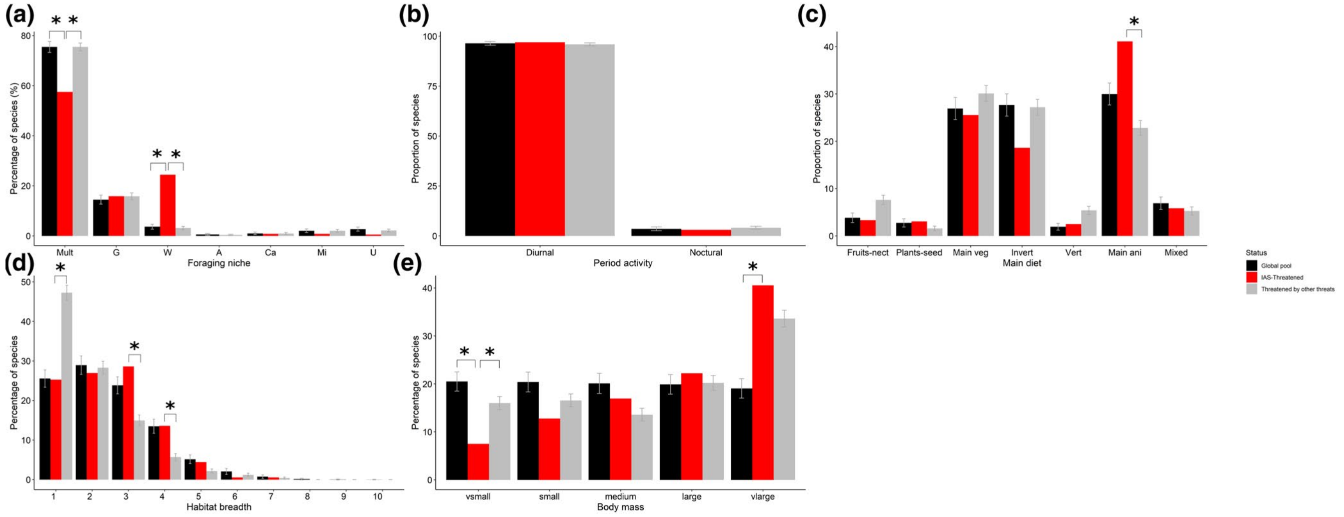

FIGURE 5 Percentage of invasive-threatened birds (in red) for the five traits considered: (a) Foraging strata (with A, aerial; Ca, canopy; G, ground level; M, multiple strata; Mi, mid-high; U, understory; W, water); (b) period of activity; (c) main diet; (d) habitat breadth; (e) body size. Their associated modalities are compared to the global pool (black bars with standard deviation errors bars) and the other-threatened species group (in gray). See Table 1 for the modality descriptions and abbreviations. * indicates the percentage of trait modalities that are significantly different between invasive-threatened and other mammal species. A difference is significant when 95% of tests have a $p < 0.05$ (see Tables S6 and S7 for value details)

scenario given the species richness. The main explanation is that invasive-threatened species are clustered in both the phylogenetic and trait space and that the projected diversity losses associated with mammals and birds will not be random. In fact, a selective process will occur across the phylogenetic tree and the ecological strategy space (Thuiller et al., 2011; Yessoufou & Davies, 2016).

We found that both invasive-threatened mammals and birds have a significantly larger body size than the rest of the pool but not when compared to other-threatened mammals. Large body mass has already been highlighted as a life-history trait that is strongly associated with increasing extinction risks due to the slow reproductive rate associated with large body mass (Hanna & Cardillo, 2013; Leclerc et al., 2020; Ripple et al., 2017). But note that body mass may hide the effects of other variables linked to reproduction, locomotion, or survival. Therefore, the effects of body size could not be direct but reflect the impact of other variables on species extinction risk. We also found that invasive-threatened species were more likely to feed in the lower strata (i.e., ground level or below the water surface) and less likely to feed in the higher strata (i.e., aerial or arboreal) compared to the other-threatened species, and more generally, the global pool. This pattern has recently been highlighted for insular species (Leclerc et al., 2020). Because most invasive-threatened species are found on islands, one possible explanation could be related to the naïveté syndrome. Indeed, ground species are more exposed to the introduction of nocturnal predators and are less capable of changing their behavior to develop new defenses (Doherty et al., 2016) while higher-strata species may develop avoidance strategies with the invasive mammals. We also found that invasive-threatened species live in a limited number of habitats and are more likely to be specialist species than generalist ones (Foden et al., 2018; Gonzalez-Suarez et al., 2013; Pacifici et al., 2017), but this tendency was not significantly different compared to the rest of the species. In fact, we found that other-threatened mammals are more likely to be specialized to a single habitat than invasive-threatened mammals, which are more likely to live in four different habitats. We also found that most invasive-threatened mammals are primarily herbivorous, which confirms the results of a recent study showing that large-bodied herbivorous mammals are more at risk of extinctions due to global threats, including biological invasions (Atwood et al., 2020). However, it would appear that the vast majority of mammals are herbivorous, meaning that this characteristic is not particularly associated with threatened species. By contrast, we did not observe that invasive-threatened bird species are more likely to be herbivorous, whereas Atwood et al. (2020) detected that large-bodied herbivorous birds are more at risk of extinctions with biological invasions. In fact, we found a disproportionately higher number of invasive-threatened birds that feed on animals compared to the rest of the species. More specifically, our findings suggest that habitat specialists and species with lower-strata feeding strategies are more likely to be filtered out of the global pool of mammals and birds. This is confirmed by the higher frequency of birds that feed on multiple strata in the global pool compared to those that are threatened by IAS. Because these traits have also been identified as highly vulnerable to other components of global changes, we can expect that IAS will further affect the global composition of bird and mammal species. In the near future, we may observe a shift in the global composition of birds and mammals toward species that have a lower body mass. Indeed, the average size of invasive-threatened species is four and eight times larger than the rest of the pool of birds and mammals, respectively. Recently, Cooke et al. (2019) predicted a potential ecological downsizing within mammals and birds due to global changes (Ripple et al., 2017). Forecast shifts in ecological traits could help us to identify the potential ecological consequences of extinctions for community and ecosystem services (Mouillot et al., 2013). Moreover, the predicted loss of habitat specialists and species with restricted foraging strata may lead to a shift toward generalist species, which may result in a global process of homogenizing ecological strategies (Clavel et al., 2011; Qian & Ricklefs, 2006; Villéger et al., 2011). In other words, biological invasions have the potential to disrupt the ecosystem structure and function.

One of the most prominent findings of this study is that the evolutionary and ecological implications of the extinction debt go far beyond a simple number of lost species. Indeed, species at risk of extinctions due to IAS will impact the ecological and evolutionary composition of future communities. We observed a clear ecological and evolutionary profile of species vulnerable to invasions. While we know that IAS is one of the most important drivers of species extinctions on islands (Bellard, Genovesi, et al., 2016), this is the first time that we documented the need to further investigate the ecological and adaptive consequences of the biological invasion threat worldwide. For this reason, we investigated whether these losses might result in the disappearance of particular profiles and/or lead to a shift in the composition of mammals and birds worldwide. Our results point to the potential disappearance of specific lineages of mammals (e.g., Myrmecobiidae, Thylacomyidae) and birds (e.g., Notiomystidae, Rhynochetidae) because all species in these families are threatened by IAS. This also includes families that are currently represented by a single species. For instance, the sole member of the Myrmecobiidae family is *Myrmecobius fasciatus*, which now has fewer than 800 individuals in Australia and continues to be threatened by several IAS (Woinarski & Burbidge, 2016). Even if IAS appear to be the primary threat to these species, other threats such as habitat degradation or natural system modifications like fire regime changes are also involved in population decline; indeed, IAS is rarely the sole threat responsible for the increasing risk of extinctions (Leclerc et al., 2018 see also Appendix S1). In fact, IAS is the only threat in less than 8% of cases in our dataset.

The potential implications of our results are multiple. For instance, we expect that the extinction debt due to IAS in terms of PD will reduce future options to adapt in a changing environment. Indeed, PD links evolutionary history to the conservation of feature diversity and potential future options (IPBES, 2019). TrD represents the ecological properties embodied by different species, which are of high concern to comprehend how ecosystems may persist in a changing world. The potential loss of TrD associated with invasive-threatened birds is very high concern for this group and may result in a reduced ability to adapt in the future. Specifically, large bird species that mostly feed in the lower foraging strata should be monitored and benefit from conservation measures. To better understand the threat posed by biological invasions, we also conducted a spatial analysis of TrD and PD threatened by biological invasions, which is a first step when establishing spatial prioritization for research and conservation actions. We found that invasive-threatened bird species located in the Oceanian realm, which is mostly comprised of islands, contribute to about half of the total invasive-threatened bird space for both PD and TrD. Moreover, the Neotropical and Australasian realms also represent hotspots of invasive-threatened mammals regarding TrD and PD. This pattern is very similar to what was observed in previous studies focusing on conservation priorities for birds and mammals (Jetz et al., 2014; Pollock et al., 2017), although it has never been revealed specifically for biological invasions. Therefore, our results imply that TrD and PD show clear differences across taxonomic groups and realms regarding the biological invasion threat, which should be considered when establishing spatial prioritizations.

Although our study brings potentially important insights into the role played by biological invasions in biodiversity losses, it is important to extend this study to other taxonomic groups before making decisions about conservation planning. The choice of life-history traits or the number of modalities and how they are categorized may also affect the results, although our sensitivity analyses of body mass modalities showed that our results are robust (Appendix S2). In addition, TrD or PD could be divided into multiple indicators (richness, divergence, originality, specialization, and rarity), all of which give complementary information that is necessary to establish a clear spatial prioritization. Because conservation is mostly undertaken at a local level, this study should be complemented with local assessments of community vulnerability to biological invasions. Moreover, IAS rarely acted alone and were often accompanied by other threats such as overexploitation and agriculture (Appendix S1). To date, it is impossible to disentangle the specific contribution of IAS compared to other threats because the large majority of threatened species are at risk of extinction due to the actions of simultaneous threats. However, our results suggest that at a minimum, IAS associated with other threats could be an important driver of TrD and PD losses in the near future. We were also able to compare ecological traits that are specifically associated with IAS compared to other threats.

Our study is a first attempt at a global scale to study the potential consequences of IAS on phylogenetic and functional diversity for birds and mammals. This study represents a first step toward integrating the multidimensional nature of diversity. We thus appeal to ecologists to investigate the consequences of biological invasions on multiple indicators of diversity and then transform this knowledge into local conservation initiatives.

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CODE AVAILABILITY

Original codes for conducting the functional analyses are available at (http://villeger.sebastien.free.fr/Rscripts.html). The R codes used to calculate TrD and PD are available on github (https://github.com/cbellard/FDPD_IAST).

DATA AVAILABILITY STATEMENT

All traits used in this study are included in the github repository and can be extracted from the Elton trait database (Wilman et al., 2014). We also used phylogeny for both birds and mammals; the data are freely available (Faurby et al., 2018; Jetz et al., 2014).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Annexe 2 : Annexes du Chapitre 1

Bernery, C., Bellard, C., Courchamp, F., Brosse, S., Gozlan, R. E., Jarić, I., ... & Leroy, B. (2022). Freshwater fish invasions: A comprehensive review. *Annual Review of Ecology, Evolution, and Systematics*, *53*.

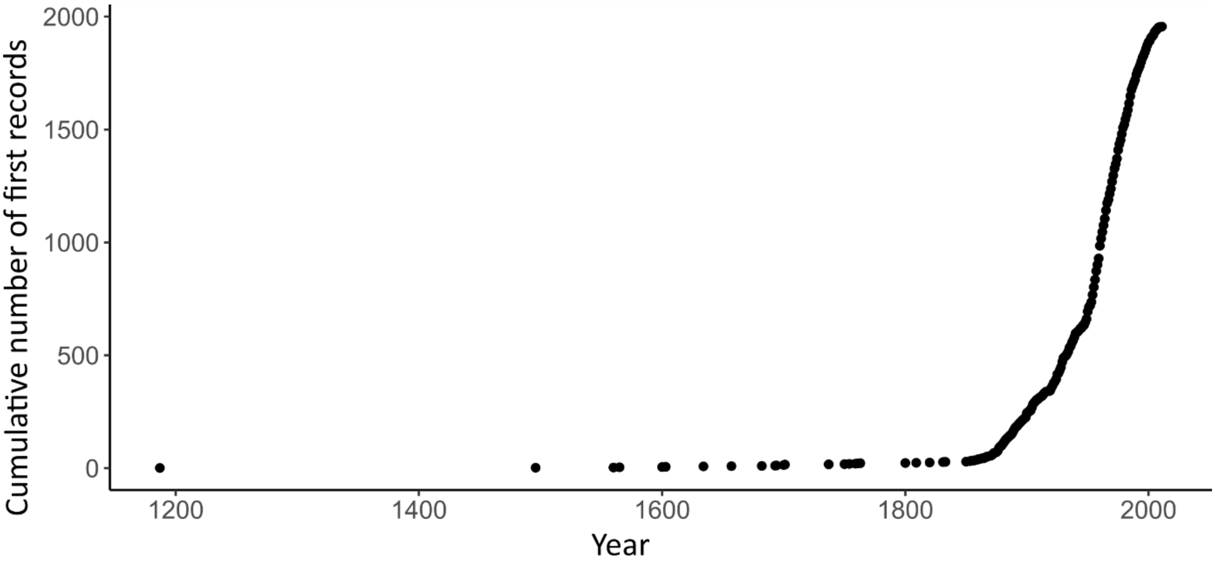

Figure S1: Cumulative number of first records for freshwater fish species (342 species considered). As first records are reported at the country scale, species may be included multiple times in the figure. Data are taken from Seebens et al. (2017)

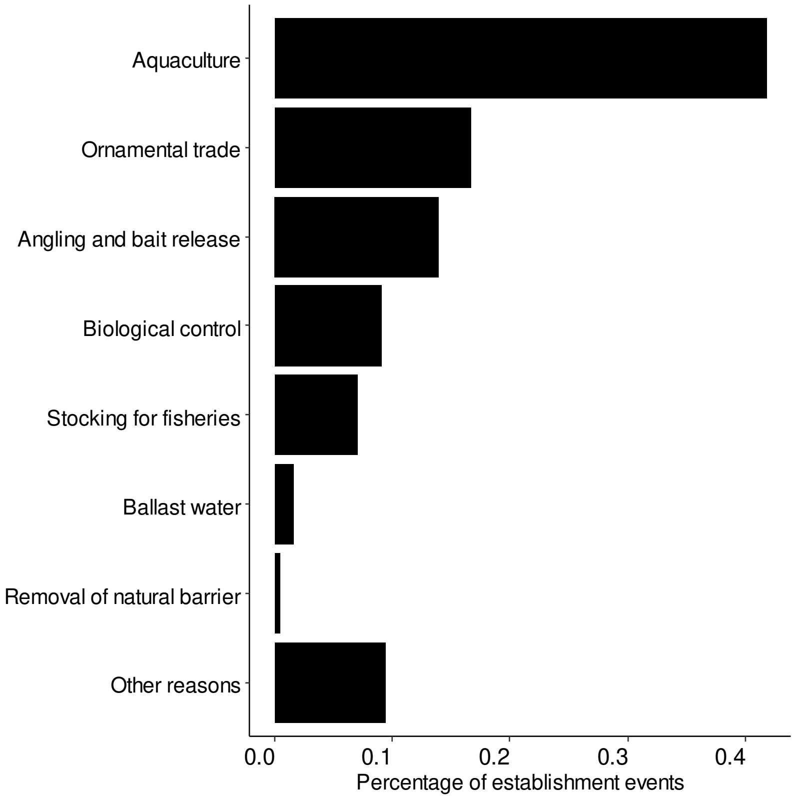

Figure S2: Percentage of establishment events of non-native freshwater fish species per introduction pathway. Note that some species may be introduced by multiple pathways, and a species can be counted multiple times for the same pathway if it becomes established at different locations along the same pathway. We used data from FishBase (Froese and Pauly, 2019) sorted to consider only freshwater fish species (i.e., species with freshwater recorded as one of their preferred habitats). We grouped several categories together (see Appendix 5) and considered 292 species and 1,649 establishment events.

Appendix 1: Additional information

Bait release in recreational fishing

In Maryland (US), 43% of anglers used fishes as bait and the majority of them release their unused bait (Kilian *et al.*, 2012). Various species of small bodied fish can be used as bait, such as those belonging to the Cyprinidae – e.g., the goldfish (*Carassius auratus*) and the fathead minnow (*Pimephales promelas*), Percidae – e.g., redfin perch (*Perca fluviatilis*) and pygmy perch (*Nannoperca sp.*), Cichlidae – e.g., *Tilapia sp.*, Gymnotidae, and Gasterosteidae (Lintermans, 2004; Kilian *et al.*, 2012; Drake and Mandrak, 2014). Fishes are among the top selling bait types, but fish baits are also captured in the wild and then released in another waterbody (Litvak and Mandrak, 1993; Mandrak and Cudmore, 2010; Drake and Mandrak, 2014). Harvest of live bait in the wild raises also the problem of bycatches because identification of species is challenging, especially for juveniles, and they can be consequently unknowingly introduced in new waterbodies (Drake and Mandrak, 2014).

Biological control

The mosquitofish (*Gambusia affinis* and *Gambusia holbrooki*), native to North America, are a classic example of biocontrol. These two closely related species have been widely introduced in many countries of southern Europe, Asia and also in Australia in the early 1920s in order to control mosquito populations responsible for malaria epidemics (Lintermans, 2004; Copp *et al.*, 2005; Beisel and Lévêque, 2010). Mosquitofishes are now distributed on multiple continents and have been included in the list of 100 of the world's worst invasive species because of their impacts (Lowe *et al.*, 2000). Other species of Poeciliidae, such as the guppy (*Poecilia reticulata*), have also been released for mosquitoes control, but not as widely as the mosquitoe fish (Lintermans, 2004). The black carp (*Mylopharyngodon piceus*) has been introduced in

North America in order to control snails, which are intermediate hosts of the yellow grub (*Clinostomum margaritum)* that parasitizes cultivated fishes (Haag, 2008)(Nico and Neilson, 2020). Other Chinese carp species such as the silver carp (*Hypophthalmichthys molitrix*) and the grass carp (*Ctenopharyngodon idella)* have been introduced in many countries to counter the proliferation of aquatic plants (Beisel and Lévêque, 2010).

Biodiversity conservation

In the early 1950s, the degradation of the native ecosystems of the huchen (*Hucho hucho*) in Poland caused its decline, and led to translocation initiatives to save the species by moving individuals out of their natural range (Nowak *et al.*, 2008; Witkowski *et al.*, 2013).

Another example is the Pedder galaxias (*Galaxias pedderensis*) species. The flooding of the Pedder lake of Tasmania in 1972 increased the abundance of predators in the small native range of the species. The Pedder galaxias was consequently translocated out of its native range and the species is now extinct from its natural range, but persists with two translocated populations at Strathgordon Dam and Lake Oberon in Tasmania (Chilcott *et al.*, 2013) (TSSC, 2016).

Ballast transport

About 3,500 million tons of ballast water are transferred annually around the world with their associated biota, via trans-oceanic shipping and shipping within inland waters (Endresen *et al.*, 2004; Mandrak and Cudmore, 2010; Bailey, 2015). Although ballast water is often cited as a medium for fish introductions, fishes represent a small part of the transported organisms, most of them being invertebrates (Wonham *et al.*, 2000; Bailey, 2015).

There are several famous examples of fishes introduced by ballast water. Gobies such as the yellowfin goby (*Acanthogobius flavimanus*) or the streaked goby (*Acentrogobius pflaumii*), native to Asia, were introduced in Australia and New Zealand via contaminated ballast water (Francis *et al.*, 2003; Lintermans, 2004). This pathway may also be responsible for six fish species introductions into the Great Lakes (Mandrak and Cudmore, 2010). Nonetheless, this pathway is less likely to drive future fish introductions, as legislations on ballast water of large ships have been put in place at a global scale (Verna and Harris, 2016).

Concerning prevention of ballast transport introductions, several management measures are implemented. For example, the International Maritime Organization (IMO) established quotas of viable organisms per cubic meter in ballast waters (Verna and Harris, 2016). IMO also imposed mid-ocean ballast water exchanges in order to release species taken in the coastal or inland waters in open ocean, where they are not supposed to survive, and replace them with saltwater species that cannot survive in inland or coastal waters (Ricciardi, 2006; Verna and Harris, 2016).

Aquaculture

Non-native fishes represent 17% of the global aquaculture production (Fuller, 2015; Ju *et al.*, 2020). China currently dominates the world in this field, accounting for 60% of the worldwide finfish inland production (i.e, 26 million tons) in 2014 (Gozlan, 2008; FAO, 2016; Ju *et al.*, 2020). In China, 91 freshwater fish species have been introduced for aquaculture, mostly from Asia, North America and Europe, and tilapia, catfish, eel and pirapatinga are the 4 most dominant fish groups cultured (Xiong *et al.*, 2015). At a worldwide scale, in 2009, 106 freshwater fish species and 24 diadromous fish species were farmed worldwide (Fuller, 2015; Gozlan, 2017; Ju *et al.*, 2020). Thus, the greater the aquaculture production, the more non-native fish species are likely to be introduced. As a results, billions of farmed fishes are intentionally or unintentionally released in nature, following the strong development of aquaculture and supplementary hatchery stocking programs (Britton and Gozlan, 2013)(Britton and Gozlan, 2013; Teletchea, 2019) and fishes non-native to their culture site contribute with 17% of the global aquaculture production.

Larger-scale introductions from aquaculture often occur through accidents and natural disasters, such as floods. In China, the destruction of aquaculture facilities by typhoons and floods in 2005 has enabled the escape of many non-native fishes (Ju *et al.*, 2020).

Between 1996 and 2012, the Center of Food Safety (2012) reported about 26 million escaped fishes from fish farms., the main species concerned being salmons and trouts.

Aquaculture is greatly influenced by the socio-economic and political situation. For instance, wars can have an impact on the species farmed, limiting the introduction of certain species and the trade between countries (Britton and Gozlan, 2013).

Interconnected waterways

Interconnected waterways were one of the earliest and most important pathways of fish introductions in the past (Mandrak and Cudmore, 2010), especially for species from the same biogeographic region (Ellender and Weyl, 2014; Nunes *et al.*, 2015). For example, the majority of species introduced in Europe through inland canals are species native to another part of Europe (Nunes *et al.*, 2015).

Factors impacting non-native fish invasion success:

Propagule pressure

It has been suggested that propagule pressure may also play a role in impacts via an additional dimension which is the colonization pressure. The colonization pressure assumes that the number of non-native taxa introduced in the new environment will affect the likelihood of introducing high-impact fishes (Richardson, 2011; MacIsaac and Johansson, 2017).

Inherent characteristics of the invaded ecosystems

Niche similarity

In California, 25% of the extant native species are invasive in other watersheds of the region: this is considered to be linked with the climatic and physiological similarities in adjacent watersheds (Moyle, 2002; Marchetti *et al.*, 2004). Conversely, aquarium fishes coming from tropical regions cannot establish easily in the cold waters of the St. Lawrence seaway in North America (Gertzen *et al.*, 2008).

Anthropization and perturbation

Another set of heavily disturbed ecosystems are estuarine ecosystems, which are subject to intensive use and alteration by humans, which has been linked to the long-term success of invasive species (Moyle and Light, 1996b).

Enemy release

In the Great Lakes, the invasive round goby (*Apollonia melanostoma*) is parasitized by only 22 species, compared to 72 in its native region (Kvach and Stepien, 2008). Moreover, Sheath *et al.* (2015) demonstrated that non-native species in England and Wales have less than 9% of the parasites species they have in their native ranges, and that parasites which survived were above all parasites with no intermediate hosts.

Invasion meltdown

It is noteworthy that already established species can facilitate the invasion of other species. For instance, the bullfrog invasion in the United States has been indirectly facilitated by the non-native sunfish: the sunfish reduced the dragonfly density, whose nymphs feed on bullfrog tadpoles (Adams *et al.*, 2003).

Furthermore, the invasive topmouth gudgeon is the healthy carrier of the rosette agent parasite *Sphaerothecum destruens*, thus leading to its invasion. This intracellular parasite then causes massive declines in native fish populations, allowing the topmouth gudgeon to overcome native competition and establish and colonize environments (Ercan *et al.*, 2015).

Impacts and mechanisms :

Homogenization and differentiation processes

The impacts of introductions and extinctions of fishes on the similarity of fish assemblages and the functions they support is a process called biotic homogenization when similarity increases, or biotic differentiation when similarity decreases. These processes have been intensively studied over the recent years (Rahel, 2000; Villeger *et al.*, 2011; Pool and Olden, 2012; Villéger *et al.*, 2014; Vargas *et al.*, 2015; Campbell and Mandrak, 2020). Species introductions appear to be the main driver of change in taxonomic and functional homogenization at regional or river basin scales (Rahel, 2000; Villeger *et al.*, 2011; Villéger *et al.*, 2014). However, not all introductions have similar impacts: translocated species (i.e. non-native species originated from the same region) may have a stronger role in taxonomic and functional homogenization upon the considered region than true non-native species (i.e. species originating from a distinct region) (Villéger *et al.*, 2014). In addition, wide-range species play a preponderant role in the taxonomic homogenization (Vargas *et al.*, 2015; Toussaint *et al.*, 2016).

The habitat alteration is also positively correlated with homogenization (Rahel, 2000; Pool and Olden, 2012). Indeed, habitat alteration increases the non-native species richness which, in turn, facilitates homogenization (Rahel, 2000; Pool and Olden, 2012).

Non-native species generally drive biotic homogenization from regional to global scales (Villéger et al. 2011, Toussaint et al. 2014, Vargas et al. 2015), with some areas homogenizing faster (e.g., Nearctic and Palearctic realms) than the others. Some areas can display taxonomic differentiation (Villeger *et al.*, 2011; Vargas *et al.*, 2015). However, this differentiation may be due to the establishment of distinct non-native species among river basins of the same region, which has been deemed to be an early signal of future homogenization, because as the number of species introductions increase, differentiation quickly turns into homogenization (Toussaint et al. 2014, Villeger et al. 2015). Functional homogenization, i.e. the increase in functional similarity of biotas through the establishment of species with already represented traits and the disappearance of species with unique traits (Olden *et al.*, 2004), has also been documented for freshwater fishes (Villéger *et al.*, 2014; Campbell and Mandrak, 2020).

The global trend of increasing biotic homogenization is expected to continue in the future because of the trends in pathways of species introductions. However, it is difficult to predict how the regionally heterogeneous trends in homogenization will evolve, because homogenization patterns are not linear and depend on the species and assemblages involved (Olden and Rooney, 2006; Pool and Olden, 2012; Villéger *et al.*, 2014; Campbell and Mandrak, 2020).

Appendix 2: Examples of trait associated with each invasion step. It is important to note that the traits filled are not exhaustive and reflect tendencies and examples of traits that are found in literature and which are known to increase the chance of success at each step. The influence of traits on the invasion steps success depends on many factors such as the physical conditions in the invaded region, and exceptions exist.

Invasion step	Specificities at each step	Example of traits associated with invasion steps success	Scale / Region	Method	References
INTRODUCTION	**Ballast water**	Small size Extensive lateral line system	World	Literature review	Wonham et al., 2000
	Aquaculture (intentional introductions)	Large size Laterally compressed	World	Observation	Su *et al.*, 2020
	Aquarium releases	Relatively large size (compared to other aquarium fishes) High popularity (high frequency in aquarium stores)	Canada and United States	Observation	Duggan *et al.*, 2006
		Aggressiveness	St. Lawrence Seaway (Canada)	Observation / Modelling	Gertzen *et al.*, 2008

ESTABLISHMENT	**Environments with highly variable conditions**	Small size Short lifespan Many spawning occasions per year Relatively low fecundity	Mediterranean streams	Observation / Literature review	Vila-Gispert *et al.*, 2005
	Environments with stable conditions	Large size Long lifespan Late maturity Few spawning occasions per year High fecundity	Mediterranean streams	Observation / Literature review	Vila-Gispert *et al.*, 2005
		Piscivorous	World	Literature review	Moyle and Light, 1996a
	All environments	Strong parental care Wide physiological tolerance	California	Observation	Marchetti, Moyle, *et al.*, 2004b
		Small body size Broad food spectrum	World	Observation	Ruesink, 2005
		Piscivorous Omnivorous Specialist feeder if their food items are highly available in the invaded ecosystem (i.e. detrivorous)	Parana river	Observation	Tonella *et al.*, 2018

	Pre-adaptation (low environmental distance)			
	Pre-adaptation (low environmental distance)	World	Literature review	Moyle and Light, 1996a
	Small size Regional origin (low geographical distance)	Iberian watershed	Observation	Ribeiro *et al.*, 2008
	Laterally compressed	World	Observation	Su et al., 2020
	Relatively fast growth Wide tolerance to temperature and salinity	Great Lakes, North America	Observation	Kolar and Lodge, 2002
	Wide salinity and temperature tolerance Higher growth rate	Great Lakes, North America	Literature review	Snyder *et al.*, 2014
SPREAD	Large size Small native range Low parental care (i.e, no parental care at all or brood hiders with no additional care) Detritivorous	Iberian watershed	Observation	Ribeiro *et al.*, 2008
	Long lifespan Not a herbivore Regional origin (low geographical distance)	California	Observation	Marchetti, Moyle, *et al.*, 2004b
	Slow relative growth rate Low tolerance to high temperatures Wide temperature tolerance	Great Lakes, North America	Observation	Kolar and Lodge, 2002 (for quickly spreading fishes compared to slowly spreading fishes)

		Slow relative growth rate Wide salinity and temperature tolerance Low tolerance to high temperatures	Great Lakes, North America	Review of articles	Snyder *et al.*, 2014
IMPACT		Small eggs Wide salinity tolerance High tolerance to low temperatures	Great Lakes, North America	Observation	Kolar and Lodge, 2002
		Small size Regional origin Not an invertivore	California	Observation	Marchetti, Moyle, et al., 2004
		Piscivorous	World	Review of articles	Moyle and Light, 1996a
		Wide physiological tolerance Small native range	Iberian watershed	Observation	Ribeiro *et al.*, 2008 *(integration)*
		Low tolerance to low temperatures Small eggs	Great Lakes, North America	Review of articles	Snyder *et al.*, 2014
		Regional origin (low geographical distance)	California	Observation	Marchetti, Moyle, *et al.*, 2004b)
		Top trophic levels (piscivorous) High fecundity (more than one million eggs per spawning season)	Great Lakes, North America	Observation	Howeth *et al.*, 2016 *(comparaison between low-impact and high-impact invaders)*

Table S1: Examples of the ecological impacts of non-native freshwater fish at each scale. The description of the impact corresponds to illustrations in Figure 2.

Scale	Impacts	Mechanism	Examples	Description of the impact	Reference
Genetic	Altering genetic resources	Hybridization	Rainbow trout (*Oncorhynchus mykiss*)	In Columbia, rainbow trout is known to hybridize with the native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), thus reducing its fitness through lower reproductive success.	Muhlfeld et al., 2009
Individual	Other – Plant/animal health	Disease – parasite transmission	Japanese eel (*Anguilla japonica*)	Japanese eel indirectly causes infections in populations of native European eel (*Anguilla anguilla*) via the nematode *Anguillicola crassus.*	Kirk, 2003
Population	Population size decline – Species range contraction	Parasitism	Sea lamprey (*Petromyzon marinus*)	Immature sea lampreys contribute to the decline of several native large predatory fish species in the American Great Lakes.	Cucherousset and Olden, 2011
Ecosystem	Reduction in native biodiversity	Predation	Nile perch (*Lates niloticus*)	The invasive Nile perch is responsible for the decline and disappearance of hundreds of endemic cichlid species in Lake Victoria.	Witte et al., 1992; Appendix 4
	Modification of nutrient pools and fluxes	Competition	Trout (e.g., brown trout *Salmo trutta*)	Invasive trout prevent the emergence of insects, which are food resources for riparian birds and spiders.	Epanchin et al., 2010
	Habitat or refuge loss / replacement	Predation	Nile tilapia (*Oreochromis niloticus*)	Laboratory experiments showed that the presence of the invasive Nile tilapia in the Gulf of Mexico estuaries resulted in the displacement of the native redspotted sunfish (*Lepomis miniatus*) from their preferred habitats.	Martin et al., 2010
	Other – Soil or sediment modification	Digging and grazing / browsing	Carp (e.g., *Cyprinus carpio*)	Common carp is responsible for increasing turbidity via sediment resuspension.	Emery-Butcher et al., 2020
Biogeographic	Biotic homogenization			In the USA, states have on average 15.4 more species in common now than before European settlement (7.2% more similar).	Rahel, 2000
				In the Lower Colorado basin, fish fauna is increasingly homogenized, both taxonomically and functionally	Pool and Olden, 2012

Appendix 3: Additional examples of ecological impacts of non-native freshwater fishes at each scale.

Scale	**Impacts categories**	**Examples of non-native species**	**Description of the impact**	**References**
Genetic	Alteration of genetic ressources	Rainbow trout (*Oncorhynchus mykiss*)	In Columbia, the rainbow trout is known to hybridize and to alter the genome of the native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), which results in a reduction of its fitness through a decrease of the reproductive success.	(Muhlfeld *et al.*, 2009)
		Pecos pupfish (*Cyprinodon pecosensis*)	In the Pecos River in Texas, the native Pecos pupfish (*Cyprinodon pecosensis*) hybridized with the non-native sheepshead pupfish (*C. variegatus*). Hybrids were shown to have better swimming endurance and to grow more rapidly than the purebred *C. pecosensis*. This led to the replacement of *C. pecosensis* population by hybrids.	(Echelle and Connor, 1989; Olden *et al.*, 2004; Rosenfield *et al.*, 2004)
Individual	Reduce/inhibits the growth of other species	Common carp (*Cyprinus carpio*), grass carp (*Ctenopharyngodon idella*), guppies, mosquito fishes (*Gambusia sp.*)	Common carps, grass carps, guppies and mosquito fishes are indirectly linked with developmental problems of several fish species worldwide (e.g. cyprinids).	(Kuchta *et al.*, 2018)
	Plant/animal health	Japaneese eel (*Anguilla japonica*)	Japaneese eels are indirectly causing infections in farmed and wild population of the native European eel (*Anguilla anguilla*) through the nematode *Anguillicola crassus*	(Kirk, 2003)
Population	Population size decline – Species range contraction	Brook trout (*Salvelinus fontinalis*)	The brook trout introductions result in the displacement and decline of many native trout species and of many endangered amphibian species, such as the marbled newt (*Triturus marmoratus*) and the Pacific tree frog (*Pseudacris regilla*)	GISD, 2015
		Peacock bass (*Cichla monoculus*)	In Lake Gatun in Panama, the peacock bass led to a decline of several native species. This decline has been sustained even 45 years after the peackock bass introduction, leading some species to be locally extirpated.	(Sharpe *et al.*, 2017)
		Sea lamprey (*Petromyzon marinus*)	Immature sea lampreys contribute to the decline of several native large predatory fish species in the Great Lakes.	(Cucherousset and Olden, 2011)
Ecosystem	Reduction in native biodiversity	Nile perch (*Lates niloticus*)	The invasive Nile perch is responsible for the decline and disappearance of hundreds of endemic cichlid species in Lake Victoria.	(Witte *et al.*, 1992)

	Largemouth bass (*Micropterus salmoides*), yellow-belly bream (*Serranochromis robustus*)	In Zimbabwe, the largemouth bass and the yellow-belly bream dramatically decrease abundances of native fishes, especially *Barbus* species whose abundance collapsed by 99% in some cases and became functionally extinct.	(Gratwicke and Marshall, 2001)
	Brown trout (*Salmo trutta*)	In New Zealand streams, trouts are responsible for the disappearance of native galaxiids, a family containing mainly threatened species, in almost all the sites where the trout has been introduced.	(Townsend and Simon, 2006; McIntosh *et al.*, 2010)
Modification of food webs / Modification of nutrient pool and fluxes / Primary production alteration	Trouts - e.g. rainbow trout *(Oncorhynchus mykiss*), brown trout (*Salmo trutta*)	Introduced trouts prevent the emergence of insects, which are food resources for rosy-finch birds and riparian spiders. This can lead to cascading effects in the terrestrial food webs.	(Baxter *et al.*, 2004; Epanchin *et al.*, 2010)
	Peacock bass (*Cichla monoculus*)	The decline of several native species of the Lake Gatun in Panama resulted in changes in the trophic structure of the Lake, which is now dominated by large-bodied non-native omnivores and piscivores, while small native insectivores are becoming scarcer.	(Sharpe *et al.*, 2017)
	Catfishes (*Pterygoplichtys sp.)*	Excretions and egestions of non-native catfishes are known to redistribute nutrients as they graze and excrete in different areas, and to produce biochemical hotspots.	(Capps and Flecker, 2013; Rubio *et al.*, 2016)
	Common carp (*Cyprinus carpio*)	Common carps are known to affect nutrient cycling, to impact the phytoplankton biomass and composition and to decrease the macrophyte biomass.	(Matsuzaki *et al.*, 2007)
Habitat or refugia loss / replacement	Nile tilapia (*Oreochromis niloticus*)	Laboratory experiments showed that the presence of the introduced Nile tilapia in the Gulf of Mexico estuaries resulted in the displacement of the native redspotted sunfish from their preferred habitats.	(Martin *et al.*, 2010)
Soil or sediment modification: modification of structure	Carps - e.g., goldfish (*Carassius auratus*) and common carp (*Cyprinus carpio*)	Goldfish and common carp are responsible for the increase of turbidity through the resuspension of sediments and excretion.	(Richardson *et al.*, 1995; Matsuzaki *et al.*, 2009; Emery-Butcher *et al.*, 2020)
	Catfishes (*Pterygoplichthys* sp.)	Catfishes are known to be responsible for bank erosion.	(Nico *et al.*, 2009); GISD, 2015
	Pumpkinseed sunfish (*Lepomis gibbosus*)	Invasive pumpkinseed sunfish (*Lepomis gibbosus*) increase the turbidity during their nest construction.	(Beisel and Lévêque, 2010)

Biotic homogenization		Rahel (2000) have shown that fish faunas between states have become more similar than before European settlement, pairs of States gaining on average 15 more species in common and fish faunas became 7.2% more similar.	(Rahel, 2000)
		In the Laurentian Great Lakes, fish communities have functionally differentiated among all lakes considered, but have been taxonomically homogenized since 1870.	(Campbell and Mandrak, 2020)
		In the Lower Colorado basin, fish fauna became increasingly homogenized, both taxonomically and functionally	(Pool and Olden, 2012)

Appendix 4: The Nile perch invasion, a relevant example of invasive fish impacts

The Nile perch (*Lates niloticus*) is a good example of the extent and the diversity of impacts that can be produced by an invasive freshwater species. The Nile perch was introduced in 1963 in Victoria Lake, an African lake characterized by its hundreds of endemic species, with a majority of endemic haplochromines species (Taabu-Munyaho *et al.*, 2016). The Nile perch introduction aimed to increase the economic value of fisheries from Victoria Lake, as Nile perch feeds on small-size haplochromines of low economic value (Cucherousset and Olden, 2011; Taabu-Munyaho *et al.*, 2016). Twenty years later, the Nile perch population in the Lake exploded, Nile perch catches rising from 5000t in 1980 to 315,000t in 1989 (Taabu-Munyaho *et al.*, 2016). Many consequences followed the Nile perch invasion.

Negative interactions

As the diet of the Nile perch consists mainly of haplochromines (Aloo *et al.*, 2017), its invasion resulted in a collapse of their populations, in addition to tilapiine species: according to Witte *et al.* (1992), about 200 endemic cichlid species were pushed to extinction, especially algae-feeding haplochromines. Moreover, haplochromines with overlapping habitats with the Nile perch are likely to experience population crash more rapidly than those with no overlap (such as species living in the littoral areas or on rocky shores), which in some cases were not even affected (Witte *et al.*, 1992). Nile perch invasion led to “the first mass extinction of vertebrates that scientists have ever had the opportunity to observe” (Kaufman, 1992) and had repercussions on the trophic network of the lake (Witte *et al.*, 2013).

However, the Nile perch’s predation was so strong that it was partly responsible for its own decline, due to the exhaustion of its prey. The decline led to a reappearance of a few native species feared extinct, but at least 200 endemic native species are definitely extinct (Matsuishi *et al.*, 2006).

- **Socio-economic consequences:**

The presence of the Nile perch has radically changed local fisheries of the Victoria Lake. It replaced previously fished native species, multiplying the annual harvest by a factor of four in less than ten years (Witte *et al.*, 1992). Such increase in harvesting was followed by the development of local processing industries, the creation of new jobs, the increase of fishing effort and the huge increase of the population around the lake (Shoko *et al.*, 2005; Matsuishi *et al.*, 2006). More than 1.2 million people and the regional development of riparian countries of the Victoria Lake highly depend on fisheries through the foreign exchanges (Matsuishi *et al.*, 2006).

Nevertheless, it seems that the Nile perch fishing is unsustainable as the Nile perch population is in decline, partly due to the intense fishing pressure (Matsuishi *et al.*, 2006).

The Nile perch also has negative impacts on the local communities, deteriorating their living conditions. Local fishers have to invest into new fishing equipment to efficiently fish Nile perch, but they cannot invest enough to ameliorate their living conditions (Onyango and Jentoft, 2010). Moreover, in about 40 years, the number of fishermen have doubled, intensifying the competition and the conflicts among fishermen and leading to the appearance of foreign leading groups controlling the equipment used and the prices paid, forcing local fishers to be price takers (Onyango and Jentoft, 2010). The disappearance of local fish species due to the Nile perch predation also raises the prices of the remaining fish species, endangering the food security of 30 million riparian people of the Victoria Lake. (Shoko *et al.*, 2005). Morever, the decreasing catches indirectly contributed to increasing prevalence of HIV/AIDS among the fisher communities, as women fishmongers have to secure the fish caught by fishermen in return of sexual relationships (Aloo *et al.*, 2017).

- **Habitat alteration**

Nile perch’s impacts on habitat are mostly indirect, driven by its exploitation by humans. Rapid growth of the human population around the Victoria Lake resulted in an increase in human activities (e.g. use of fertilizers, farming), and consequently in the elevated nutrient input to the lake and its eutrophication (Shoko *et al.*, 2005). Moreover, it was also triggered by the Nile perch processing industry which is different from the one used for native fish. The Nile perch needs to be smoked, which requires firewood, leading to an aggravation of the deforestation around the lake, and in turn contributing to the increase of soil erosion, siltation and eutrophication (Aloo et al., 2017). The marked eutrophication experienced by the lake since the late 90ties decreased the water transparency and water oxygen content, worsening the loss of cichlids species diversity by reducing species home range and mating efficiency (Balirwa *et al.*, 2003).

Appendix 5: Gathering pathways together

New categories	**Fishbase categories**
Biological control	"mosquito control", "other pest control", "snail control", "weed control" , "phyto-zooplankton control"
Aquaculture	"aquaculture", "Aquaculture"
"Unknown"	"no data", "unknown", "unknown", “forage”, “research”
Stocking for fisheries	fisheries
Accidental release	"accidental"
Ballast water	"accidental with ships"
Other reason	"off-site preservation", "fill ecological niche", "other reasons", "diffused from other countries"
Angling and bait release	"angling/sport", "bait"
Removal of natural barrier	"removal of natural barrier", "Lessepsian migration"
Ornamental trade	"ornamental"

References – Annexes du Chapitre 1

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Annexe 3 : Annexes du Chapitre 2

P. J Haubrock*; **C. Bernery***; R. N. Cuthbert*; C. Liu; M. Kourantidou; B. Leroy; A. J. Turbelin; A. M. Kramer; L. Verbrugge; C. Diagne; F. Courchamp; R. E. Gozlan (2022). Knowledge gaps in economic costs of invasive alien fish worldwide. *Science of the Total Environment*, 803, 149875

*Co-premiers auteurs

Supplement 1: Description of the procedure used for collecting and describing cost data in the InvaCost database (adapted from Diagne et al. 2020).

Cost data were collated as they appear in the original source (‘Raw cost estimate local currency’ column). When several cost estimates were provided in a study, we also collated the minimum and maximum estimates provided. We also retrieved temporal information under the ‘Period of estimation’, ‘Probable starting/ending years’ and the ‘Time range’ (*year* if the estimate is given yearly or for a period up to one year, *period* if the estimate is given for a period exceeding a year).

For each cost estimate recorded, we provided information on including *(a)* the reference from which the cost was extracted, *(b)* the taxonomy of the associated species, *(c)* the spatial and temporal coverage of the study, *(d)* the typology of each cost estimate and *(e)* the evaluation of the reliability of the estimation method(s). Using the World Bank Open Data and the Organisation for Economic Cooperation and Development (OECD), we expressed all retrieved costs (raw costs and costs per year) in US dollars (US$) for the year 2017 using the following formula to convert and standardise each cost estimate:

$C_e = (M_V/C_F) \times I_F$

with Ce = Converted cost estimate (to 2017 US dollars based on exchange rate or PPP)

M_V = Cost estimate (either the ‘Raw cost estimate local currency’ extracted from analysed paper or the ‘Cost per year local currency’ transformed by us)

C_F = Conversion factor (either the official market exchange rate or the purchasing power parity, in US dollars)

I_F = Inflation factor since the year of cost estimation, calculated as $CPI_{2017}/CPIy$ with CPI corresponding to the Consumer Price Index and y the year of the cost estimation ('Applicable year').

Table 1: Below, we presented the categories used for each descriptive variable that corresponds to a specific column in the InvaCost database.

Column title	Description
Acquisition method	The method used to provide the cost estimate as a *report/estimation* (gathered or derived from field-based information) or *extrapolation* (cost modelled beyond the original spatial and/or temporal observation range)
Applicable year	The year of the 'Currency' value (not the year of the cost occurrence) considered for the conversion/standardization of the cost estimate
Authors	The authors of the material analysed
Availability	The accessibility of the material as a searchable document (*yes*/*no*)
Benefit value(s)	The mention of if any benefit value was found in the analysed material; this might cover different types of benefits (*e.g.* real benefits provided by direct use or exploitation of invasive species or benefits that are actually avoided costs) - the figure was not recorded or described as being out of the scope of INVACOST
Common name	The non-scientific (or vernacular) name(s) provided by the authors, or by the International Union for Conservation of Nature (UICN) when not provided
Contributors	The name of collaborator(s) having recorded the cost estimate; currently, it is only the initials of the authors, but each future contributor will be consistently acknowledged here
Cost estimate per year local currency	The 'Raw cost estimate local currency' transformed to a cost estimate per year of the 'Period of estimation' (obtained by dividing the raw cost estimate by the number of years* of the 'Period of estimation')
Cost estimate per year 2017 USD exchange rate	The 'Cost estimate per year local currency' standardised from local 'Currency' and 'Applicable year' to 2017 USD based on ER** (See the formula in the 'Standardisation of cost data' section)

Cost estimate per year 2017 USD PPP	The ‘Cost estimate per year local currency’ standardised from local ‘Currency’ and ‘Applicable year’ to 2017 USD based on PPP*** (See the formula in the ‘Standardisation of cost data’ section)
Cost ID	A unique numerical identifier for the cost estimate
Currency	The currency of the ‘Raw cost estimate local currency’ as extracted from the material
Details	When necessary, narrative elements deemed important either to understand the cost estimate or to support choices made for completing the database; this column was left unchanged from the original entries in order to allow trace-back investigations
Environment	The type of habitat (*aquatic*, *terrestrial*, *semi-aquatic*) where the cost estimate occurred
Geographic region	The geographical region(s) where the cost estimate occurred (*Africa*, *Asia*, *Central America*, *Europa*, *North America*, *Oceania-Pacific islands*, *South America*)
Impacted sector	The sector impacted by the cost estimate in our socio-ecosystems (e.g. *agriculture*, *health*, *public and social welfare*; see Table 2 for details on each category)
Implementation	This states – at the time of the estimation – whether the reported cost was actually *observed* (i.e. cost actually incurred) or *potential* (i.e. not incurred but expected cost)
Location	When provided, the precise location (e.g., region, city, area) where the cost estimate occurred
Max Raw cost estimate local currency	The higher boundary of the ‘Raw cost estimate local currency’ (if a range of estimates was provided by the authors)
Method reliability	The assessment of the methodological approach used for cost estimation as of *(i) high* reliability if either provided by officially pre-assessed materials (peer-reviewed articles and official reports) or the estimation method was documented, repeatable and/or traceable if provided by other grey materials, or *(ii) low* reliability if not (see Figure 2 for more details)
Min Raw cost estimate local currency	The lower boundary of the ‘Raw cost estimate local currency’ (if a range of estimates was provided by the authors)
Occurrence	The status of the cost estimate as *potentially ongoing* (if the cost can be expected to continue over time) or *one-time* (if the cost was explicitly considered as over by the authors)

Official country	The country or official territory where the cost is incurred; sometimes, this is not congruent with the geographic regions as some territories (e.g. Overseas areas) are situated on other continents than their country of attachment
Period of estimation	If provided, the exact period of time covered by the costs estimated, otherwise the raw formulation (e.g. late 90's, during 5 years)
Previous materials	If any, the list of successive materials checked before reaching the material originally providing the cost estimate
Probable starting year Probable ending year	The year range in which the cost is known or assumed to occur. When not explicitly provided by the authors, we mentioned 'unspecified' in both columns unless the authors provided a clear duration time. In this case, we considered the 'Publication year' as a reference for the probable starting/ending year from which we added/subtracted the number of years* of the 'Period of estimation'. In the case of a cost estimate provided for a one-year period straddling two calendar years, we mentioned the latest year of the cost occurrence in both columns. When vague formulations were used (e.g. early 90's), we still translated them in probable ending/starting year (e.g. 1990-1995). We will harmonise the way these specific cases are dealt with when reviewing and validating new lines proposed by new contributors.
Publication year	The publication year of the material analysed
Raw cost estimate local currency	The cost estimate directly retrieved from the analysed materials
Raw cost estimate 2017 USD exchange rate	The 'Raw cost estimate local currency' standardised from local 'Currency' and 'Applicable year' to 2017 US$ based on ER** See the formula in the Standardisation of cost data section
Raw cost estimate 2017 USD PPP	The 'Raw cost estimate local currency' standardised to 2017 US$ based on PPP*** See the formula in the Standardisation of cost data section
Reference ID	The numerical identifier of the material analysed, which allows correspondence with Data citation 1 that provides bibliographic details
Reference title	The title of the material analysed
Repository	The original source of each material: 'Web of Science (*WoS*)', 'Google Scholar (*GS*)', 'Google search engine (*Go*)' or 'Targeted collection (*TC*)'

Spatial scale	The spatial scale considered for estimating the cost: global (worldwide-scale), intercontinental (sites from two or more geographic regions) continental ('geographic region' level), regional (several countries within a single geographic region), country, site (for cost evaluated at intra-country level, including USA states) and unit (for costs evaluated for a well-defined surface area or entity)
Taxonomy	For each species recorded, the taxonomic information from kingdom to species level using the Global Biodiversity Information Facility (GBIF) as a reference
Time range	The time range considered by the authors for providing the cost estimate: *year* (when costs were if the estimate is given yearly or for a period up to one year) or *period* (when costs were provided for a period exceeding a year)
Type of cost	The type of the cost includes: damages and losses incurred by an invasion (*e.g.* damage repair, medical care, value of crop losses), or means dedicated to understand or predict (*e.g.* research), prevent (*e.g.* education, biosecurity), early detect (*e.g.* monitoring, surveillance) and/or manage (*e.g.* control, eradication) the invaders
Type of applicable year	The assessment of the applicable year as *effective* if explicitly stated by the authors or *publication year* if no explicit information provided
Type of material	The type of material analysed (*i.e.* scientific *peer-reviewed article* or grey literature); for grey literature, the exact nature of the material was indicated (*e.g.*, *official report*, *press release*)

* The number of years of the 'Period of estimation' is the difference between the 'Probable ending year' and the 'Probable starting year"

** Market exchange rate (local currency unit per US$) provided by the World Bank Open Data (available at https://data.worldbank.org/indicator/PA.NUS.FCRF?end=2017&start=1960).

*** Purchase Power Parity (local currency unit per US$) provided by the World Bank Open Data (available at https://data.worldbank.org/indicator/PA.NUS.PPP?end=2017&start=1990) and the Organisation for Economic Cooperation and Development (available at https://data.oecd.org/conversion/purchasing-power-parities-ppp.htm).

Table 2. Description of the sectors considered in the InvaCost database

Sector	**Description**
Agriculture	Considered at its broadest sense, food and other useful products produced by human activities through using natural and/plant resources from their ecosystems (e.g. crop growing, livestock breeding, beekeeping, land management)
Authorities-Stakeholders	Governmental services and/or official organisations (e.g. conservation agencies, forest services, associations) that allocate efforts for the management sensu lato of biological invasions (e.g. control programs, eradication campaigns, research funding)
Environment	Impacts on natural resources, ecological processes and/or ecosystem services that have been valued by authors such as disruption of native habitats or degradation of local habitats
Fishery	Fish-based activities and services such as fishing and aquaculture
Forestry	Forest-based activities and services such as timber production/industries and private forests
Health	Every item directly or indirectly related to the sanitary state of people such as vector control, medical care and other derived damage on human productivity and well-being
Public and social welfare	Activities, goods or services contributing - directly or indirectly - to the human well-being and safety in our societies, including local infrastructures (e.g. electric system), quality of life (e.g. income, recreational activities), personal goods (e.g. private properties, lands), public services (e.g. transports, water regulation), and market activities (e.g. tourism, trade)

Supplementary Material 2: Database available online :

https://ars.els-cdn.com/content/image/1-s2.0-S0048969721049500-mmc2.csv

Supplementary Material 3: Search-string used for (a) invasive fish species, (b) birds, and (c) mammals :

(a)

(invasi* OR alien OR non-indigenous OR nonindigenous OR nonnative OR alien OR exotic OR introduced OR naturali* OR invader) NOT (cancer* OR cardio* OR surg* OR carcin* OR engineer* OR rotation OR ovar* OR polynom* OR purif* OR respirat* OR "invasive technique" OR carbon OR fuel OR therap* OR vehicle OR cell* OR drug OR fitness OR "operational research" OR banking OR liberalization) AND fish

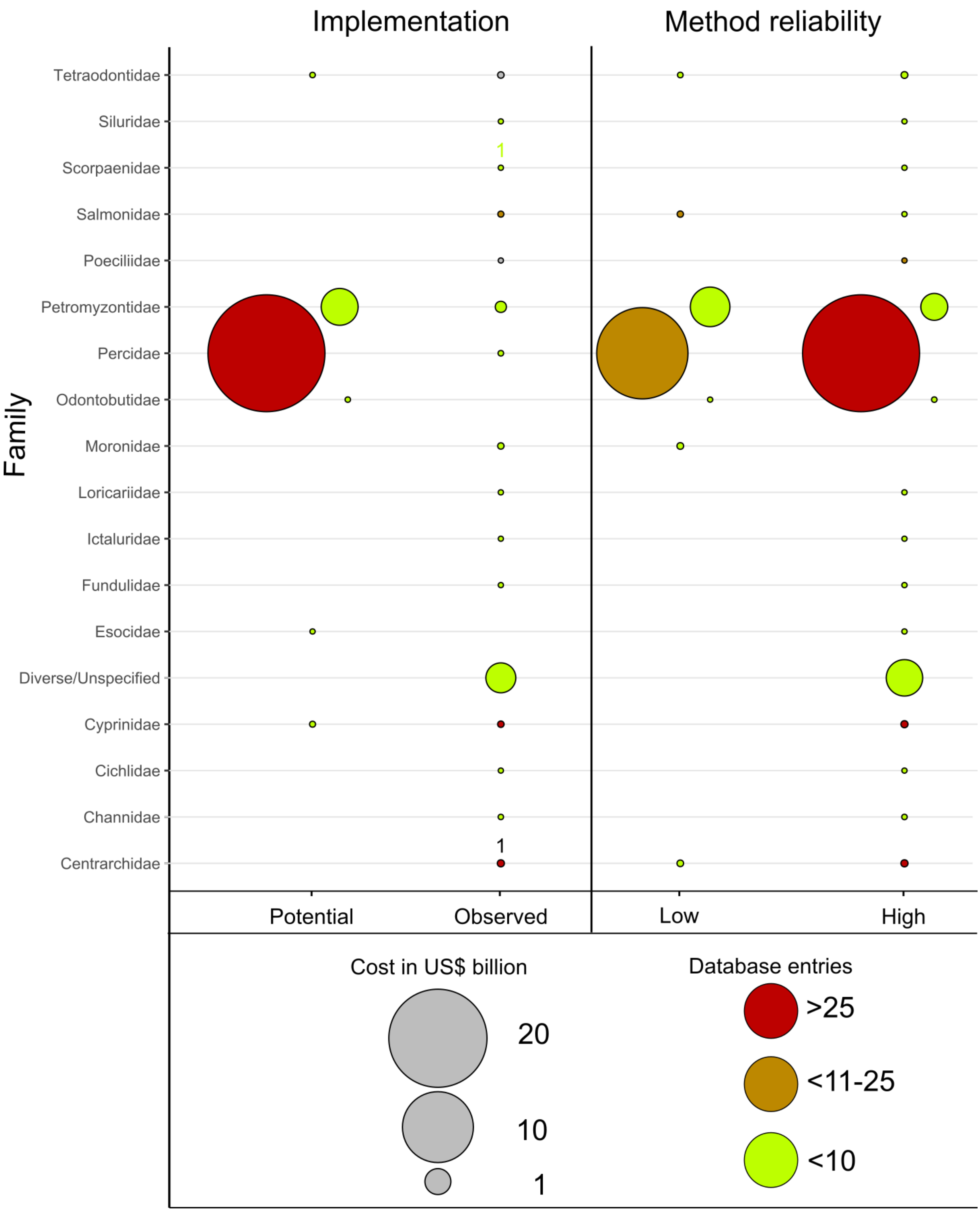
(b)

(invasi* OR alien OR non-indigenous OR nonindigenous OR nonnative OR alien OR exotic OR introduced OR naturali* OR invader) NOT (cancer* OR cardio* OR surg* OR carcin* OR engineer* OR rotation OR ovar* OR polynom* OR purif* OR respirat* OR "invasive technique" OR carbon OR fuel OR therap* OR vehicle OR cell* OR drug OR fitness OR "operational research" OR banking OR liberalization) AND bird

(c)

(invasi* OR alien OR non-indigenous OR nonindigenous OR nonnative OR alien OR exotic OR introduced OR naturali* OR invader) NOT (cancer* OR cardio* OR surg* OR carcin* OR engineer* OR rotation OR ovar* OR polynom* OR purif* OR respirat* OR "invasive technique" OR carbon OR fuel OR therap* OR vehicle OR cell* OR drug OR fitness OR "operational research" OR banking OR liberalization) AND mammals

Supplementary Material 4: Ballonplot showing implementation of costs (observed vs. potential) and method reliability (high vs. low) for all families of fish listed in InvaCost.



Annexe 4 : Annexes du Chapitre 3

C. Bernery; C. Bellard; F. Courchamp; S. Brosse; B. Leroy. Important characteristics to become a successful freshwater fish invader.

Appendix 1: Reclassification of pathway categories

New pathway categories	**FishBase pathway categories**
Aquaculture	Aquaculture
Sport/Angling	Angling/Sport
Species control	Weed control – mosquito control – other pest control – phyto-zooplankton control – snail control
Diffusion	Lesseptian migration – spread from other countries – removal of natural barrier
Accidental	Accidental – accidental with ships
Fisheries	Fisheries
Ornamental	Ornamental
Pathways not considered	Unknown – no data – other reasons – bait – forage –fill ecological niche – off-site preservation – research

Appendix 2: Countries and locations considered after reclassifying locations

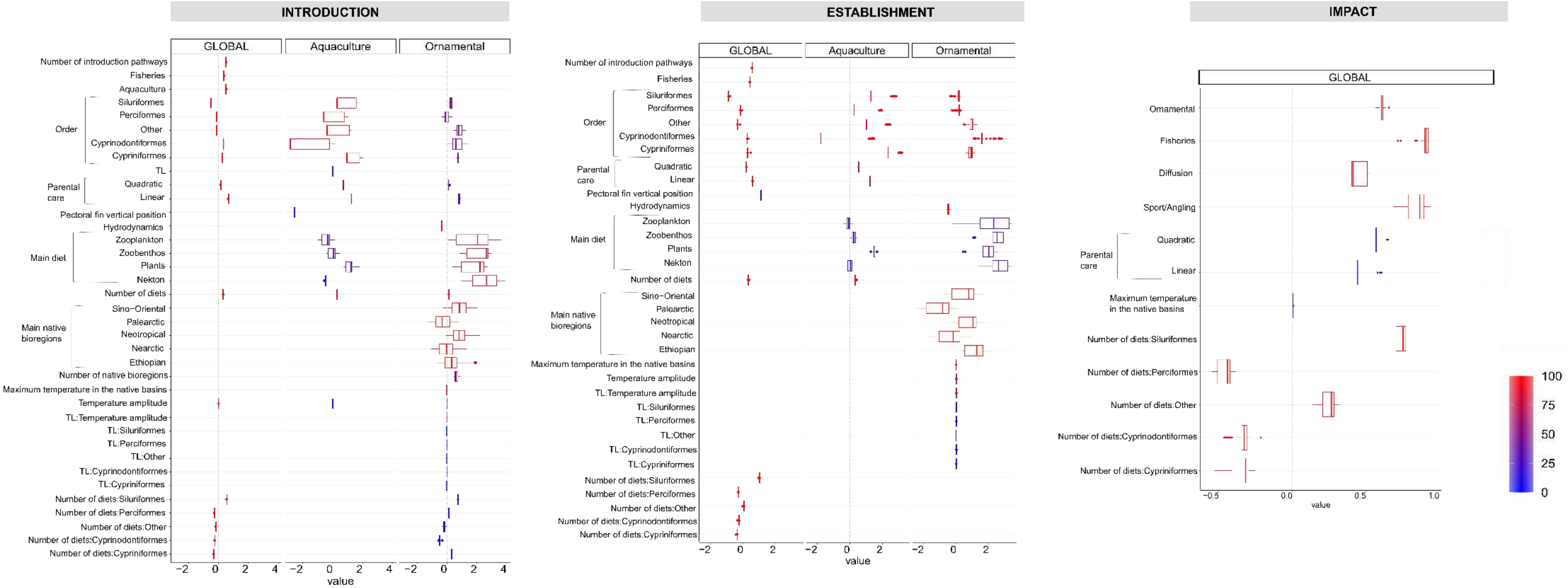
1	Afghanistan
2	Alaska
3	Albania
4	Algeria
5	American Samoa
6	Angola
7	Antigua-and-Barbuda
8	Argentina
9	Armenia
10	Australia
11	Austria
12	Azerbaijan
13	Azores Is.
14	Bahamas
15	Bangladesh
16	Barbados
17	Belarus
18	Belgium
19	Belize
20	Benin
21	Bermuda
22	Bhutan
23	Bolivia
24	Borneo
25	Bosnia Herzegovina
26	Botswana
27	Brazil
28	Brunei Darussalam
29	Bulgaria
30	Burkina Faso
31	Burundi
32	Cambodia
33	Cameroon
34	Canada
35	Caroline Island
36	Cayman Is.
37	Central African Republic
38	Chile
39	China
40	Colombia
41	Comoros
42	Congo
43	Cook Islands
44	Costa Rica
45	Cote d'Ivoire
46	Croatia
47	Cuba
48	Curacao
49	Cyprus
50	Czech Republic
51	Czechoslovakia
52	Denmark
53	Dominica
54	Dominican Republic
55	East Timor
56	Ecuador
57	Egypt
58	El Salvador
59	Eritrea
60	Estonia
61	Ethiopia
62	Falkland Islands
63	Federated States of Micronesia
64	Fiji
65	Finland
66	France
67	French Guiana
68	French Polynesia
69	Gabon
70	Galapagos Is.
71	Georgia
72	Germany
73	Ghana
74	Greece
75	Greenland
76	Grenada
77	Guatemala
78	Guinea
79	Guyana
80	Haiti
81	Hawaii
82	Honduras
83	Hungary
84	Iceland
85	India
86	Indonesia
87	Iran
88	Iraq
89	Ireland
90	Israel
91	Italy
92	Jamaica
93	Japan
94	Kazakhstan
95	Kenya
96	Kerguelen
97	Kiribati
98	Korea
99	Kuwait
100	Kyrgyzstan
101	Laos
102	Latvia
103	Lebanon
104	Lesotho
105	Liberia
106	Libya
107	Liechtenstein
108	Lithuania
109	Luxembourg
110	Macedonia
111	Madagascar
112	Madeira Is.
113	Malawi
114	Malaysia
115	Maldives
116	Malta
117	Mariana Islands
118	Marshall Islands
119	Martinique
120	Mauritius
121	Mexico
122	Moldova
123	Mongolia
124	Morocco
125	Mozambique
126	Myanmar
127	Namibia
128	Nauru
129	Nepal
130	Neth Antilles
131	Netherlands
132	New Caledonia
133	New Zealand
134	Nicaragua
135	Nigeria
136	Niue
137	North Korea
138	Norway
139	Oman
140	Pakistan
141	Palau
142	Panama
143	Papua New Guinea
144	Paraguay
145	Peru
146	Philippines
147	Poland
148	Portugal
149	Puerto Rico
150	Qatar
151	Reunion
152	Romania
153	Russia
154	Rwanda
155	Samoa
156	Sao Tome and Principe
157	Saudi Arabia
158	Serbia
159	Montenegro
160	Seychelles
161	Shanghai
162	Sierra Leone
163	Singapore
164	Slovakia
165	Slovenia
166	Solomon Islands
167	South Africa
168	South Korea
169	Spain
170	Sri Lanka
171	St. Vincent and the Grenadines
172	Sudan
173	Suriname
174	Swaziland
175	Sweden
176	Switzerland
177	Syria
178	Taiwan
179	Tajikistan
180	Tanzania
181	Thailand
182	Tibet
183	Togo
184	Tonga
185	Torres Strait Islands
186	Trinidad
187	Tunisia
188	Turkey
189	Turkmenistan
190	Tuvalu
191	Uganda
192	UK
193	Ukraine
194	United Arab Emirates
195	Unknown
196	Uruguay
197	US Virgin Islands
198	USA
199	USSR
200	Uzbekistan
201	Vanuatu
202	Venezuela
203	Vietnam
204	Wallis and Futuna
205	Yemen
206	Zaire
207	Zambia
208	Zimbabwe

Appendix 3: Variables used in each model

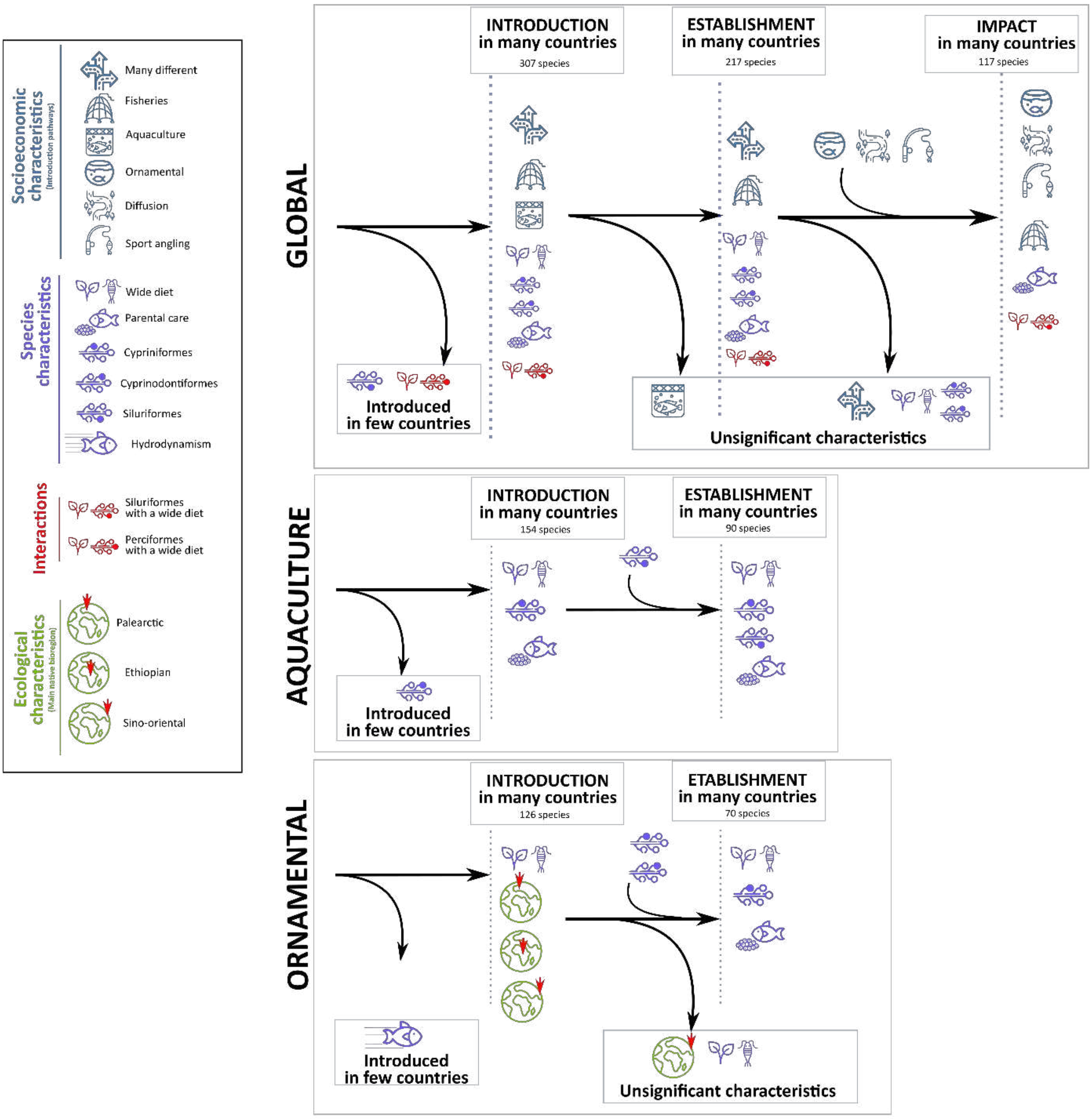
Introduction – Global Establishment – Global Impact – Global	**Life history traits** Main diet Number of diets Hydrodynamics Pectoral fin vertical position Parental care Total Length Order **Ecological characteristics** Temperature amplitude in the native basins Maximum temperature in the native basins Main native bioregion Number of native bioregions	**Socioeconomic characteristics** Aquaculture Sport/Angling Accidental Ornamental Fisheries Diffusion Species control Number of introduction pathways Human use **Interactions** Between Temperature amplitude and TL Between Order and Number of diets Between Order and TL Between Ornamental and TL Between Sport/Angling and TL Between Aquaculture and TL
Introduction – Aquaculture Introduction – Ornamental Establishment – Aquaculture Establishment – Ornamental	**Life history traits** Main diet Number of diets Hydrodynamics Pectoral fin vertical position Parental care TL Order **Ecological characteristics:** Temperature amplitude in the native basins Maximum temperature in the native basins Main native bioregion Number of native bioregions	**Interactions** Between Temperature amplitude and TL Between Order and Number of diet Between Order and TL

Appendix 4: Sensitivity analysis

Boxplots represent the estimates (without standard errors) of 100 models. We varied the main diet of species with several main diets and the main native bioregion of species with several main native bioregions. The color gradient represents the number of models in which the considered variable is significant (1: blue, 100: red). “TL” refers to total length.



Appendix 5: Main characteristics to succeed at each invasion step for the global pool and for species introduced through the ornamental and aquaculture pathways



Appendix 6: Differences in characteristics between introduced and non-introduced species

Methods

Introduction status

We took as introduced all species introduced to at least one location (i.e., species with at least one location listed in the "TO" column of the *introduction()* table). It should be noted that some species were simply imported to the location without being introduced to the wild. These species were impossible to separate from others, although they represent only a very small part of the data (Nicolas Bally, pers. com.). Thus, these were taken as species introduced to the wild.

Statistical analysis

To compare the characteristics of the introduced species with those of the non-introduced species, we conducted univariate comparisons between the introduced and non-introduced species for each characteristic. First, we directly compared introduced versus non-introduced species. Second, we accounted for the class imbalance between non-introduced species (majority class) and introduced species (minority class) by performing a repeated random sub-sampling approach. In this latter approach, we reduced the majority class (non-introduced species) to a random sample of size equal to the minority class (introduced species) and then made 999 repetitions. To test the significance of the results, we used a Fisher test for each modality when the considered characteristic was a qualitative variable and a Wilcoxon test for quantitative variables. We considered a test to be significant when $p<0.05$ (see Appendix 7 for the p-values of each test).

We performed these analyses for the entire pool of species and then specifically analyzed each pathway in order to detect any interactions between pathways and species characteristics. As the main diet and main native region of some species were chosen randomly from several possibilities, we also performed sensitivity analysis on the main diet and main native region. To do so, we randomly selected (100 repetitions) the main diet and main native region between the different modalities for the concerned species.

Results

We examined the characteristics that were overrepresented in the introduced species pool compared to the non-introduced pool of species (Fig. 1). We found that introduced species had a higher temperature amplitude in their native basins, a higher number of diets and native regions, and were more often used by humans than non-introduced ones. These differences were found in the majority of the considered introduction pathways, except for the ornamental and species control pathways.

In addition, the native regions of the introduced species strongly differed for the different pathways (Fig. S1). For example, species mainly native to the Palearctic and Sino-Oriental regions were more represented among introduced species than non-introduced ones in the global pool. By contrast, the Neotropical region was more represented among species introduced through the ornamental trade pathway compared to other species. Species introduced by the ornamental pathway also had ventral pectoral fins and were rather small (compared to long fish introduced by fisheries and sport/angling). Accidentally introduced species tended to have lateral pectoral fins and were more represented in the Cypriniformes order than other fish. Concerning species introduced by sport/angling, they were more represented in the guarder strategy for parental care and in the nekton category for main diet compared to other fish. Finally, species introduced for species control were more represented in the bearer strategy for parental care, in the Cyprinodontiformes order, and had lateral pectoral fins compared to other species.

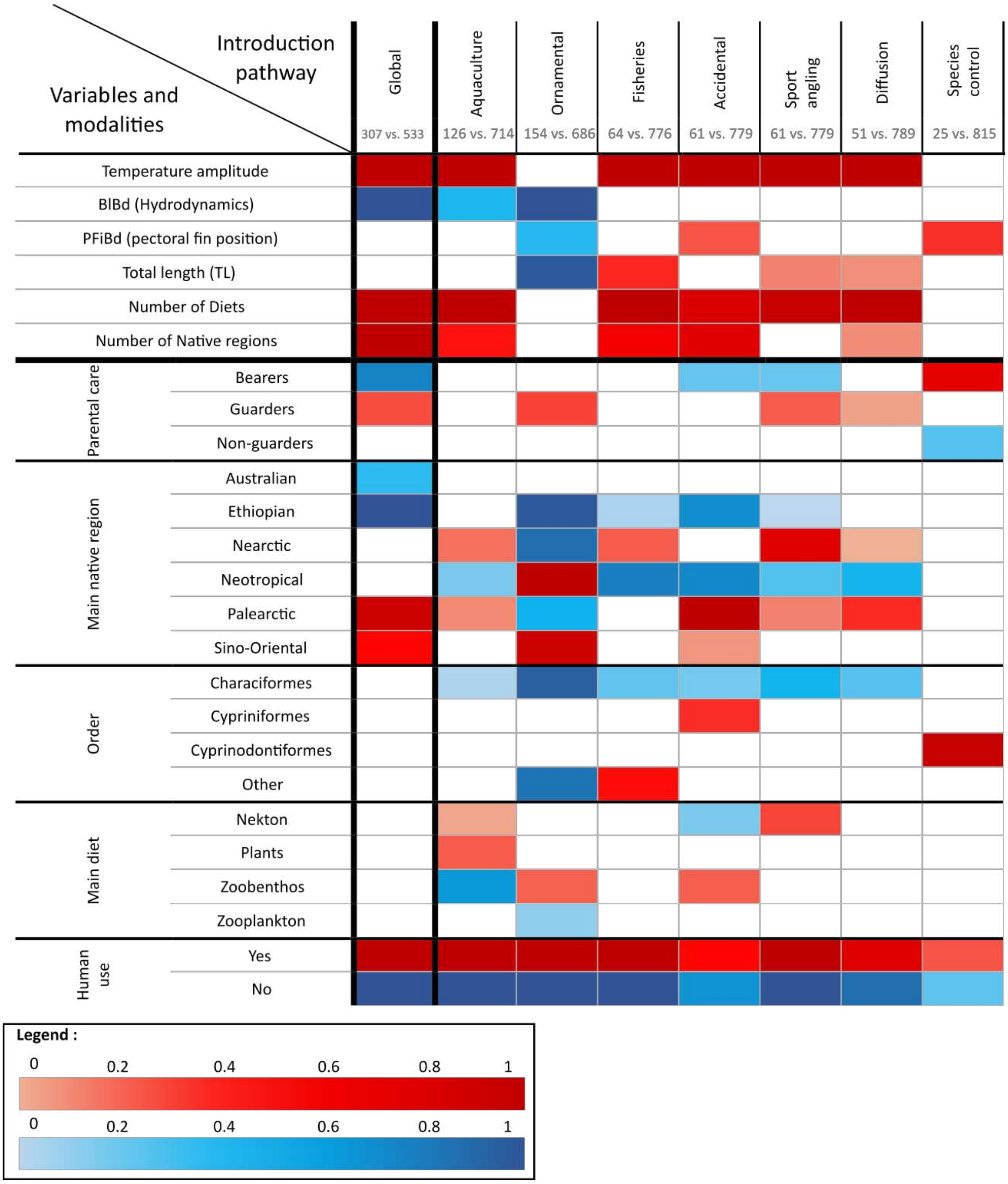


Figure S1: Results of Wilcoxon tests and F-tests per modality for each variable and each introduction pathway (see Appendix 7 for p-values). Red (blue) color indicates when introduced species are significantly more (less) represented or have a significantly higher (lower) value than non-introduced species using comparisons with all species. The gradient of colors represents the proportion of significant tests using the resample method. Only variables with a significant difference are presented. The p-values of tests with all species are available in the

Appendix 7. It is important to note that these results do not describe the main characteristics of the introduced species (see Appendix 6bis) but rather the differences between the introduced and non-introduced species.

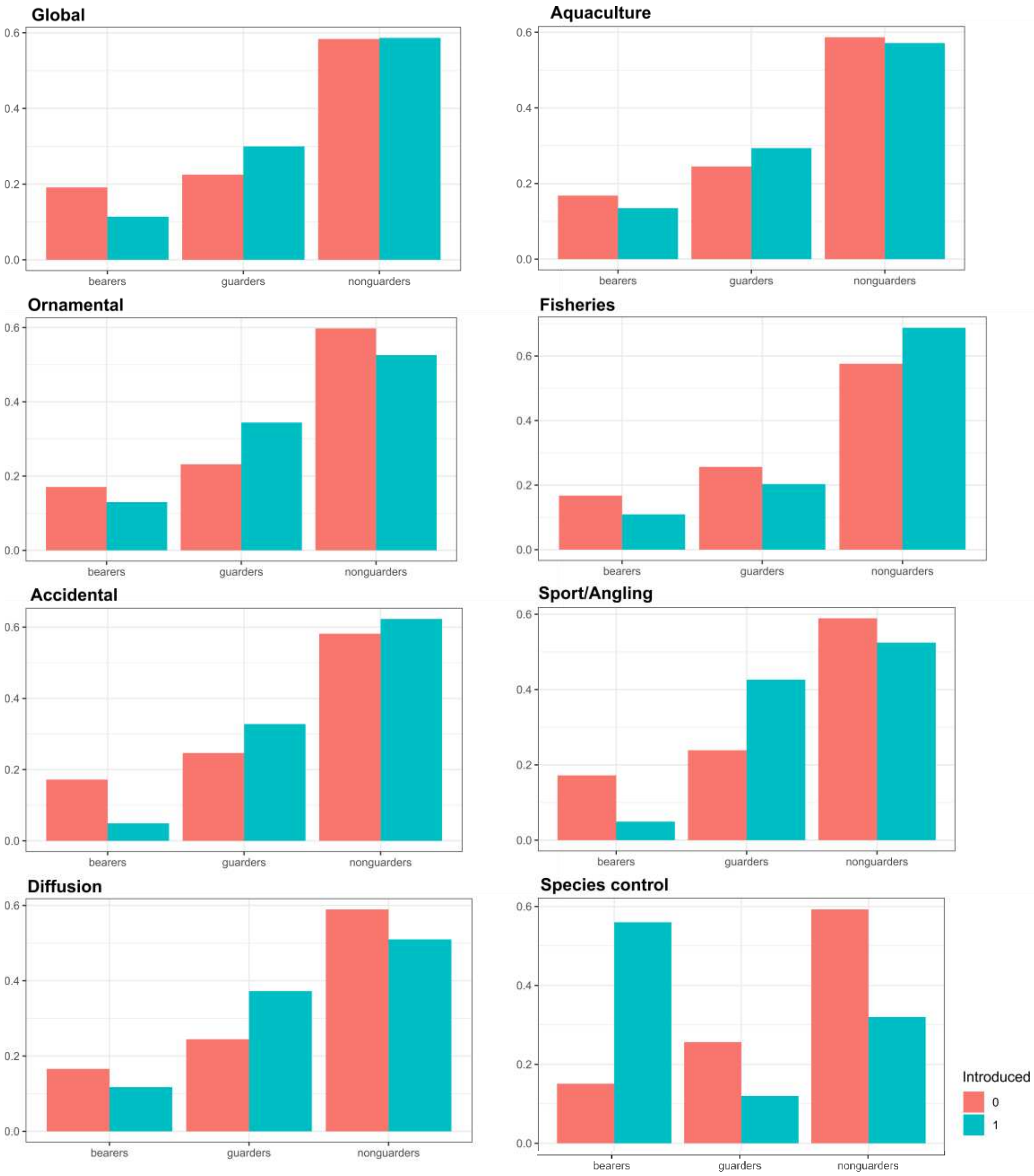
Discussion

We demonstrated the importance of a high number of diets and a high temperature tolerance to differentiate introduced species from non-introduced ones at the global scale. These findings are supported by the literature at the local scale (e.g., North America, Kolar and Lodge, 2002; Parana River, Tonella et al., 2018). In addition, human use is unsurprisingly related to a greater likelihood of introduction and has already been highlighted to differentiate invasive and native species (Alcaraz et al., 2005). Moreover, species from a higher number of native regions were also more introduced, perhaps because they have greater opportunities to be in contact with human activities. Nonetheless, some species with only one native bioregion can also be introduced in numerous countries: for example, the common carp (*Cyprinus carpio*), native to the Sino-Oriental region, has the highest number of introduced countries in our pool (i.e. 133 countries).

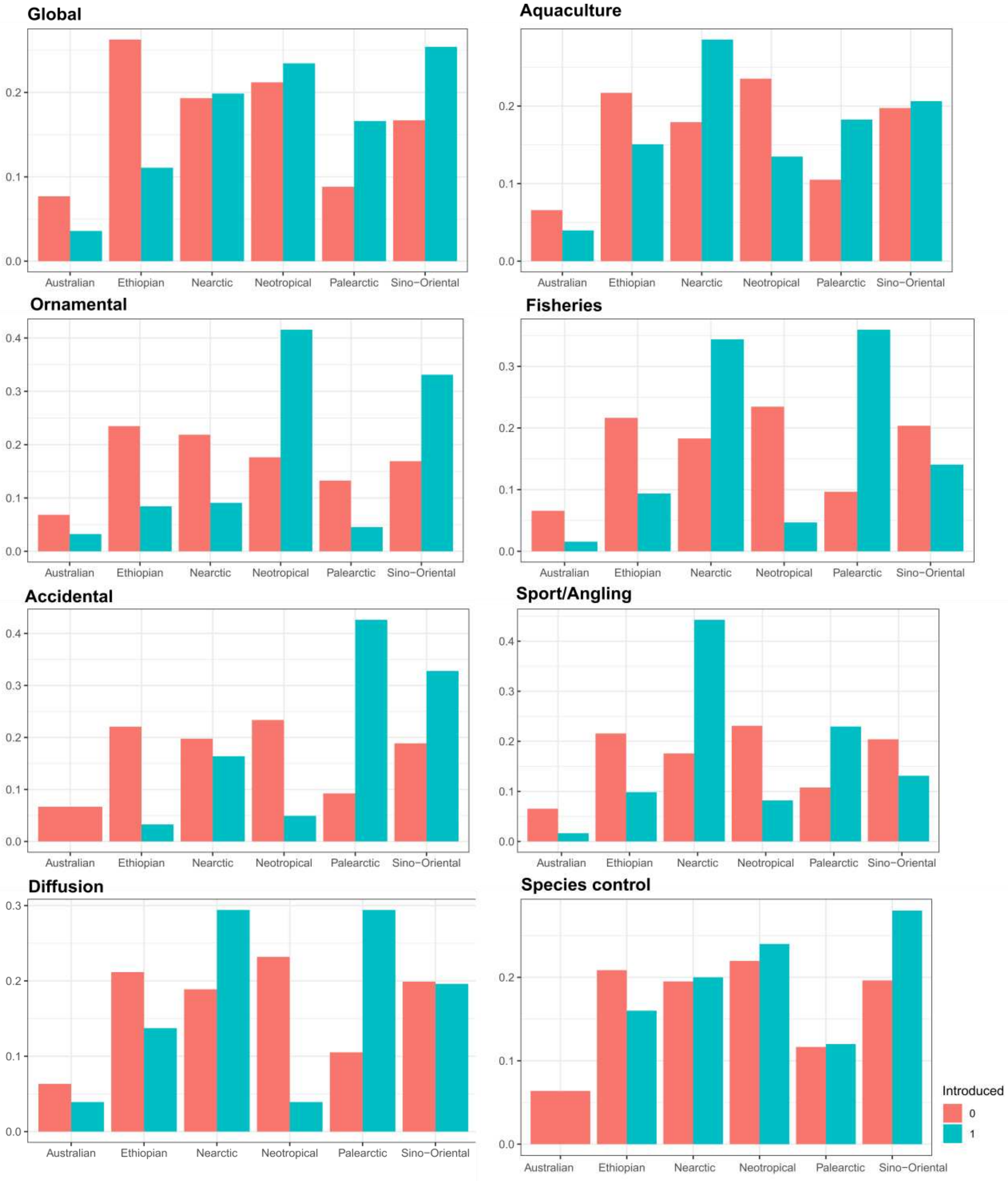
Appendix 6bis: Representation of qualitative data for each introduction pathways, concerning A. Parental care, B. The main native region, C. the order, D. The main diet, E. The human use. Proportions of species in each modalities are represented. Introduced species are represented in blue, and non-introduced species are represented in red;

Overall, successfully introduced species were mainly used by humans, adopted a non-guarder strategy for parental care, were represented by the Perciformes or Cypriniformes orders, and had a zoobenthos main diet. The only exceptions were for species introduced through the species control pathway. Species introduced for species control were mainly from the Cyprinodontiformes order and adopted a bearer strategy for parental care (Appendix 6bis, A, C, D, E). We found that species mainly native to the Sino-Oriental, Neotropical, and Nearctic regions were frequently introduced species (Appendix 6bis, B).

A. Parental care

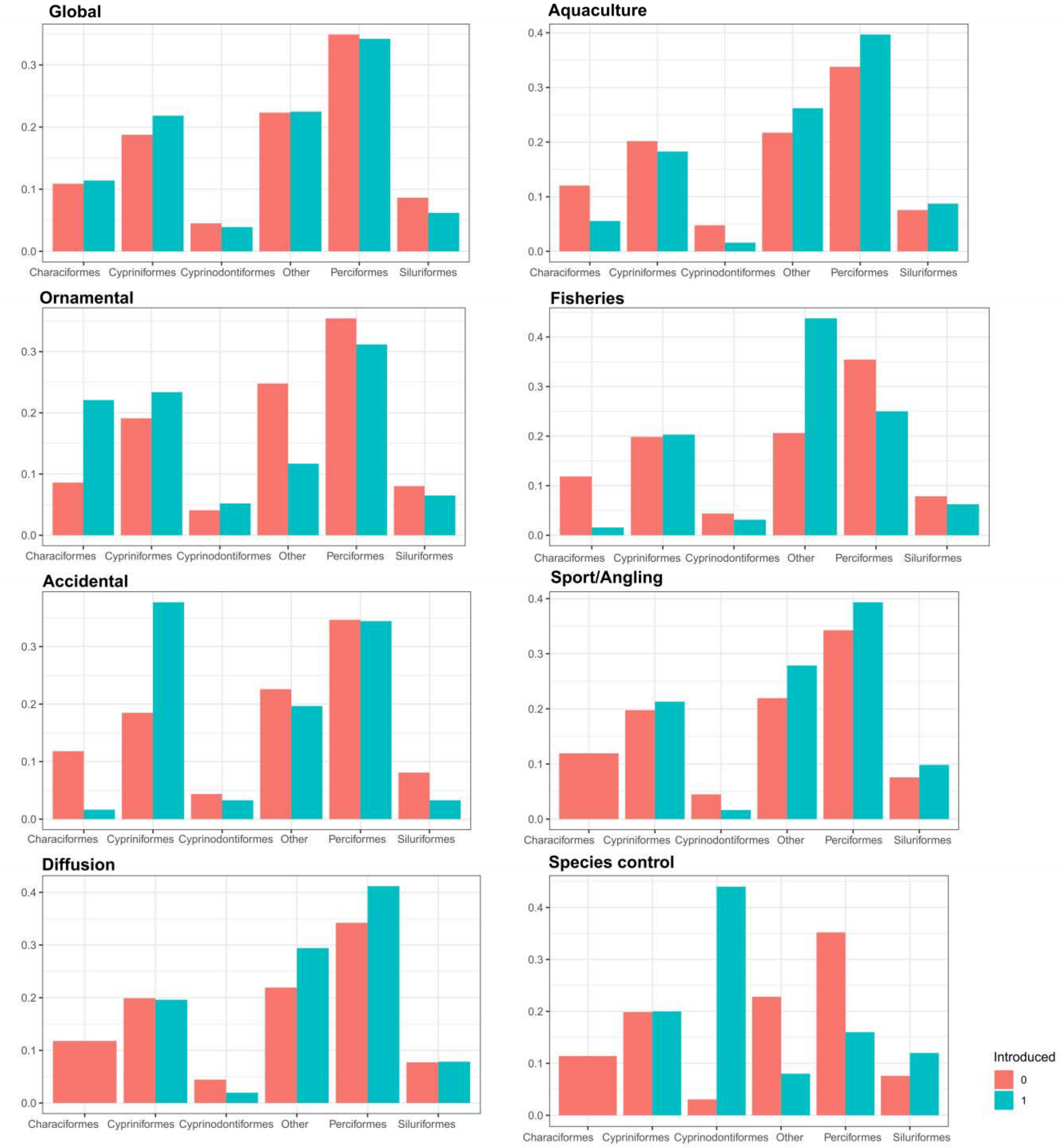


B. Main native region

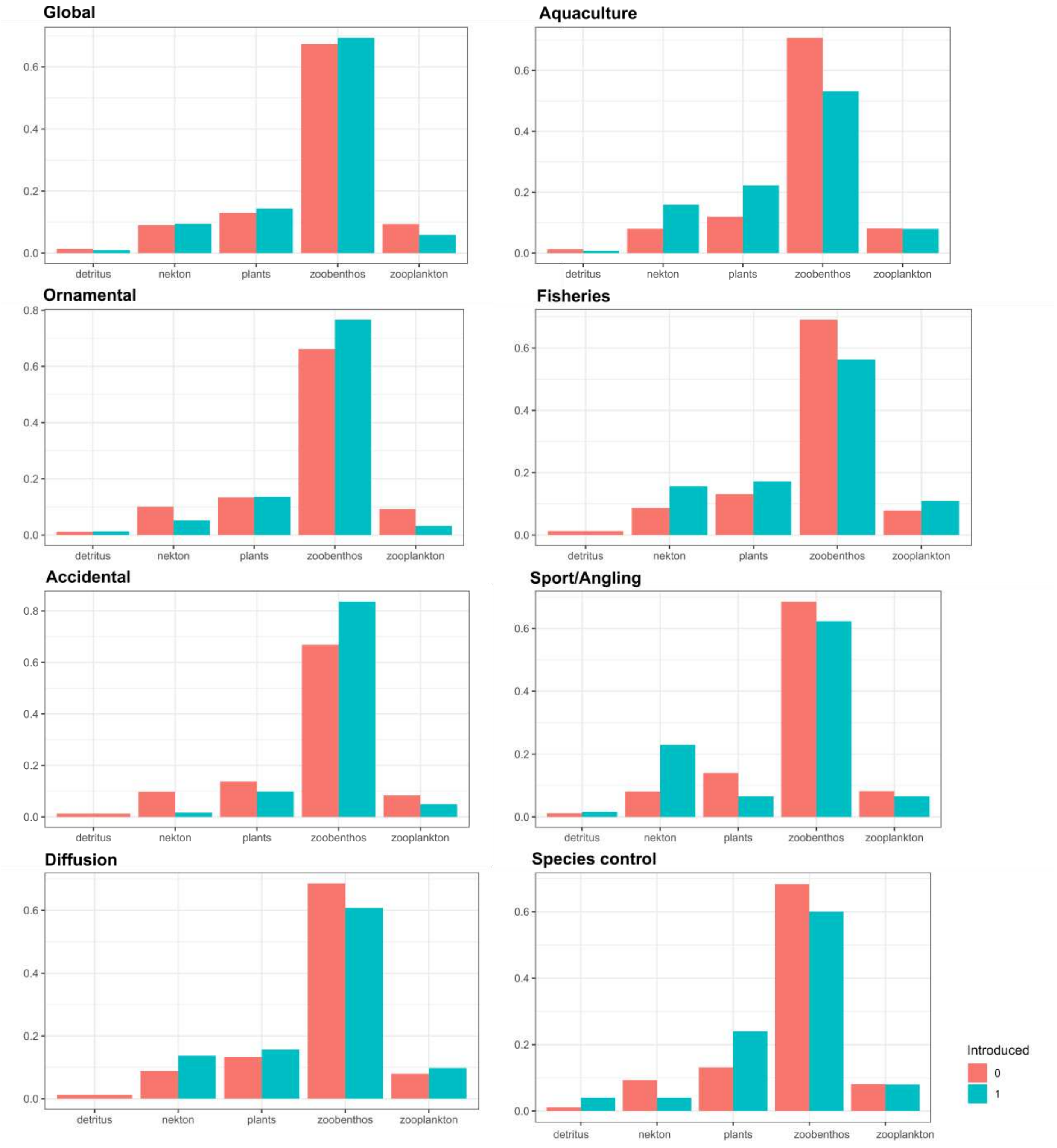


C.Order

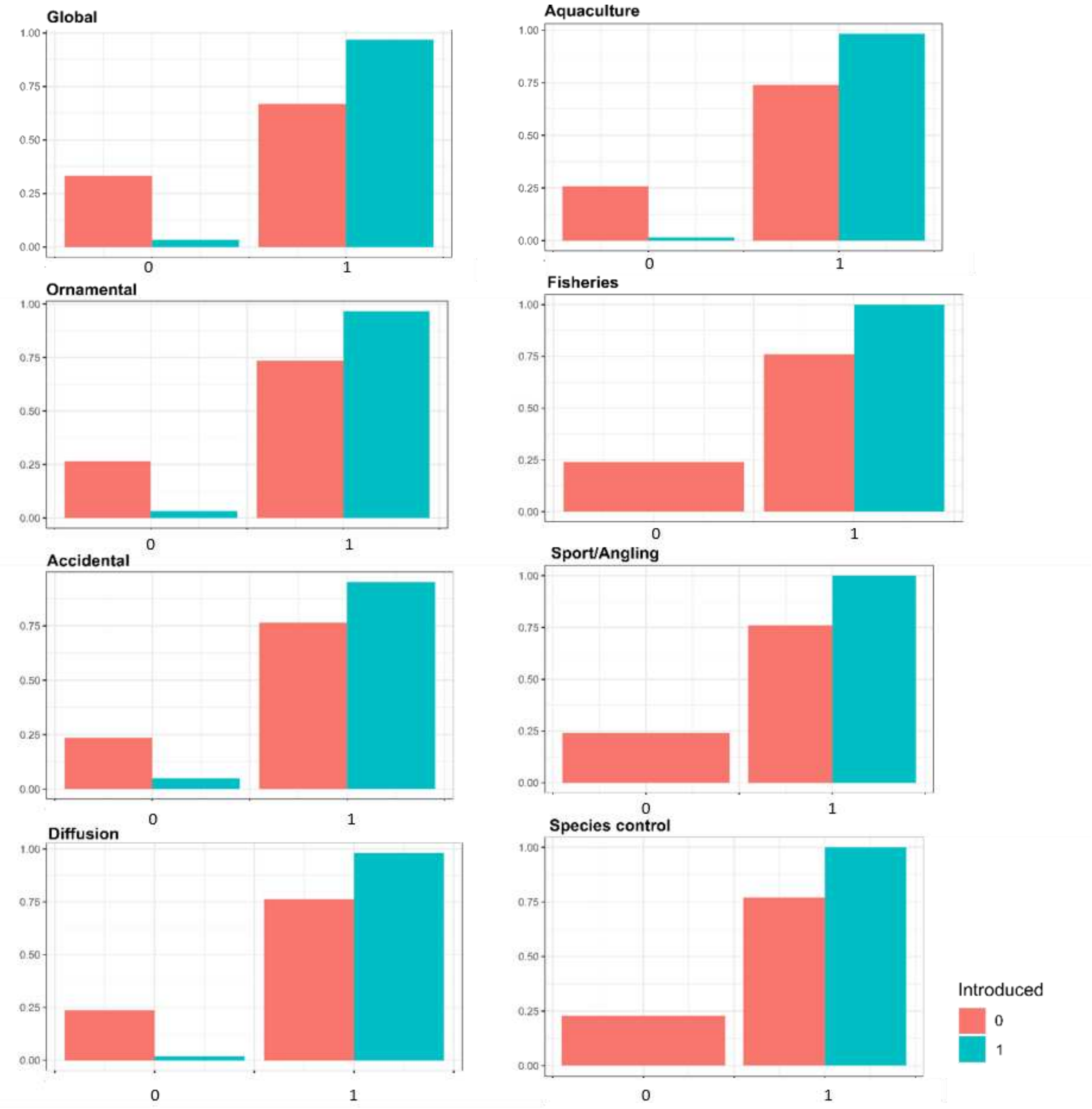
Order



D. Main diet


Global
Aquaculture
Ornamental
Fisheries
Accidental
Sport/Angling
Diffusion
Species control
0.0
0.2
0.4
0.6
0.8
detritus
nekton
plants
zoobenthos
zooplankton
Introduced
0
1

E. Human use (0 = no human use; 1= with a human use)



Appendix 7: Results of Wilcoxon tests (A) and Fisher tests (B)

The cells in white correspond to the p-values of the direct comparisons between introduced and non-introduced species for each characteristic. The cells in gray show the proportion of significant tests performed using the repeated random subsampling approach. With this latter approach, we reduced the majority class (non-introduced species) to a random sample of size equal to the minority class (introduced species) and performed 999 repetitions.

A.	Amplitudetemp		BlBd		TL		NbDiet		NbNativeRegion		PFiBd	
GLOBAL	2.51E-10	1	1.04E-06	1	0.737604	0	6.78E-12	1	0.000143	0.998999	0.485032	0.001001
Aquaculture	2.02E-11	1	0.002798	0.725726	0.07099	0.189189	1.74E-13	1	0.00031	0.820821	0.664508	0.014014
Species control	0.173449	0.066066	0.337548	0.049049	0.616464	0.021021	0.78624	0.001001	0.264231	0.072072	0.000931	0.685686
Ornamental	0.368074	0.032032	1.95E-11	1	2.21E-05	0.988989	0.053015	0.263263	0.152031	0.096096	0.003518	0.698699
Fisheries	6.85E-12	1	0.914416	0.005005	0.00101	0.723724	4.04E-08	0.997998	3.40E-06	0.922923	0.462093	0.038038
Accidental	9.54E-15	1	0.346491	0.036036	0.265602	0.057057	2.36E-05	0.95996	3.38E-07	0.954955	0.00684	0.515516
Sport angling	9.51E-10	1	0.483734	0.026026	0.024289	0.317317	2.36E-06	0.986987	0.055281	0.155155	0.831201	0.025025
Diffusion	2.60E-07	0.995996	0.928826	0.011011	0.044861	0.251251	6.97E-08	1	0.017359	0.263263	0.11614	0.111111

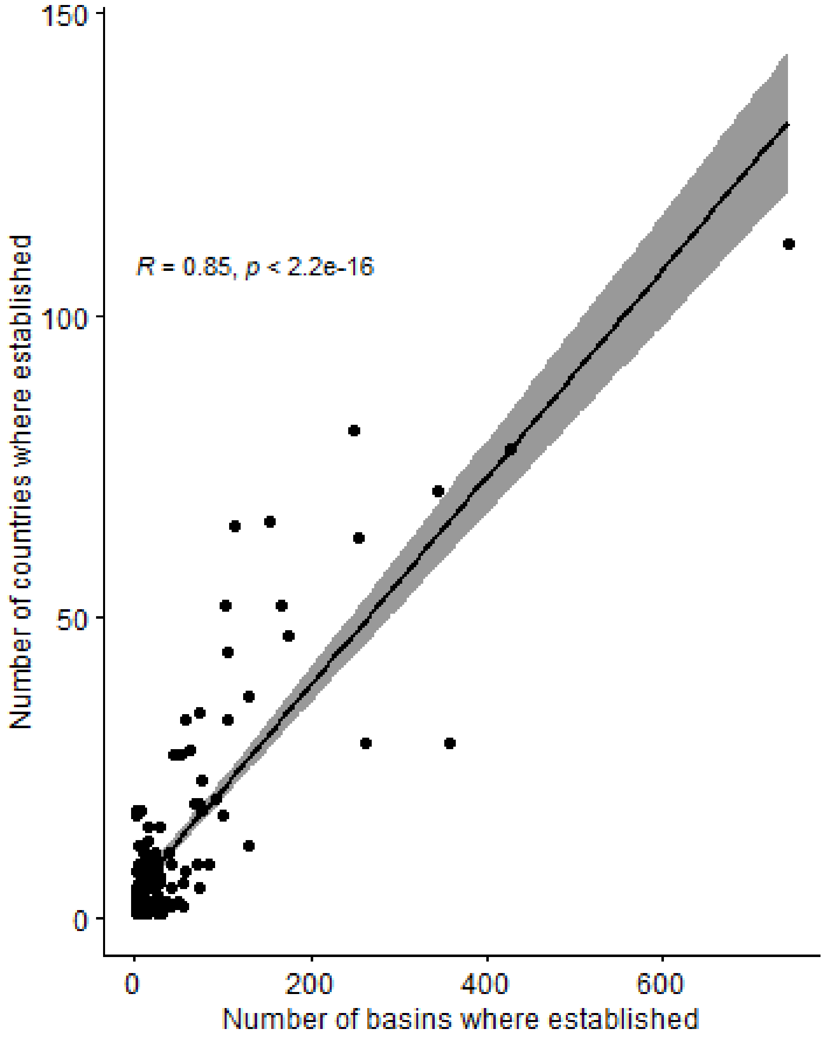
B.	Detritus		Nekton		Plants		Zoobenthos		Zooplankton	
GLOBAL	0.754013	0	0.732406	0	1	0	0.298897	0.011011	0.24669	0.007007
Aquaculture	1	0	0.030585	0.145145	0.005761	0.492492	0.000293	0.866867	0.861305	0.003003
Species control	0.261987	0	1	0	0.163433	0.066066	0.293126	0.024024	1	0
Ornamental	1	0	0.062202	0.193193	1	0.002002	0.012419	0.457457	0.024228	0.347347
Fisheries	1	0	0.098381	0.078078	0.59911	0.001001	0.058526	0.153153	0.234538	0.031031
Accidental	1	0	0.009727	0.421421	0.369087	0.016016	0.008623	0.471471	1	0
Sport angling	0.531461	0	0.000393	0.587588	0.074201	0.135135	0.338183	0.016016	0.810137	0.001001
Diffusion	1	0	0.249888	0.014014	0.8451	0.002002	0.231947	0.028028	0.427364	0.014014

	Australian		Ethiopian		Nearctic		Neotropical		Palearctic		Sino-Oriental	
GLOBAL	0.014608	0.680681	1.35E-07	1	0.856894	0	0.489266	0.002002	0.001116	0.980981	0.00432	0.878879
Aquaculture	0.413994	0.007007	0.119417	0.094094	0.007232	0.386386	0.013894	0.415415	0.01604	0.284284	0.905013	0.001001
Species control	0.392562	0.002002	0.801416	0.001001	1	0	0.807353	0.001001	1	0	0.319174	0.022022
Ornamental	0.058244	0.203203	1.39E-05	0.985986	0.00018	0.952953	1.29E-09	1	0.001306	0.778779	1.30E-05	0.976977
Fisheries	0.167867	0.047047	0.02303	0.263263	0.004606	0.477477	0.000129	0.921922	8.82E-08	0.990991	0.257193	0.037037
Accidental	0.043255	0.168168	0.000113	0.893894	0.616514	0.006006	0.000311	0.896897	1.08E-10	1	0.019535	0.224224
Sport angling	0.252548	0.025025	0.031938	0.203203	4.83E-06	0.947948	0.00577	0.564565	0.010836	0.315315	0.185659	0.058058
Diffusion	0.761908	0	0.282508	0.03003	0.070263	0.103103	0.000393	0.75976	0.00032	0.711712	1	0.001001

	Characiformes		Cypriniformes		Cyprinodontiformes		Other		Perciformes		Siluriformes	
GLOBAL	0.820158	0	0.28317	0.016016	0.727339	0	1	0	0.880377	0	0.228691	0.008008
Aquaculture	0.03098	0.251251	0.716595	0.001001	0.148842	0.068068	0.296494	0.027027	0.222938	0.044044	0.592005	0.001001
Species control	0.099416	0.05005	1	0	5.24E-10	0.994995	0.090298	0.1001	0.054311	0.135135	0.433603	0
Ornamental	1.18E-05	0.978979	0.263526	0.024024	0.512046	0.002002	0.000259	0.937938	0.349136	0.02002	0.618217	0.002002
Fisheries	0.006354	0.506507	0.87193	0	1	0.001001	6.87E-05	0.852853	0.10166	0.095095	0.809885	0.001001
Accidental	0.009741	0.444444	0.000722	0.698699	1	0	0.749652	0.006006	1	0.001001	0.219148	0.02002
Sport angling	0.001034	0.772773	0.740696	0.006006	0.507933	0.006006	0.337598	0.026026	0.484922	0.019019	0.460308	0.004004
Diffusion	0.004267	0.541542	1	0.002002	0.718426	0.001001	0.225614	0.051051	0.362274	0.012012	1	0

	Bearers		Guarders		Non-guarders		Human use: yes		Human use: no	
GLOBAL	0.003544	0.905906	0.020779	0.548549	0.942193	0	1.80E-28	1	1.80E-28	1
Aquaculture	0.432483	0.009009	0.266134	0.021021	0.769127	0.008008	1.05E-12	1	1.05E-12	1
Species control	4.53E-06	0.937938	0.160819	0.04004	0.011815	0.372372	0.002570427	0.522522523	0.002570427	0.522522523
Ornamental	0.230178	0.027027	0.005401	0.597598	0.104478	0.131131	1.24E-12	1	1.24E-12	1
Fisheries	0.290759	0.023023	0.453784	0.009009	0.087399	0.112112	6.54E-08	1	6.54E-08	1
Accidental	0.010633	0.484484	0.169103	0.038038	0.590419	0.009009	0.000318095	0.876876877	0.000318095	0.876876877
Sport angling	0.010633	0.481481	0.002016	0.488488	0.346531	0.025025	1.84E-07	0.998998999		
Diffusion	0.438486	0.014014	0.046671	0.167167	0.305122	0.02002				

Appendix 8: Correlation between the number of countries and the number of basins where species have established (161 species considered)



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Annexe 5 : Annexes du Chapitre 4

C. Bernery*, C. Marino*, C. Bellard. Differences in exotic species characteristics along an establishment gradient.

* Co-premières autrices

Appendix 1. Material and methods used to link the establishment abilities with the ecological impact.

For each group of the establishment gradient, we calculated the proportion of exotic fish that had an ecological impact recorded in their exotic range. To this aim, we gathered impact data for each species as a binary variable (0 = no impact, 1 = presence of impact) using FishBase (Froese and Pauly, 2019). In this database, ecological impact relates to the significant ecological interactions an exotic species can have in a system where it has been introduced. We considered the presence of impact for a species when it was reported as having an adverse effect or a probable adverse effect on the ecosystem (Froese and Pauly, 2019). We finally compared the proportion of fish with impact in each group along the gradient using chi-squared tests. See Fig. S1 and Table S4 for the results of this analysis.

Reference: Froese, R. and Pauly, D. 2019. FishBase. World Wide Web electronic publication. www.fishbase.org.

Supplementary figures

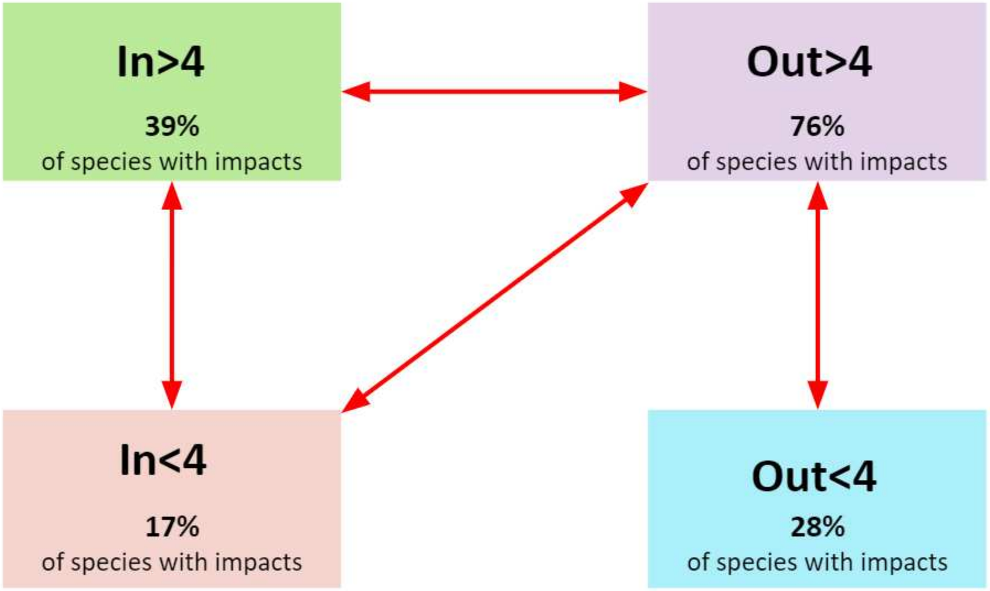

Fig. S1. Proportion of exotic freshwater fish species having ecological impacts in each group along the gradient of establishment. Groups showing significantly different proportions of species with impact are connected with red arrows. The Chi-squared tests and associated p-values are detailed in Table S4.

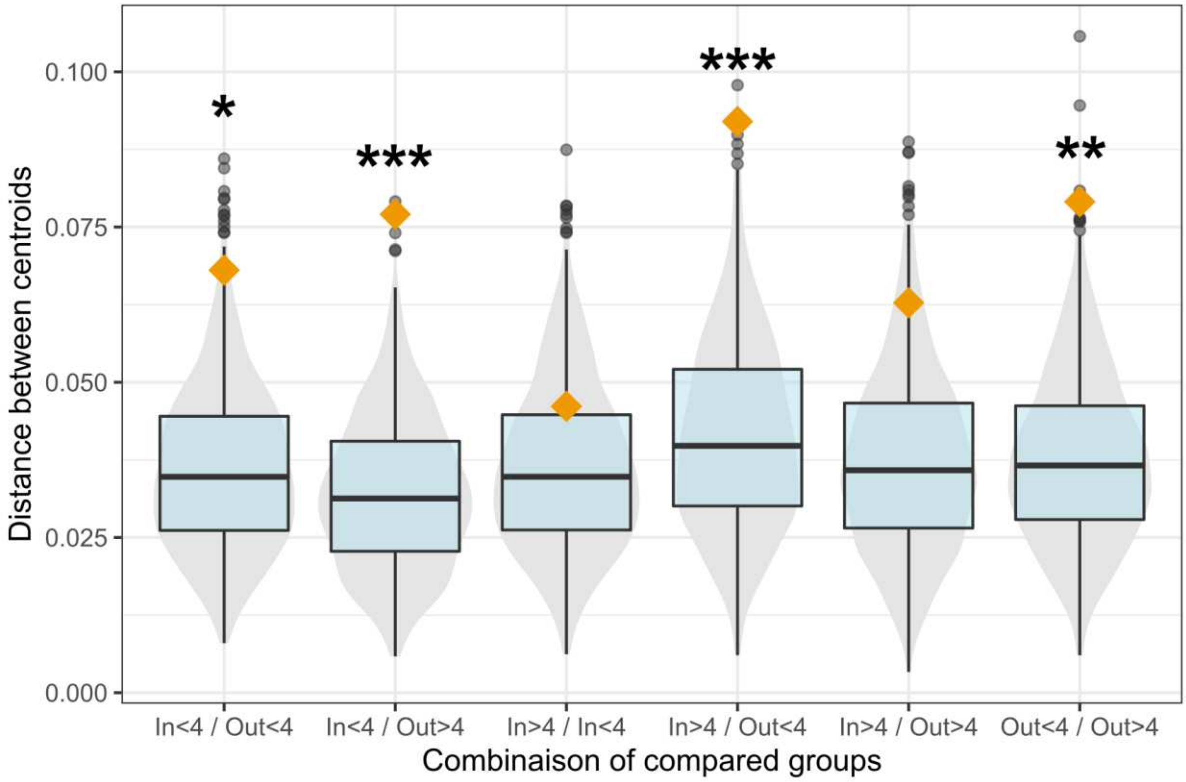

Fig. S2. Distances between centroids of the hypervolumes encompassed by the four groups of fish along the establishment gradient. The orange losange represents the observed value of distance between each group pair. Gray violins and boxplots represent the distribution of the distances obtained under the null model (n=9999). Stars show significant differences between the observed value and the simulated ones.

Supplementary Tables

Table S1. Sensibility to cut-off at four basins for defining the groups of fish according to the number of basins they are established into. We evaluated the consequences of a cut off change on the p-values evaluating the significance of the differences between each establishment outcome, for each axis of the PCA. The four different groups correspond to the establishment gradient: species introduced inside their native bioregion in four basins or less (In<4), inside their native bioregion in more than four basins (In>4), outside their native bioregion in in four basins or less (Out<4), and outside their native bioregion in more than four basins (Out>4).

			P-values of the Chi-squared tests				
Axis	**Group 1**	**Group 2**	**Cut at 2**	**Cut at 3**	**Cut at 4**	**Cut at 5**	**Cut at 6**
V1	In<4	Out<4	0,5921	0,5117	0,6867	0,5182	0,5094
V1	In<4	In>4	0,218	0,2904	**0,0236**	0,108	0,3299
V1	In<4	Out>4	**0,0355**	**0,0443**	**0,0081**	**0,025**	**0,0304**
V1	Out<4	In>4	**0,0409**	0,0786	**0,0267**	0,0781	0,1504
V1	Out<4	Out>4	**0,0089**	**0,0122**	**0,0033**	**0,0065**	**0,0118**
V1	In>4	Out>4	0,8205	0,8785	0,9675	0,9476	0,8296
V2	In<4	Out<4	**1,00E-04**	**1,00E-04**	**1,00E-04**	**0**	**0**
V2	In<4	In>4	**0,0481**	0,1102	**0,0238**	**0,0244**	**0,0238**
V2	In<4	Out>4	**0**	**0**	**0**	**0**	**0**
V2	Out<4	In>4	0,0543	0,0967	0,3186	0,5013	0,4766
V2	Out<4	Out>4	0,1932	0,3608	0,3738	0,3132	0,476

V2	In>4	Out>4	**0,0073**	**0,0096**	**0,016**	0,0622	0,1106
V3	In<4	Out<4	0,0713	**0,0136**	**0,0046**	**8,00E-04**	**0,001**
V3	In<4	In>4	**0,04**	0,3238	0,2619	0,4934	0,1644
V3	In<4	Out>4	0,763	0,5016	0,4635	0,3517	0,4099
V3	Out<4	In>4	**0**	**3,00E-04**	**1,00E-04**	**4,00E-04**	**9,00E-04**
V3	Out<4	Out>4	**0,0278**	**0,0077**	**0,0013**	**5,00E-04**	**0,0037**
V3	In>4	Out>4	**0,0107**	0,0716	0,2424	0,5412	0,2987
V4	In<4	Out<4	0,0672	**0,0154**	**0,0074**	**0,0154**	**0,0157**
V4	In<4	In>4	0,5428	0,4907	0,2913	0,2644	0,3931
V4	In<4	Out>4	0,5826	0,7959	0,5119	0,3427	0,4485
V4	Out<4	In>4	0,3384	0,234	0,4605	0,7638	0,7484
V4	Out<4	Out>4	0,465	0,1442	0,1036	0,1943	0,1414
V4	In>4	Out>4	0,6982	0,7259	0,6169	0,6308	0,6352

Table S2. Correlation between species traits and the first four axes of principal component analysis containing the 222 exotic freshwater fish. Spearman coefficients and p-values are reported. The only non-numeric trait (parental care) was converted into an ordered factor from the lowest level of parental care to the highest: 1 = nonguarder, 2 = guarder, 3 = bearer. converted into binary variables to compute the correlations. The strongest correlations (r < -0.4 or r > 0.4) and their associated significant p-values are shown in bold.

	PC1			**PC2**			**PC3**			**PC4**		
Trait	**Coeff.**	**Stat**	***p***	**Coeff.**	**Stat**	***p***	**Coeff.**	**Stat**	***p***	**Coeff.**	**Stat**	***p***
Morphology												
EhBd	-0.164	0.027	0.015	0.064	0.004	0.341	0.144	0.021	0.032	-0.139	0.019	0.038
BlBd	-0.276	0.076	<0.001	-0.064	0.004	0.34	**-0.394**	**0.155**	**<0.001**	0.116	0.013	0.085
PFiBd	-0.172	0.03	0.01	0.189	0.036	0.005	0.26	0.067	<0.001	**-0.369**	**0.136**	**<0.001**
MoBd	-0.16	0.025	0.017	0.18	0.032	0.007	0.245	0.06	<0.001	-0.28	0.078	<0.001
Maximum length	-0.178	0.032	0.008	0.183	0.034	0.006	-0.144	0.021	0.032	0.152	0.023	0.024
Ecology												
Diet detritus	**0.746**	**0.556**	**<0.001**	0.212	0.045	0.002	**0.333**	**0.111**	**<0.001**	-0.078	0.006	0.244
Diet nekton	**-0.39**	**0.152**	**<0.001**	**0.801**	**0.642**	**<0.001**	**0.111**	0.012	0.1	**0.366**	**0.134**	**<0.001**
Diet plants	**0.788**	**0.62**	**<0.001**	-0.12	0.014	0.074	0.08	0.006	0.234	**0.498**	**0.248**	**<0.001**
Diet zoobenthos	0.017	0	0.8	0.352	0.124	<0.001	-0.038	0.001	0.574	0.193	0.037	0.004
Diet zooplankton	**0.538**	**0.289**	**<0.001**	**0.579**	**0.336**	**<0.001**	**-0.394**	**0.155**	**<0.001**	**-0.4**	**0.16**	**<0.001**
Temp. amplitude	0.012	0	0.854	0.087	0.008	0.196	**-0.69**	**0.477**	**<0.001**	0.122	0.015	0.071
Beahavior												
Parental care	-0.043	0.014	0.077	0.218	0.147	<0.001	**0.811**	**0.636**	**<0.001**	**-0.306**	**0.086**	**<0.001**

Table S3. Results of Kolmogorov-Smirnov (KS) tests and associated p-values when comparing density distributions along the four axes of the PCA for both dimensions of establishment gradient.

Dimension	**Axis**	**D**	**p**
Number of basins	PC1	**0.298**	**<0.001**
Number of basins	PC2	**0.248**	**0.002**
Number of basins	PC3	0.13	0.31
Number of basins	PC4	0.102	0.609
Location of establishment	PC1	0.105	0.57
Location of establishment	PC2	**0.196**	**0.029**
Location of establishment	PC3	**0.259**	**0.001**
Location of establishment	PC4	0.17	0.081

Table S4. Results of the Chi-squares tests evaluating the differences in proportion of species with ecological impact between groups along the gradient of establishment. The four different groups correspond to the establishment gradient: species introduced inside their native bioregion in four basins or less (In<4), inside their native bioregion in more than four basins (In>4), outside their native bioregion in in four basins or less (Out<4), and outside their native bioregion in more than four basins (Out>4). In bold are statistically significant differences (p<0.05).

Establishment group 1	Establishment group 2	p-value	X-squared	Df
In<4	**In>4**	**0.0149**	**5.9317**	1
In<4	Out<4	0.2335	1.4196	1
In<4	**Out>4**	**1.713e-11**	**45.274**	1
In>4	Out<4	0.3959	0.7207	1
In>4	**Out>4**	**0.0005**	**12.134**	1
Out<4	**Out>4**	**4.167e-06**	**21.186**	1

Annexe 6

A. Turbelin, C. Diagne, E. J. Hudgins, D. Moodley, M. Kourantidou, A. Novoa, P. J Haubrock, **C. Bernery**, R. Gozlan, R. A. Francis, F. Courchamp (2022). Introduction pathways of economically costly invasive alien species. *Biological Invasions*. 1–19.

Implication dans le projet : J'ai participé à la conception du projet et à la compilation des données de coûts par voies d'introduction.

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ORIGINAL PAPER

Introduction pathways of economically costly invasive alien species

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Abstract Introduction pathways play a pivotal role in the success of Invasive Alien Species (IAS)—the subset of alien species that have a negative environmental and/or socio-economic impact. Pathways refer to the fundamental processes that leads to the introduction of a species from one geographical location to another—marking the beginning of all alien species invasions. Increased knowledge of pathways is essential to help reduce the number of introductions and impacts of IAS and ultimately improve their management. Here we use the *InvaCost* database, a comprehensive repository on the global monetary impacts of IAS, combined with pathway data classified using the Convention on Biological Diversity (CBD) hierarchical classification and compiled from CABI Invasive Species Compendium, the Global Invasive Species Database (GISD) and the published literature to address five key points. Data were available for 478 individual IAS. For these, we found that both the total and annual average cost per species introduced through the 'Stowaway'

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(US$144.9bn; US$89.4m) and 'Contaminant' pathways (US$99.3bn; US$158.0m) were higher than species introduced primarily through the 'Escape' (US$87.4bn; US$25.4m) and 'Release' pathways (US$64.2bn; US$16.4m). Second, the recorded costs (both total and average) of species introduced unintentionally was higher than that from species introduced intentionally. Third, insects and mammals, respectively, accounted for the greatest proportion of the total cost of species introduced unintentionally and intentionally respectively, at least of the available records; 'Stowaway' had the highest recorded costs in Asia, Central America, North America and Diverse/Unspecified regions. Fourthly, the total cost of a species in a given location is not related to the year of first record of introduction, but time gaps might blur the true pattern. Finally, the total and average cost of IAS were not related to their number of introduction pathways. Although our findings are directly limited by the available data, they provide important material which can contribute to pathway priority measures, notably by complementing studies on pathways associated with ecologically harmful IAS. They also highlight the crucial need to fill the remaining data gaps—something that will be critical in prioritising limited management budgets to combat the current acceleration of species invasions.

Keywords Introduction pathways · *InvaCost* · Invasive alien species · Monetary impact · Exotic mammals · Non-native insects · Management · Policy

Introduction

All alien species invasions begin with the intentional or accidental transportation of individuals or propagules by humans outside of their historical biogeographic boundaries (Blackburn et al. 2011; Lehan et al. 2013; Essl et al. 2015). Introduction pathways (henceforth 'pathways') refer to the fundamental processes that leads to the introduction of a species from one geographical location to another (Richardson et al. 2011). Consequently, pathways play a pivotal role in the success of Invasive Alien Species (IAS)—the subset of alien species that have a negative environmental and/or socio-economic impact—as they influence the number, frequency and geographic range of propagules dispersed (Pyšek et al. 2020; Gippet and Bertelsmeier, 2021). Increased knowledge of pathways is crucial to help reduce the movement and impacts of IAS (Leung et al. 2002; Essl et al. 2015) and ultimately improve their management (Simberloff and Rejmanek 2011; Novoa et al. 2020). In recent years, research and policy have focused on identifying and classifying pathways and prioritising which pathways to manage in order to prevent biological invasions. This was illustrated by the Strategic Plan for Biodiversity 2011–2020 (Target 9; Convention on Biological Diversity 2014; https://www.cbd.int/sp/targets/rationale/target-9/) in which parties aspired that *'by 2020, invasive alien species and pathways are identified and prioritized'*.

Many pathways have already been identified through assessments at regional levels and across ecosystems. These assessments help advance our understanding of IAS flows and support the development of policy tools (Hulme et al. 2008; Essl et al. 2015; Katsanevakis et al. 2013; Pyšek et al. 2011; Nunes et al. 2015; García-Berthou et al. 2005; Pergl et al. 2017). Global databases of IAS such as the IUCN's Global Invasive Species Database (GISD, www.iucngisd.org) and the CABI Invasive Species Compendium (CABI ISC, www.cabi.org/isc) list between 34 and 80 different pathways through which alien species can be introduced to new locations. Examples of pathways include horticulture (e.g. purple loosestrife, *Lythrum salicaria*; Maki and Galatowitsch 2004), agriculture (e.g. sisal hemp, *Agave sisalana;* Ortega et al. 2019), pet trade (e.g. Burmese python, *Python bivittatus*; Wilson et al. 2011) and biofouling (e.g. zebra mussel, *Dreissena polymorpha*; Carlton 2008). Such lists are neither exhaustive nor static; as societies evolve and economic activities continue to grow, and so more pathways are expected to emerge. To facilitate comparative studies on pathways, Hulme et al. (2008) proposed a pathway classification, which was further developed and subsequently adopted by the Convention on Biological Diversity (CBD, 2014). The CBD's hierarchical framework encompasses three levels; the first level is three broad mechanisms through which

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species may arrive to a new location: movement of commodities, arrival of a transport vector, and/or natural spread from a neighbouring region. These three mechanisms then encompass six primary pathways (Hulme et al. 2008): 'Release' (intentional introduction as a commodity for release), 'Escape' (intentional introduction as a commodity but unintentional escape; includes the release of alien organisms from captivity), 'Contaminant' (unintentional introduction with a specific commodity), 'Stowaway' (unintentional introduction attached to or within a transport vector), 'Corridor' (unintentional introduction via human infrastructures linking previously unconnected regions), and 'Unaided' movement (unintentional introduction through natural dispersal of alien species across political borders). These six pathways are further divided into 44 subcategories, covering pathways applicable to alien species from a wide range of taxonomic groups and environments (Pergl et al. 2020) (Fig. 1).

Prioritizing the management of high-risk pathways is necessary to achieve cost-effective management of IAS, essentially by preventing additional introductions of species that have already been introduced as well as new harmful alien species (McGeoch et al. 2016). IAS can generate substantial costs in terms of damage to ecosystems, impacts on human well-being and expenditures on management (Diagne et al. 2021a). At the same time, there is evidence that investing in the prevention of IAS introduction (proactive management) is less costly—and likely more efficient—compared to allocating resources and funds to reactive management once they establish and become invasive (Leung et al. 2002; Ahmed et al., this Special Issue).

Pathways can be prioritized using (i) the number of IAS introduced per pathway and/or (ii) an assessment of the observed or potential impact caused by species introduced through different pathways (Essl et al. 2015; McGeoch et al. 2016). Studies investigating the number of species per pathway have found that, where pathway information had been deduced, movement of commodities was associated with the most documented introductions. Indeed, 'Escape' is identified as the most prevalent pathway for IAS (Faulkner et al. 2016; McGrannachan, et al. 2020), predominantly through horticulture trade (Turbelin et al. 2017) and the most important for plants and vertebrates (Saul et al. 2017). It is worth noting that pathway information is still lacking for a number of IAS, particularly plant and invertebrate taxa (Faulkner et al. 2016). Other studies showed that invaders associated with a high number of pathways are more likely to have an ecological impact in newly invaded sites (Pergl et al. 2017; Saul et al. 2017). Particularly for plants, both the number and types of pathways may influence invasion success and the likelihood of impact (Pysek et al. 2011; Pergl et al. 2017). Plants introduced through 'Release', 'Corridor' and 'Unaided' pathways are more likely to have an ecological impact than when introduced as 'Contaminants' (Pergl et al. 2017). Plants introduced through these pathways are also more likely to successfully establish and be accepted in society when grown as animal food or for environmental uses (van Kleunen et al. 2020). Similarly, certain pathways may favor successful invaders, e.g. pet trade particularly favors invasive species (Gippet and Bertelsmeier, 2021).

Whilst a number of publications have examined the links between ecological impacts and pathways of IAS (e.g. Pergl et al. 2017; Saul et al. 2017), there are currently no studies assessing relationships between pathways and economic impacts of IAS. Although economic impact may overlook aspects of ecological impacts, it is a very useful metric of the impact of IAS, as it can be quantitative, and if costs are standardized, they can be compiled across regions or taxa and compared between pathways. A better understanding of the economic costs of invasions is also a key way to raise global awareness about IAS, optimise transboundary legislation and help the prioritisation of management actions (Diagne et al. 2020a).

In this paper, we investigate pathways of economically-harmful IAS using the most up-to-date compilation of monetary cost information on IAS—the *InvaCost* database (Diagne et al. 2020b) and pathway data classified using the CBD hierarchical classification (CBD, 2014; Hulme et al. 2008) and compiled from CABI ISC, the GISD and the published literature. Specifically, we address the following questions: (*i*) Have some introduction pathways facilitated the introduction of more economically costly species than others? (*ii*) Are there differences in costs between species introduced intentionally and unintentionally? (*iii*) How are costs taxonomically and spatially distributed across introduction pathways? (iv) Is there a relationship between the cost of species and the year of first record of introduction? and (*v*) Is there a

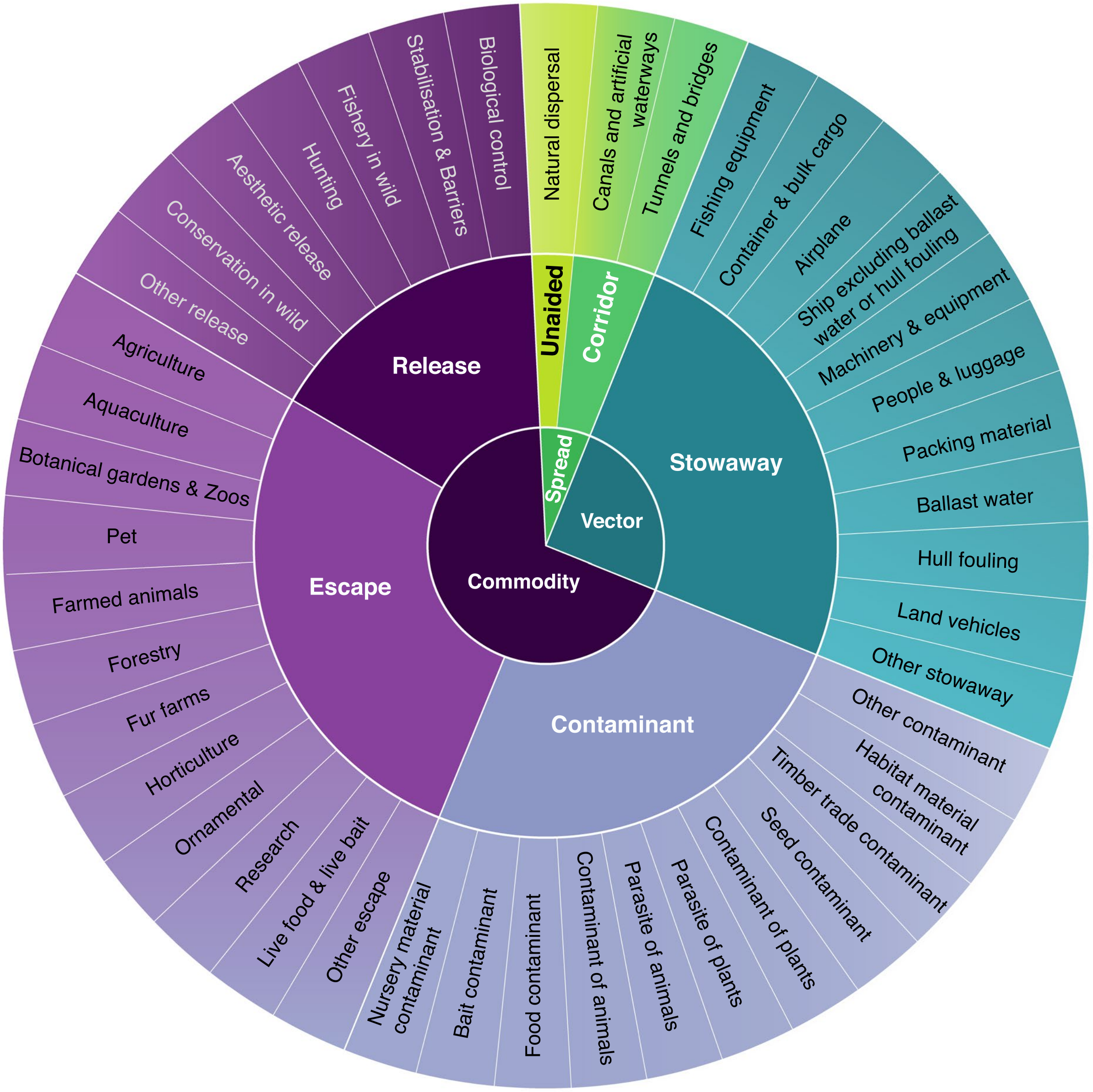

Fig. 1 Convention on Biological Diversity (CBD) pathway classification. This framework uses a hierarchical approach in which alien species may arrive in a new location through three broad mechanisms (i.e. movement of a commodity, arrival of a transport vector, or spread from a neighbouring region), 6 main pathways (i.e. release, escape, contaminant, stowaway, corridor, and unaided) and 44 pathway subcategories (e.g. ornamental, aquaculture, seed contaminant, etc.). Changes adopted from suggestions by Harrower et al. (2018) include the addition of ‘Other contaminant’ and the removal of ‘Release in nature for use’. Figure adapted from Harrower et al. (2018). ‘Intentional’ pathways include ‘Release’ and ‘Escape’ and ‘Unintentional’ pathways include ‘Contaminant’, ‘Stowaway’, ‘Corridor’ and ‘Unaided’

relationship between the number of possible introduction pathways of IAS and their costs?

Methods

Cost data collection and filtering

To assess the economic impact of IAS over the last 50 years (1970–2020), we relied on cost data recorded in the latest version of *InvaCost* (version 4.0, openly available at https://doi.org/10.6084/m9.figshare.12668570.v4), which is the most complete and up-to-date global dataset of the reported economic costs attributable to biological invasions (Diagne et al. 2020b). *InvaCost* has been built by a combination of both systematic literature searches (e.g., specific search strings used in Web of Science and Google Scholar) and direct solicitations (e.g., stakeholders, scientific experts) in more than 10 languages, to gather any cost information available in written documents. After ensuring the relevance of each document, cost information was collated, standardised to a common and up-to-date currency in the database (i.e. 2017 US dollars), and finally classified into categories using a range of descriptive fields (complete description and details on these descriptive fields are available at https://doi.org/10.6084/m9.figshare.12668570)(See Table 1 for a description of the fields used in this study). This updatable and publicly available resource contains 13,123 cost entries (as of June 2021), therefore providing an essential basis for worldwide research and policymaking targeting IAS (Diagne et al. 2020a; 2020b). The 'living' nature of the dataset allows for the taxonomic and geographic gaps in cost information to be addressed over time, and then keeps all users and stakeholders informed on cost dynamics and distribution (Diagne et al. 2021a).

We used successive filters from the *InvaCost* database to identify relevant cost entries for our analysis and obtain a conservative and realistic estimate of costs. First, we extracted costs empirically "observed" in the invaded environment and left out all "potential" costs (not yet actually realised but rather expected and/or predicted over time within or beyond their actual distribution area). Second, we then retained costs classified as "high" reliability—therefore discarding "low" reliability costs—thereby keeping only cost estimates either provided by officially pre-assessed documents (peer-reviewed articles

Table 1 Definition of fields from the InvaCost Database. Source: https://doi.org/10.6084/m9.figshare.12668570

Field	Definition
Method reliability (Method_reliability column)	Assessment of the methodological approach used for cost estimation as of (i) high reliability if either provided by officially pre-assessed materials (peer-reviewed articles and official reports) or the estimation method was documented, repeatable and/or traceable if provided by other grey literature, or (ii) low reliability if not
Implementation (Implementation *column*)	This states — at the time of the estimation — whether the reported cost was actually observed (i.e., cost actually incurred) or potential (i.e., not incurred but expected cost)
Cost type (Type_of_cost_merged column)	Categories of the Type of cost column reassigned into **damage** (economic losses due to direct and/or indirect impacts of invaders, such as yield loss, health injury, land alteration, infrastructure damage, or income reduction), **management** (monetary resources allocated to mitigate the spread or impacts of invaders, such as prevention, control, research, long-term management, eradication) or **mixed** (when costs included both 'damage' and 'management' components); every cost for which the exact nature of cost was not clearly defined was assigned to **unspecified**
Management type (*Management_type* column)	**Pre-invasion management** (monetary investments for preventing successful invasions in an area—including quarantine or border inspection, risk analyses, biosecurity management, etc.), **post-invasion management** (money spent for managing invasions in invaded areas—including control, eradication, containment), **knowledge/funding** (money allocated to all actions and operations that could be of interest at all steps of management at pre- and post-invasion stages—including administration, communication, education, research, etc.), or **mixed** was assigned when costs include at least (and without possibility to disentangle the specific proportion of) two of the previous categories; every cost for which the exact nature of cost was not clearly defined was assigned to **unspecified**. Every entry that has partly or fully associated with damage costs was assigned to **NA**
Geographic Region (*Geographic_region* column)	Geographical region(s) where the cost occurred (**Africa, Antarctic-Subantarctic, Asia, Central America, Europe, North America, Oceania, Pacific islands, South America**) In this analysis Oceania and Pacific islands are classified as one category: "Oceania / Pacific islands". Diverse/Unspecified is assigned when costs are incurred over multiple regions or the geographic location was not specified

and official reports) or associated with an estimation methodology that was deemed reproducible when building the database (Diagne et al. 2020b). Lastly, we focused on cost estimates exclusively attributed to individual species, therefore multi-species costs or genus-level costs were removed (e.g. when the value in the *Species* field included "sp." or "spp." or was simultaneously associated with several species without any possibility to disentangle specific contribution of each taxon to the overall cost). Following these filtering steps, our dataset (hereafter called *filtered_subset*) contained 7,175 entries (Supplementary Material 1). Finally, we extracted the list of individual species with recorded costs. After checking for discrepancies in species names (i.e., where entries for the same species have different scientific names, we opted for the internationally preferred scientific name as described in CABI), the number of individual species with cost records amounted to 606.

Collection and compilation of pathway information

Pathways were categorised using Harrower et al. (2018), a guidance document for interpreting the Convention on Biological Diversity (CBD, 2014) pathway classification framework (Fig. 1). This pathway classification system has limitations, especially regarding uncertainty linked to subcategories (Faulkner et al. 2016, 2020; Pergl et al. 2020), however McGrannachan et al. (2021) suggested that it is a reliable framework for reporting on IAS pathways at a global level. Pathway mechanisms and categories are defined, and subcategories are listed in Supplementary Material 2. We compiled pathway data for each of the 606 species with reported economic costs in our *filtered_subset* (Supplementary Material 3, which contains all columns hereafter mentioned) mainly using information from CABI ISC (www.cabi.org/isc/) and the GISD (http://www.iucngisd.org/gisd), resulting in a total of 478 species with information on their specific pathways. When the pathway information needed was not available in one of these repositories, we opportunistically extended our searches to other databases on biological invasions (e.g. the Galapagos Species Checklist), and performed targeted searches in the published literature. Pathway descriptions provided in databases or publications were recorded, along with the source of the data (CABI ISC, GISD, etc.), in our pathways dataset. These descriptions do not always match the CBD pathway sub-categories. Each pathway description was initially matched to the CABI ISC pathway description and then classified into the mechanisms, categories, and subcategories of the CBD scheme using the published guidelines for the scheme (i.e. Harrower et al. 2018). Pathways were further classified into pathway types with 'Intentional' pathways including 'Release' and 'Escape' and 'Unintentional' pathways including 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'.

As stated by Harrower et al. (2018; p.88): "*Moreover, the pathway category assigned to a species is typically the pathway(s) that relates directly to the species being introduced. However, the introduction of a species may also be indirectly dependent on another pathway, particularly when the species is contaminant of another species or product. Although these dependent pathways are not directly related to the species they play a part in understanding the process of introduction and are, therefore, important for decision-making and particularly in relation to prevention through management of pathways. As these dependent pathways are important they should be recorded, but as they are not directly related to the species it is important they are not confused with the pathway information that directly relates to the species.*" As such, to highlight pathway dependency, we classified pathways as 'Direct' or 'Indirect' to indicate whether the pathway was related directly to the species being introduced (*Direct)* or when the pathway was related to a species or product that the species being introduced is dependent upon (*Indirect*) (*Direct_or_Indirect* column).

Finally, as IAS can have multiple pathways, we determined the most important pathways for each species and classified each pathway as 'primary' or 'secondary' (*Primary_or_Secondary* column) based on the above-mentioned source information. A pathway was categorised as 'primary' when it was clearly recognised as one of the most important in the source document, i.e. likely leading to successful long-distance introductions as a result of increased propagule pressure (number, frequency and range of propagules) or by facilitating escape. Conversely, a pathway was categorised as 'secondary' when it was less likely to lead to the successful establishment of a species, generally due to either low propagule pressure (i.e. low number of introduction events, low number of individuals per introduction event) or due to it mainly promoting short distance/local dispersal of the species. We classified pathways as ‘secondary’ only when the information provided in databases or publications enabled us to identify primary pathways. Otherwise, pathways were classified as primary. It was thus possible for a species to have more than one primary pathway. See Supplementary Material 4 for an example of how species pathways were classified as ‘direct’ or ‘indirect’ and ‘primary’ or ‘secondary’.

There is a level of inherent uncertainty associated with the compilation of data collated in large-scale databases. We minimized the level of uncertainty associated with pathway-related data input in two ways depending on the source of uncertainty. First, data collation and the merging of different data sources may be a source of potential confusion and errors. Therefore, we checked for and then systematically corrected obvious mistakes in pathway assignment resulting from the merging of datasets using our expert judgement. For example, if the pathway recorded in the database of an invertebrate was ‘Forestry’ but this was a known contaminant, then the new pathway description would be ‘Contaminant of plants’. Second, given that uncertainty may also arise from the varying quality of the source attributing a pathway to a particular species, we assessed pathways based on (i) information from the peer-reviewed literature—providing evidence of transport of a species from one region to another, (ii) indirect evidence of pathway use reported in grey literature (e.g. individuals found near botanic gardens), and (iii) assumptions/deductions made from similar species’ introduction pathways (Harrower et al. 2018).

Data processing

We used the *expandYearlyCosts*() function from the ‘invacost’ package version 0.3–4 (Leroy et al. 2020) in R version 4.0.3 (R Core Team 2020) to ensure that each cost entry—which could correspond to either a single or a multi-year estimate—was consistently recorded on an annual basis for the amount of years that the cost was incurred. The expanded version of our *filtered_subset* contained 21,250 cost entries (hereafter called *expanded_subset*). Finally, we used the R package dplyr (version 1.0.2.)(Wickham et al. 2020) to merge the *expanded_subset* with the pathways dataset (Supplementary Material 3) and generate our *final dataset,* available in Supplementary Material 5. Our *final dataset* contained 77,826 entries covering over 108 countries.

We organised this *final dataset* for further analyses (see below). First, IAS were classified into 13 broad “organism types” based on information from the *Kingdom*, *Phylum*, and *Class* columns: amphibian, arthropods, bird, decapod, fish, fungi, insect, mammal, mollusc, plant, reptile, animalia diverse and other organisms. “Animalia diverse” include invertebrate species from the *Kingdom* Animalia that are not listed in the above animal categories, namely species of the phylum Nematoda, Cnidaria, Platyhelminthes and class Ascidiacea. The category “other organisms” is made up of all organisms not included in the aforementioned categories (e.g. species with *Kingdom* column entries Bacteria, Virus, Chromista). Second, we included information from the *Type_of_cost_merged* column (Table 1) in our *final dataset*, which classifies the cost estimates as “damage” (i.e. economic losses due to direct and/or indirect impacts of invaders, such as yield losses, damage repair, etc.), “management” (i.e. economic resources allocated to actions related to the prevention, management and control of alien species) or “mixed” (i.e. when costs incorporate both ‘damage’ and ‘management’ elements) costs.

Data analyses

To estimate the economic cost of invasive species for the period 1970–2020, we calculated the total cost per pathway observed over this period, by summing all cost estimates provided in the *Cost_estimate_per_year_2017_USD_exchange_rate* column of our *final dataset*. We also calculated (i) the annual average cost per species, by averaging the total cost per year calculated for every species and (ii) the average annual average cost per species per pathway by averaging the annual average cost per species for each pathway.

To assess the potential effects of unknown pathways on the cost distribution shown, we randomly assigned one of the 6 main pathways (‘Release’, ‘Escape’, ‘Contaminant’, ‘Stowaway’, ‘Corridor’, ‘Unaided’) to each species from the InvaCost database which lacked pathway information. We then calculated the total cost per pathway and the average annual average cost per species for each pathway. The probability of a species being assigned a pathway was dependent on the organism group of that species as it was weighted by the proportion of species in each pathway for a given organism group. We repeated that process 200 times and recorded the average, minimum and maximum of the total cost per pathway and the average annual average cost per species for each pathway.

To compare the total and annual average cost per species across pathway categories and subcategories and for "types of cost" (Table 1), we used the Kruskal–Wallis rank sum test. Multiple comparisons were further carried out with pairwise Wilcoxon rank sum tests (95% family-wise confidence level). All these analyses were conducted for 'direct primary' pathways only.

We used a linear regression and Spearman's rank correlation to assess the correlation between the cost of species and the year of first record of introduction. First records data are from the Global Alien Species First Record Database (Seebens et al. 2017).

To determine if the number of pathways influenced the cost of a species, the number of pathways per species was calculated for both pathway categories and subcategories by (i) summing the number of direct pathways (*CBD_pathway* column) and (ii) summing the number of direct pathways subcategory (*CBD_subcategory* column) for each species. We used Spearman's rank correlation to assess the correlation between the total and annual average cost per species and the number of pathways subcategories.

For all analyses we use 'direct primary' pathways to minimise the duplication of cost across pathways, except when (i) investigating the relationship between the number of pathways and cost of species where both primary and secondary pathways are considered and (ii) identifying indirect pathways subcategories of species introduced unintentionally where we use 'indirect' pathways.

We used ggplot2 (v.3.3.2, Wickham 2011) R package and Adobe illustrator to generate and format all figures.

Results

Our final dataset contained cost data for 606 individual species. Pathway information was available for 478 species (79%), whilst 128 species (21%) currently have unknown pathways.

Have some pathways facilitated the introduction of more economically costly species than others?

As shown in Fig. 2, when considering direct primary pathways only, we found that 'Stowaways' and 'Contaminants' were globally associated with the highest monetary losses and expenditures. This pattern was consistent when considering both the *(i)* total cost per species over the last 50 years (1970–2020) (KW test = 56.666; $p < 0.001$; Supplementary Material 7) as well as *(ii)* the annual average cost per species per pathway (KW test = 84.438; $p < 0.001$; Fig. 2b). See Supplementary Material 6 for the annual average cost and total cost per species per pathway and Supplementary Material 7 for details on Kruskal–Wallis rank sum test and Wilcoxon pairwise comparisons. Contrastingly the greatest number of species was found to be introduced through 'Escape' (243) followed by 'Contaminant' (159), 'Release' (121) and 'Stowaway' (113) pathways (see Supplementary Material 8). Equally when randomly assigning a pathway to the 128 species with unknown pathways 'Stowaways' and 'Contaminants' were still associated with the highest monetary losses and expenditures with a maximum total cost of \$159.5bn and \$126.7bn respectively. Whilst 'Escape' and 'Release' had a maximum total cost of \$56.7bn and \$26.8bn respectively (Supplementary Material 8).

'Corridor' and 'Unaided', were generally classified as secondary pathways and thus their contribution to economic costs in this study was minimal (Fig. 2a); nevertheless for a relatively small amount of species (n = 18) (e.g. *Salvinia molesta, Gymnocephalus cernuus*) these were also classified as the primary means of dispersal. The total costs incurred as a result of species introduced through 'Corridors' and 'Unaided' pathways over the last 50 years were the lowest, costing \$0.04bn and \$2.2bn, respectively. However, the average annual cost per species spread through 'Corridor' was \$0.5m and 'Unaided' \$25.0m and the median species costs were comparable to the other pathways (\$0.5 and \$7.5m respectively).

Supplementary Material 9 shows that over the last 50 years, species introduced unintentionally through 'Packing material' and 'Contaminant of plants'

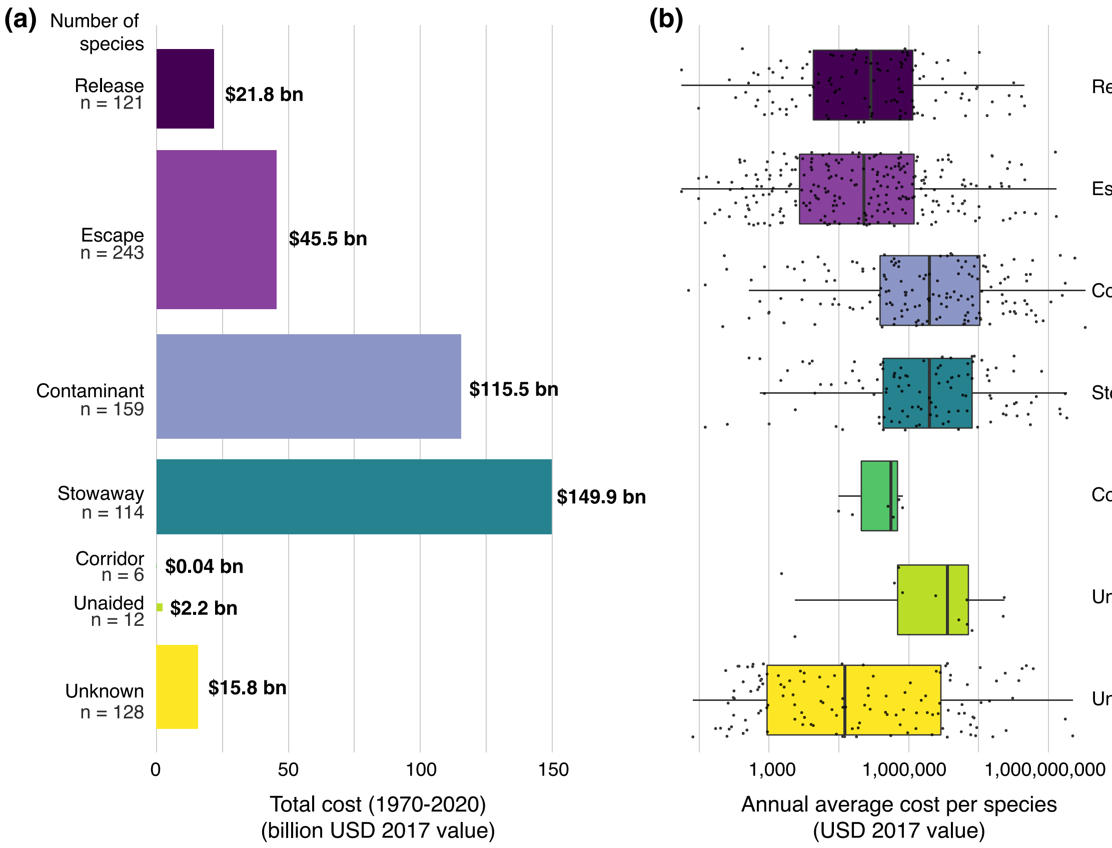

Fig. 2 Cost of species by introduction pathways. (a) Total cost of invasive alien species by pathway for the period (1970–2020) and (b) annual average cost per invasive alien species per pathway. The solid line in (b) shows the median, the lower and upper hinges of the box correspond to the 25th and 75th percentiles. The upper [lower] whisker extend to the largest [smallest] value no further than 1.5 * the distance between the first and third quartiles from the hinge. Species can have multiple pathways although in this figure we only present direct 'primary' pathways that are likely to lead to successful long-distance introductions (see methods), which reduces the number of pathways per species. The width of the bars in (a) is equivalent to the number of species. 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'

accounted for the highest total costs ($83bn and $73bn, respectively). For intentional pathways, species introduced through 'Pet trade', 'Other release' and 'Live food & live bait' amassed the highest total cost of $14bn, $11bn and $10bn. In Fig. 3 we see that the three direct, primary pathway subcategories with the highest median annual average cost per species were 'Timber trade contaminant, 'Food contaminant' and 'Parasites on animals' whilst the three pathway subcategories with the lowest median annual average cost per species were 'Fishery in the wild', 'Agriculture', and 'Ornamental'. Species sample size becomes more varied across pathway sub-categories and may generate higher uncertainty in the results. It is important to take this into consideration when interpreting pathway subcategories results as these are likely to change with time. As shown in Supplementary Material 10, we found that the 'indirect' pathways unintentional introductions of species were most frequently associated with were: 'Agriculture', 'Horticulture' and 'Ornamental trade'.

Are there differences in costs between species introduced intentionally and unintentionally?

Figure 4 shows the total and average cost per species of intentional and unintentional introductions by cost type. The total cost of species introduced

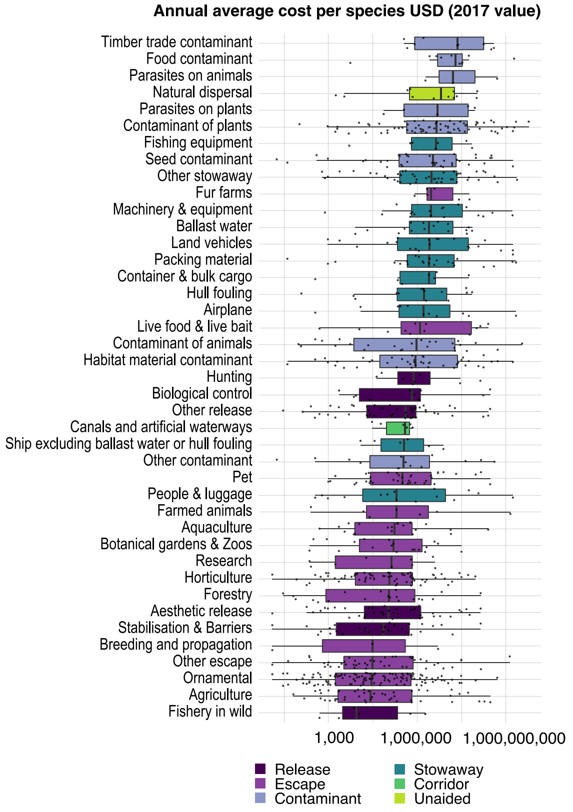

Fig. 3 Annual average cost per invasive alien species by introduction pathway sub-category (1970–2020) (USD 2017 value). Species can have multiple pathways. Only direct 'primary' pathways are included in this figure. Boxes are coloured based on the main CBD pathway classification and ranked according to the median cost of species in each pathway sub-category. The solid line shows the median, the lower and upper hinges of the box correspond to the 25th and 75th percentiles. The upper [lower] whisker extend to the largest [smallest] value no further than 1.5 * the distance between the first and third quartiles from the hinge. 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'

unintentionally is more than four times the cost of species introduced intentionally ($207bn vs. $48bn respectively). The annual average cost per species tended to be higher for species introduced unintentionally in terms of damage (KW test = 3.381; $p = 0.066$), management (KW test = 27.994; $p < 0.001$) and mixed costs (KW test = 20.191; $p < 0.001$) than species introduced intentionally (Fig. 4a). Similar to this trend, over the period 1970–2020, total costs due to species introduced unintentionally were found to be more in terms of damage, management and mixed costs than species introduced intentionally (Fig. 4b). When considering the different types of management costs (e.g. pre-invasion, post-invasion), unintentional introductions still generated more costs than intentional introductions (see Supplementary Material 11).

How are costs taxonomically and spatially distributed across pathways?

Figure 5 shows the total cost and number of IAS by pathway and organism group (See Supplementary Material 12 for all values). The cost of species introduced as 'Contaminants' and 'Stowaways' were the highest for insects, with a total cost of $78bn and $116bn, respectively, followed by plants ($$22bn) for 'Contaminants' and mammals ($24bn) for 'Stowaways'. The cost of species introduced intentionally and released into nature ('Release') was the highest for mammals ($13bn), followed by plants ($3.5bn). Whilst the cost of species introduced intentionally and subsequently escaped ('Escape') is highest for plants ($17bn), followed by mammals ($16bn). Plants accounted for the highest number of species introduced intentionally (n = 68 for 'Release' and n = 174 for 'Escape') and insects had the highest number of species introduced as 'Contaminants' (n = 74) and 'Stowaways' (n = 43).

Figure 6 shows the total cost of IAS by pathway and geographical region. The total cost associated with each IAS pathway varied across regions. 'Stowaways' had the highest costs in Asia, Central America, North America and Diverse/Unspecified regions, whilst Antarctic-Subantarctic incurred the greatest costs from species intentionally released into nature ('Release'). In Africa, Europe and Oceania/Pacific Islands, 'Contaminants' generated the highest costs, followed by 'Escape' species.

As shown in Supplementary Material 13, when considering the average yearly cost per species for each pathway, 'Escape' species were the costliest in South America, 'Contaminants' were the most costly in Africa and Oceania/Pacific Islands region and 'Stowaways' cost the most in Antarctic-Subantarctic, Asia, Europe, Central and North America and Diverse/Unspecified.

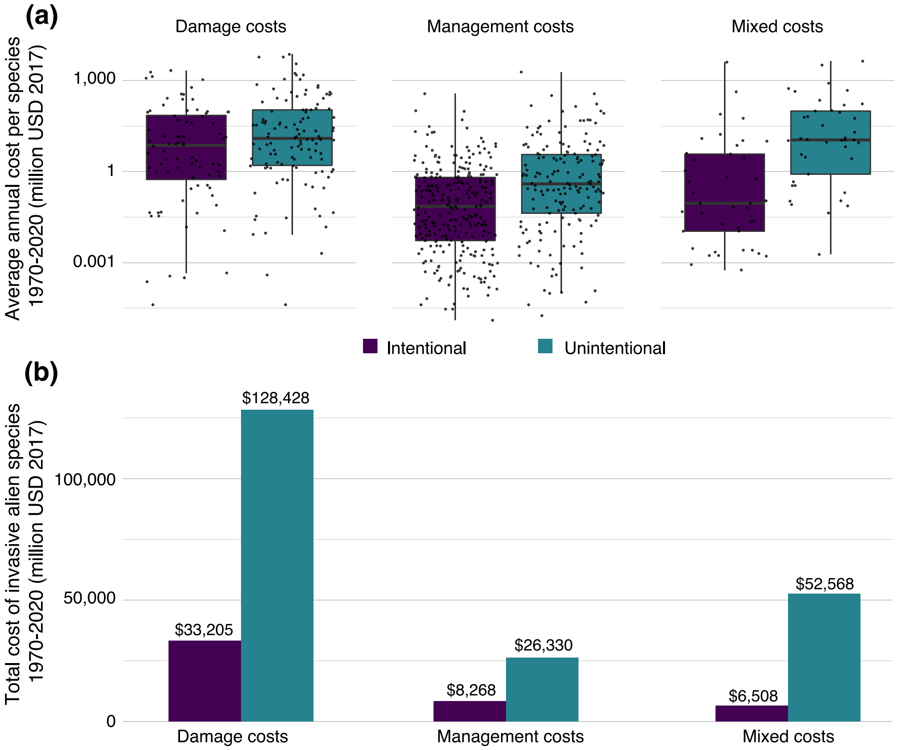

Fig. 4 Cost of intentional and unintentional introductions by cost type (1970–2020) (USD 2017 value). Figure showing **a** a boxplot of the average cost of species introduced intentionally and unintentionally by cost type and **b** bar plot of the total cost of species introduced intentionally and unintentionally by cost type. The solid line in (**a**) shows the median, the lower and upper hinges of the box correspond to the 25th and 75th percentiles. The upper [lower] whisker extend to the largest [smallest] value no further than 1.5 * the distance between the first and third quartiles from the hinge. Only 'primary' and 'direct' pathways of introduction are included in this figure

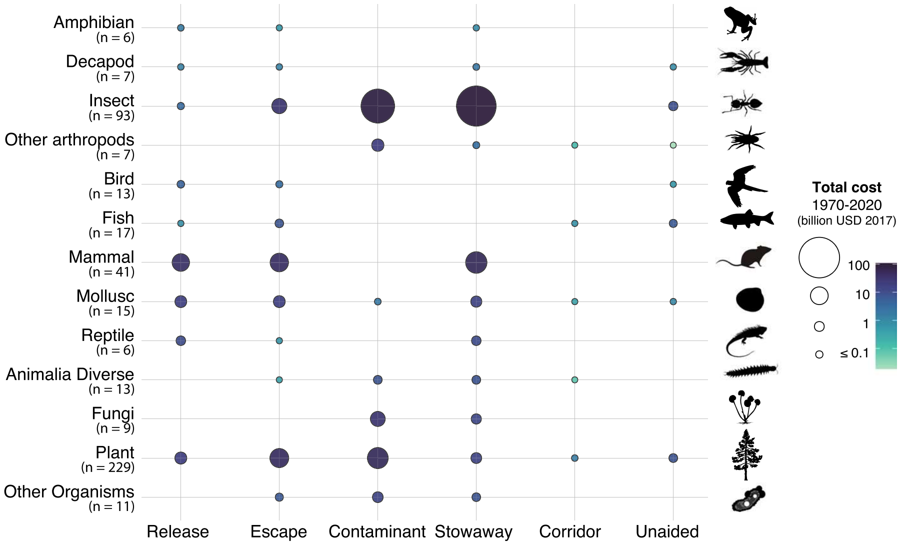

Fig. 5 Total cost of invasive alien species by introduction pathway and organism group (1970–2020) (USD 2017 value). Only direct 'primary' pathways are included in this figure. The colour and the size of the bubble represents the total cost of invasive alien species by broad organism group and pathway. For example, the total cost incurred for plants introduced through 'escape' for the period 1970–2020 is $ 16.9 billion. 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'

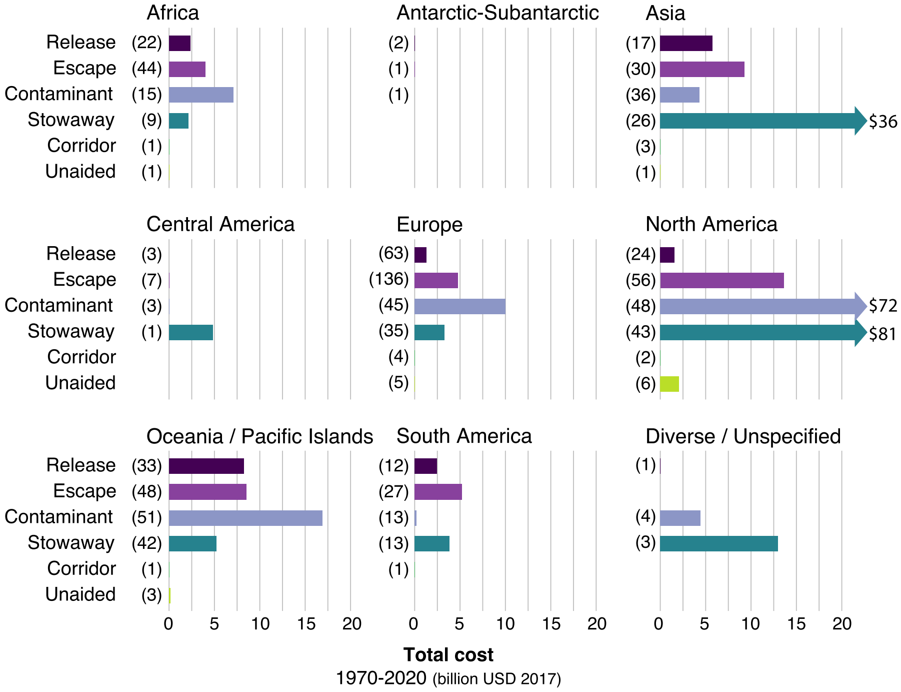

Fig. 6 Total cost of invasive alien species by introduction pathway and geographical region (1970–2020) (USD 2017 value). Only direct 'primary' pathways of introduction are included in this figure. 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'. Values in brackets represent the number of species with reported costs introduced in each pathway/region

Is there a relationship between the cost of species and the year of first record of introduction?

Figure 7 plots the total cost of a species over the period 1970–2020 in a given location against the year of first record of introduction of the species in that location. We found no significant relationship between the total cost of a species and the year of first record of introduction (Spearman's rho = -0.056; $p = 0.202$). So, although there was a slight decreasing trend between the cost of IAS and the year of first record of introduction, the observed total cost of recent introductions is not significantly lower than the observed total cost of species introduced in earlier years.

In Supplementary Material 14, we individually plotted the total cost of species introduced intentionally, both intentionally and unintentionally and unintentionally against the year of first record of species. Again, there was no significant relationship between the total cost of a species over the period 1970–2020 against the year of the first record of introduction of the species. There was a slight decreasing trend for species introduced intentionally and both intentionally and unintentionally whilst for species introduced unintentionally we found a slight increasing trend.

Is there a relationship between the number of pathways and species cost?

Figure 8 depicts the total cost of a species for the period 1970–2020 against the number of pathways attributed to that species. There was a slight decreasing trend between costs of IAS and the number of pathways through which they are transported. However, we found no significant relationship between the total cost and the number of pathways (Spearman's rho = -0.025; $p = 0.521$) or pathway sub-categories (Spearman's rho = -0.025; $p = 0.594$). Although we note that perhaps it has not been long enough since the first introduction date for many of the species transported via multiple pathways to have accrued additional impacts due to these sources of introductions, we see no reason why these time lags would be absent for species transported via a single pathway.

Discussion

Using data from the global database of reported monetary costs of IAS—*InvaCost*—we set out to address five principal questions. First, we found that the total cost of species, as well as the annual average cost

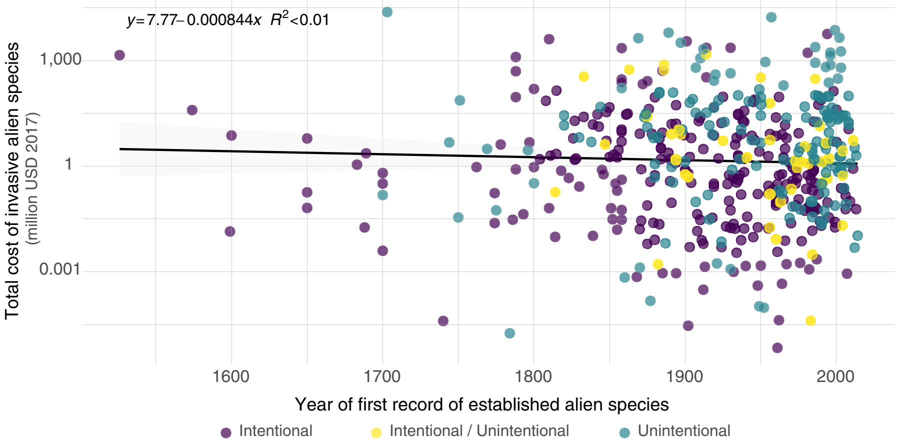

Fig. 7 Invasive alien species cost (1970–2020) (million USD 2017) against the year of the first record of the species in a given location. Only 'primary' and 'direct' pathways are included in this figure. The colours represent whether the primary pathway for a species in a given location is intentional (purple), unintentional (teal) or both intentional and unintentional (yellow). Species were assigned both categories when it was not possible to identify a primary pathway

per species introduced through 'Contaminants' and 'Stowaways' were more costly than species introduced primarily through 'Escape' and 'Release', with 'Unaided' and 'Corridor' being the least costly (Fig. 2; Supplementary Material 6). Second, the total cost of species and the average annual cost per species tends to be much higher for species introduced unintentionally than species introduced intentionally. This pattern is the same across different types of costs (i.e. damage, management and mixed costs) (Fig. 4). Third, patterns vary spatially and across taxonomic groups, which is an important consideration when formulating policies (Fig. 5 and 6). Fourth, the observed total cost of recent introductions is not

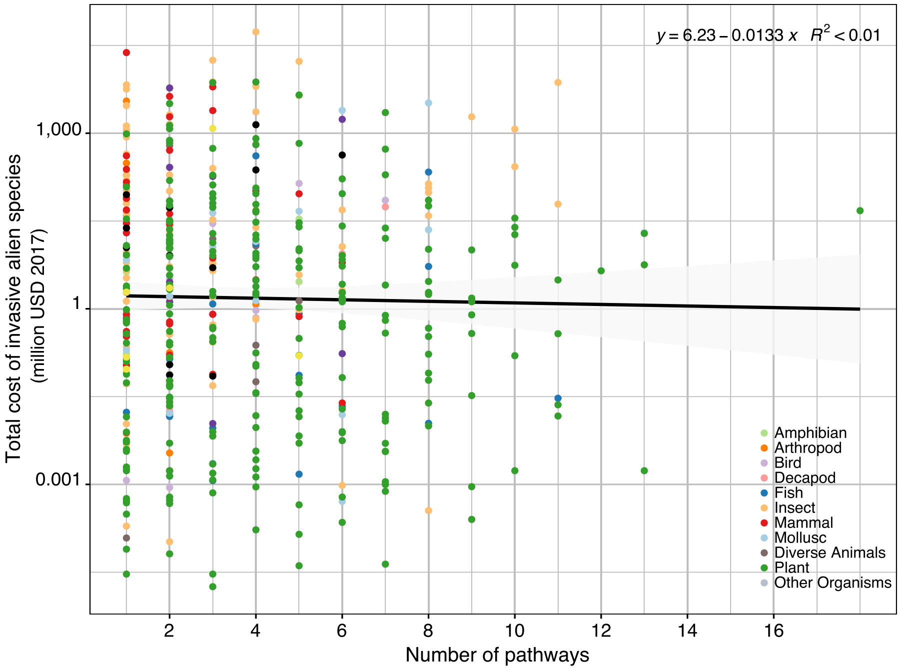

Fig. 8 Total cost per invasive alien species (1970–2020) (million USD 2017) against the number of introduction pathways. Both primary and secondary pathways are considered; however only direct pathway subcategories are included in this figure. The colours represent the broad organism group each species belongs to

significantly lower than the observed total cost of species introduced in earlier years (Fig. 7). Finally, unlike ecological impacts—where multiple pathways increase the likelihood of species' having an impact (Pergl et al. 2017)—we found no relationship between the total and annual average cost per species and the number of pathways through which it is transported (Fig. 8).

More than 40% of species with cost records had 'Escape' as a primary pathway of introduction making it the most common IAS pathway, followed by 'Contaminants' (26%), 'Release' (20%) and 'Stowaways' (19%) (Supplementary Material 8). Although species introduced through 'Escape' and 'Release' are more numerous than species introduced as 'Contaminants' or 'Stowaways', their annual average and overall costs are significantly lower (see Fig. 1). While the patterns and trends depicted here are based on only a subset of known IAS—i.e. those recorded in the *InvaCost* database vs. 3352 species in GRIIS considered to have evidence of impacts (Chamberlain and Bartomeus, 2021), our results are aligned with previous findings in terms of proportion of IAS by pathways (Saul et al. 2017) and proportion of introduction events by pathways (McGrannachan et al. 2021). Hence, our study provides a sound basis for further improved pathway-based cost assessments for many more IAS.

Observed patterns can be attributed to several factors including lack of records, possibly in turn affected by species' charisma, perceived utility, and ease of management. IAS charisma—"characteristics that affect people's perceptions, attitudes, and behaviors toward them"—can influence public support or contribute to social conflicts thereby affecting perceptions of costs and management actions (Jarić et al. 2020, p. 346; Kourantidou et al. 2021). As such, charismatic species are not only more likely to be introduced intentionally through, for example, the ornamental trade (van Kleunen et al. 2018) but are also more likely to receive social acceptance in the receiving region and generate public opposition to control measures (Jarić et al. 2020). This could lead to low reports of damage costs and paltry investment in management actions. For example, proposed controlled measures of the grey squirrel (*Sciurus carolinensis*) in the UK and Italy generated strong backlash from the public despite its known impact on native red squirrel (*Sciurus vulgaris*) populations and potentially high economic damage cost (Bertolino and Genovesi 2003; Gurnell et al. 2004; Mayle and Broome 2013). Moreover, intentional releases and escapes should in theory be more straightforward to monitor and control (Hulme et al. 2008) and therefore less costly. Although further evidence is needed to support this hypothesis, Pluess et al. (2012) suggest that eradication campaigns were more likely to succeed for plants introduced for cultivation and subsequently escaped, than for plants introduced through unintentional pathways in semi-natural environments. Another theory that would require further research is that species introduced unintentionally may be able to spread undetected for longer, leading to greater economic costs compared to species introduced intentionally, for which one expects that better measures are already in place to prevent and control invasions.

In line with vertebrates being often characterized as deliberate 'Releases', plants as 'Escapes' and invertebrates as 'Contaminants' (Hulme et al. 2008), in our dataset mammals drive the total cost of intentional 'Release' (61%), plants account for the greatest proportion of 'Escape' costs (37%), whilst insects drive the total costs of unintentional introductions (68%) (Supplementary Material 9). Indeed, domesticated cats (*Felis catus*), wild boars (*Sus scrofa*) and rabbits (*Oryctolagus cuniculus*) represent 57% of intentional 'Release' costs (Supplementary Material 6). Their close proximity and value to humans either as game animals or as pets is a likely cause for their uncontrolled range and population expansion, consequently leading to extensive damage costs. On the other hand, insects are inconspicuous, so their sheer numbers and predominant impacts on sectors such as agriculture, health and forestry probably contribute to their high costs. The high reported costs of insects are the opposite of what we would expect if detection bias drove our results. Contrastively the low costs attributed to fungi and other microorganisms is likely due to detection bias. When looking at the annual average cost per species, fungi and mammals, notably rats, stand out as the most costly 'Stowaway' species, and fungi and arthropods (other than insects) have the highest annual average species cost for 'Contaminants' (Supplementary Material 12). Indeed, rats are amongst the most impactful IAS with both global and multi-sectoral economic impacts, pertaining to disease transmission, damage to infrastructures and social disruption among others (WHO 2019; Diagne et al., 2021b).

Pergl et al. (2017) found that plants introduced through 'Release', 'Corridor' and 'Unaided' are more likely to have ecological impacts than those introduced as 'Contaminants'. We found that the annual average cost per plant introduced as 'Contaminants' and the total cost of plants introduced as 'Stowaways' were higher compared to other pathways, despite more plant species being introduced intentionally. Moreover, Pyšek et al. (2011) note that plants introduced deliberately have a higher establishment success rate than plants introduced unintentionally, although 'Contaminants' were as widely distributed as intentionally introduced species, and invaded a wider range of semi-natural habitats. This could explain the higher costs caused by 'Contaminants', despite the high number of 'Escape' plant species as one may expect a high number of low impact 'Escape'.

Some plants with the greatest associated costs were originally released through the aquarium trade or for aquatic horticulture (e.g. *Eichhornia crassipes, Hydrilla verticillata, Hydrocotyle ranunculoides, Lagarosiphon major*) (Brundu et al. 2013; Brunel 2009; Madeira et al. 2007). Aquatic ecosystems are susceptible to invasions due to the discrete nature of their coevolved communities (i.e. individual lakes) combined with the accelerating levels of human transport among them that may spread plant propagules (Francis et al. 2019). Increased awareness of biosecurity issues around the trade in aquatic plants is needed to help counter the future emergence of costly invasions (Champion et al. 2010), just as there has been increased recognition of the risks of fish introductions through this mechanism (Gertzen et al. 2008; Nunes et al. 2015; Lockwood et al. 2019).

Costs incurred as a result of unintentional introductions are the greatest globally and for most regions, except for Antarctic-Subantarctic, where costs from 'Release' species have accrued the most over the last 50 years, mostly in the earlier years. With low levels of human activity in the Antarctic region, it is not surprising that cost records mainly relate to management measures of intentionally introduced mammals, even though both deliberate and accidental introductions have been reported (Frenot et al. 2005). Monetary quantification of damage from invasions may be more difficult when the impact is primarily environmental; especially since humans are perhaps more inclined to spend money to mitigate impacts that cause economic losses. It is worth noting that all costs in our dataset were standardised based on the classical exchange rates, meaning that the purchasing power of different currencies was not equalised between countries. We did not consider costs standardised based on the Purchase Power Parity (PPP) in *InvaCost* (Diagne et al. 2020b) because (i) this information is still missing for a number of countries and years from the official sources (i.e. World Bank website; see Diagne et al. 2020b for details) and (ii) of limitations of PPP as an adequate conversion factor (Avalos and Alley, 2014). Thus we should be cautious about the geographic patterns shown here.

Our results should not be taken as leads to recommendation of lower investment in the management of pathways where the recorded costs were shown to be lower, at least for two main reasons. ***First***, the trends and patterns drawn here only reflect a snapshot of a portion of the cost data available in the InvaCost database at the time of writing (i.e. only observed highly reliable costs). Our work should therefore be seen as the first state-of-the-art on the topic, given both qualitative and quantitative findings will be refined as knowledge on pathways and costs of IAS will continue to increase in the future. Precise knowledge on pathways is still lacking for a number of IAS—as illustrated by the costs associated with the category 'unknown' pathway (Fig. 2). Nonetheless, we can assume that our findings are not only driven or blurred by data availability. Indeed, if the magnitude of cost information available across pathways was likely to have directly driven the cost distribution evidenced here, one could expect that the higher the number of species or cost data recorded for a particular pathway, the higher the estimated costs. However, we found that 'stowaway'—the pathway associated with the costliest estimates—is among the pathways with the lowest number of cost information currently recorded in the database. ***Second***, although our results currently highlight 'contaminant' and 'stowaway' as the costliest pathways, we must keep in mind that the impacts of IAS are far beyond their estimated economic burden and affect health and biodiversity in ways that are often hard to quantify in monetary terms (Charles and Dukes 2008; Hanley and Roberts 2019). As such, considering all dimensions of IAS impacts (ecological, economic and sanitary) is key when prioritising pathways in terms of management actions.

Therefore, our results should, rather, be viewed as (i) a sound basis providing avenues for future improvement on this research topic, (ii) complementary knowledge to existing studies on IAS impacts and pathways to improve prioritization and (iii) a call to further invest in the management of all pathways given their massive—and likely much underestimated—costs to our society. Moving from our empirical results to actual management recommendations requires, for instance, (i) deciphering how pathways—and associated number/identity of introduced species—vary across space and time, (ii) identifying how local contexts influence the introduction opportunities from specific pathways (e.g. implementation of regulations), and (iii) bridging current gaps (e.g. CBD pathway classification scheme is heavily biased towards Europe; Faulkner et al. 2020) in research on pathways. This objective is beyond the scope of our manuscript which rather aims at using evidence from the relationship between pathways and costs to highlight the need for transdisciplinary approaches in invasion science, at the interface between science and society (Vaz et al. 2017; Novoa et al. 2018; Diagne et al 2020a, b, 2021a). Accordingly, given the high economic impacts depicted here, managing unintentional pathways (i.e. 'Stowaway' and 'Contaminants') should be a key item for future biosecurity efforts, which must adapt to growing trends in global shipping (Sardain et al. 2019), and increased survivability of stowaways due to climate change (Pyke et al. 2008; Della Venezia et al. 2018; Kourantidou et al. 2015; Kaiser and Kourantidou 2021). Embracing emerging technologies for safer shipping such as eDNA detection techniques, recyclable plastic pallets (i.e. IKEA's OptiLedge), and the application of fouling-resistant paints to ship hulls will help meet these challenges (Callow and Callow 2011; Guan et al. 2019). At the level of international policy, agreements such as the Ballast Water Management (BWM) which finally entered into force in 2017 (close to 27 years after its initial design and 13 years after its adoption) (IMO 2020) and the creation of global biofouling policy are instrumental to establishing a worldwide standard to mitigate stowaways on ship hulls (Davidson et al. 2016; Ojaveer et al. 2018; Galil et al. 2019). The upholding of existing international ballast water regulations, as well as improved ballast water management in Arctic regions, will be key in the face of warming arctic waters (Goldsmit et al. 2019; Kourantidou et al. 2015; Kaiser and Kourantidou 2021). Stricter enforcement of wood packing material protocols such as ISPM15 can help limit the transport of wood boring insects in wood pallets (Leung et al. 2014). Similarly, adopting a 'pest free status' (ISPM10) prior to the export of goods—especially through 'Agriculture', 'Horticulture', and 'Ornamental trade'—may help reduce costs associated with 'Contaminants' and 'Stowaways'. Interception of IAS by trained staff at ports of entries (airports, seaports) could also be a very efficient measure. More broadly, we advocate for the implementation of measures and actions ever-increasingly proposed in the recent scientific literature to improve at-border systems. These aimed at controlling both intentional and unintentional introduction events through, for instance, (i) appropriate sampling strategies, (ii) suitable inspection methods, (iii) continuous, transnational recording of organisms detected, and (iv) risk assessment and education (Essl et al. 2015; Saccaggi et al. 2016 and references therein; Carpio et al. 2020).

To conclude, using the most up-to-date compilation of monetary cost information on IAS we show that 'Stowaway' and 'Contaminant' pathways (particularly 'Timber trade' and 'Food' contaminants) have a particularly high economic impact globally. In line with existing research, our work supports the need to prevent and control unintentional species introductions in order to reduce the overall economic burden of IAS. We also stress the importance of conducting risk assessments before introducing species into new environments and raising public awareness of the potential impacts of non-native species, especially those introduced through the pet and aquarium trade. Moreover, we expect that our findings can stimulate the need for more and better cost assessments and their association with IAS pathways and impacts, in line with existing evidence that targeted management implemented to prevent IAS introduction is the most efficient way to limit further impacts to our ecosystems and our economies.

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Author contributions AJT, CD and FC managed the project. All co-authors contributed to the design of the study. AJT, EJH, CB, PJH, MK, REG and AN compiled the pathway dataset. AJT, CD, DM and REG checked the pathway dataset. AJT carried out the analyses and generated the graphical items with help from FC and input from all co-authors. AJT took the lead in writing the first draft of the paper with inputs from CD followed by all co-authors. All co-authors read and approved the final manuscript.

Data availability All data used in this study were made fully accessible as supplementary files (Supplementary file 1; Supplementary file 3; Supplementary file 4).

Declarations

Conflict of interest The authors have declared that no competing interests exist.

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Annexe 7

M. Robuchon, **C. Bernery**, C. A. K. M. Dia, F. Courchamp, C. Diagne, G. Heringer, N. Kirichenko, S. Pavoine, D. Renault, V. Rezende, A-C. Vaissière, C. Bellard. The conservation paradox of exotic species of economic concern. *In prep*

Implication dans le projet : J'ai participé à la conception du projet, à la construction de la base de données des espèces d'oiseaux et de mammifères exotiques à l'échelle mondiale. J'ai procédés aux analyses portant sur la comparaison des espèces exotiques avec des coûts aux espèces exotiques sans coût en regardant l'originalité fonctionnelle, phylogénétique, et le statut du risque d'extinction. J'ai aussi analysé la relation entre le coût économique en terme de dommages et de gestion, et l'originalité fonctionnelle et phylogénétique

Assessing conservation paradoxes in invasive alien species of economic concern

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Abstract

1. Several studies have highlighted the existence of species that constitute conservation paradoxes because they are invasive in some places and worth-conserving in others. However, only a few cases have been discussed, and only considering ecological impacts of invasions and species' threat status as a criterion making them worth-conserving. Therefore, a global quantification of these conservation paradoxes encompassing their economic impacts and going beyond the sole consideration of species' threat status to include their evolutionary history or ecological functions is needed.
2. Here, our aim was to reveal, quantify and identify such conservation paradoxes for mammals, birds and plants worldwide. We used the InvaCost database to calculate an economic cost for each invasive alien species (IAS) of economic concern present in this database. To reveal potential conservation paradoxes within IAS of economic concern, we (i) explored the threat status of all IAS that have a recorded cost and (ii) investigated the phylogenetic and functional distinctiveness of such IAS. We further focused on the costliest species to reveal whether conservation paradoxes occur in this subset of species.
3. Among the 397 species of mammals, birds and plants with economic costs, we found that 126 species are worth-conserving – either because they are threatened and/or belong to the most phylogenetically or functionally distinctive species. Such conservation paradoxes represent almost one third of the species with economic costs, and exactly one third of the costliest species.
4. We further found that (i) more species constitute a conservation paradox because they are among the most phylogenetically or functionally distinctive species (119 species) than because they are threatened (9 species) and (ii) most of the economic costs documented for these species concern management costs to limit the number of individuals and potential spread of the species.

5. *Synthesis and applications.* Our work stresses to an unprecedented level the fact that some species simultaneously need to be controlled and/or eradicated in their invasive ranges and conserved in their native ranges. The management of such species needs to be tightly coordinated between alien and native ranges to optimise cost-effective actions and maximise conservation benefits.

Keywords

Birds, coordinated management, functional distinctiveness, InvaCost, mammals, phylogenetic distinctiveness, plants, threat status

Introduction

When exotic species get established outside of their native areas, some of them can have dramatic impacts on local biodiversity and, consequently, on ecosystem functioning and potentially on nature's contribution to people (or ecosystem services) (e.g. Blackburn, Cassey, Duncan, Evans, & Gaston, 2004; Magliozzi et al., 2020; Simberloff et al., 2013). They can also cause substantial losses and damages to human health and activities (e.g. Bradshaw et al., 2016; Mazza, Tricarico, Genovesi, & Gherardi, 2014; Paini et al., 2016). Such exotic species having negative impacts are referred to as invasive alien species (IAS) (Russell & Blackburn, 2017). To mitigate the negative impacts of IAS, funding are mobilised to implement management measures to prevent, control or even eradicate the populations of IAS at the invaded place (Pyšek et al., 2020). For instance, nearly 600 terrestrial populations of island native species benefited from eradication plans of invasive mammals (Jones et al., 2016).

Yet, while IAS populations can have negative effects in the introduced ecosystems they are invading, they can also present some conservation needs in their native area. One such case is the wattle-necked turtle (*Palea steindachneri*). On the one hand, this species is considered as critically endangered in its native range in China and Vietnam due to its high value in food trade. On the other hand, it has been introduced and probably farmed into Hawaiian Islands, Honk Kong and Mauritius, where it causes severe alterations of the native freshwater species, which are often unique and endemic. This questions the need for controlling or eradicating IAS populations that suffer from extirpation in their native range and may provide valuable information (ecological and life-history data) as well as genetic rescue to be used as insurance for the species' survival in their native area (Marchetti & Engstrom, 2016). In other words, while controlling or eradicating those alien populations would help protect the invaded ecosystems, it may concomitantly further jeopardise the future of the whole species on Earth.

The high degree of threat that species experience globally is one of the strong criteria that is being used to justify species' conservation: protecting species threatened at a global scale is a way to avoid irreversible species' extinctions, which has been suggested as the main criteria to define biodiversity targets in public policies (Rounsevell et al., 2020). However, at least two other criteria may complete the need and justification for species' conservation: their unique evolutionary history (Faith, 1992) and their unique ecological functions (Cooke, Eigenbrod, & Bates, 2020). Indeed, on the one hand, protecting species exhibiting unique evolutionary history is a way to conserve the evolutionary heritage of our planet as well as the evolutionary potential of these species. In addition to its intrinsic value, such evolutionary heritage, measured as phylogenetic diversity (PD), represents option values, i.e. a reservoir of yet-to-be discovered benefits for humanity (Faith, 1992; IPBES, 2019). On the other hand, protecting species exhibiting unique ecological functions is a way to preserve the integrity of ecological processes and functions (Cooke et al., 2020).

IAS that need to be managed (because of their negative impacts) and are at the same time worth-conserving (because of at least one of the three above-mentioned criteria) could thus be considered as conservation paradoxes. Such a conservation paradox in the case of species simultaneously endangered and invasive has been discussed by Marchetti & Engstrom (2016), who provided a dozen examples of this kind of species. The conservation paradox of the notorious European wild rabbit *Oryctolagus cuniculus* invasive in many places but endangered in Iberia has also been extensively discussed (Lees & Bell, 2008). However, only a few cases have been discussed, and only about the threat status of the species, overlooking their evolutionary history or ecological functions. Consequently, and based on those case by case discussions, we argue that a global quantification of these conservation paradoxes is much needed. Moreover, the cost of IAS management is huge with $66.3 billions for 1970-2017 period (Diagne et al., 2021), and it seems crucial to be consistent between money spent in management actions that aim to protect native areas and control in the alien ranges. As a consequence, in order to optimise cost-effective management and conservation actions, we need to unravel those conservation paradoxes.

In this study, our aim was to reveal, quantify and identify such conservation paradoxes for mammals, birds and plants worldwide. We focused on those taxonomic groups as they were the ones having sufficient data in the four areas of concern: threat status, phylogeny, functional traits and economic costs caused in invaded areas. We used the recently published InvaCost database version 4.1 - which compiles the recorded economic costs of biological invasions worldwide (Diagne et al., 2020) - to calculate an economic cost for each species present in the database and therefore representing IAS of economic concern. To reveal potential conservation paradoxes within IAS of economic concern, we first explored the threat status of all IAS that have a recorded cost. We then investigated the phylogenetic and functional distinctiveness of such IAS, respectively corresponding to their overall contribution to phylogenetic and functional diversities (Kondratyeva, Grandcolas, & Pavoine, 2019; Pavoine, Bonsall, Dupaix, Jacob, & Ricotta, 2017). Finally, we focused our attention on the costliest species to reveal whether conservation paradoxes occur in this subset of species.

Material and methods

Economic cost collection

We used the InvaCost database to calculate the economic cost associated with invasive alien mammals, birds and plants over the 1960-2020 period. InvaCost is a living, publicly available database compiling the monetary losses incurred by IAS worldwide. The database was generated following a systematic, standardised methodology to collect information from scientific articles, grey literature, stakeholders and expert elicitation (Diagne et al., 2020). Each cost estimate collated was standardised to a common and up-to-date currency (i.e., 2017 US dollars). The used version of this database (version 4.1) is accessible here: https://doi.org/10.6084/m9.figshare.12668570. We filtered out all entries that were ambiguously attributed to a single species, and also ignored cost data associated with different subspecies, or mix of species.

Estimation of the average cost per species

We obtained the average cost for each species following Diagne et al. (2020). First, we homogenised costs on an annual basis using the *expandYearlyCosts* function of the 'invacost' R package (Leroy, Kramer, Vaissière, Courchamp, & Diagne, 2021). Hence, costs spanning over multiple years (e.g. $20 million between 2006 and 2010) were divided according to their duration (e.g. $4 million for each year between 2006 and 2010). Second, we calculated the average annual cost for each species by dividing the annualised costs by the number of cost entries in the expanded database where costs were homogenised on an annual basis. Note that we focused on average annual costs (rather than total cumulated costs) over time to weight the differences in both number and temporal coverage of cost entries across recorded species in the database. We could not calculate an average annual cost for all species documented in InvaCost as some cost entries did not provide enough information to estimate such average annual cost. Finally, we estimated this average annual cost separately for the two main types of cost in the InvaCost database: the "economic damages" caused by the IAS and the "management investments" to mitigate their impacts. After these necessary steps of data standardisation and quality check, we ended up with 397 IAS for the three taxonomic groups considered in the study (44 mammals, 20 birds, and 333 plants), and we retrieved costs for 382 species (39 mammals, 20 birds, and 323 plants). These include damage costs for 146 species (21 mammals, 13 birds, and 112 plants) and management costs for 338 species (36 mammals, 15 birds, and 287 plants).

Finally, for each taxonomic group and based on the calculated costs, we further identified the top 5 costliest species both in terms of damage and management cost.

Conservation need: threat status, phylogenetic distinctiveness and functional distinctiveness

To identify potential conservation paradoxes, we relied on the three following conservation criteria: threat status, phylogenetic distinctiveness and functional distinctiveness. We collected the global threat status of bird, mammal and plant species from the version 2020-2 of the IUCN Red List database (IUCN, 2020). Importantly, the IUCN threat status is assigned for "wild populations inside their natural range, and to populations resulting from benign introductions" (IUCN Species Survival Commission, 2012), thus excluding IAS populations. We downloaded phylogenies and traits for bird and mammal species from VertLife (https://vertlife.org/data/). Specifically, we used the mammal phylogeny based on the tip-dated backbone tree published by Upham, Esselstyn, & Jetz (2019), the bird phylogeny based on the fossil-calibrated backbone tree by Ericson et al. (2006) published by Jetz et al. (2014), and the species-level foraging attributes of the world's birds and mammals published by Wilman et al. (2014). Foraging attributes include information on diet-related traits (percentage of use of each diet type), traits related to time and place of activity (percent of use of each foraging place and binary traits indicating if the species is mainly pelagic and mainly nocturnal), and body mass (in grams). For diet-related traits, we completed missing information for three mammal species (*Myzopoda aurita*, *Mystacina robusta*, and *Mystacina tuberculata*) with data from the Phylacine database (Faurby et al., 2018). We used the cube-root transformation for body mass. For plant species, we chose the most comprehensive phylogeny of seed plants published by Smith & Brown (2018), and the 'Global Inventory of Floras and Traits' (GIFT) database for species traits (Weigelt, König, & Kreft, 2020). As the species coverage in GIFT varied greatly among traits, we selected the five traits with more than 50% species coverage (woodiness, growth form, epiphyte, climber and parasite, ranging from 54 to 61% species coverage).

Calculation of phylogenetic and functional distinctiveness

We calculated scores of phylogenetic and functional distinctiveness for all the world's mammals, birds and plants for which we had phylogenetic and trait information thanks to the function 'distinctTree' from the R package adiv (Pavoine, 2020) using the evolutionary distinctiveness 'ED' metric as a parameter (Isaac, Turvey, Collen, Waterman, & Baillie, 2007; Redding, 2003). For mammal and bird phylogenetic distinctiveness, following the approach of Robuchon et al. (2021) to take into account phylogenetic uncertainty, we calculated species scores on a subset of 100 phylogenetic trees from the available posterior distributions of phylogenetic trees and we calculated the median score. For plant phylogenetic distinctiveness, we calculated species scores based on the only available tree. For mammal and bird functional distinctiveness, we calculated four scores: one score of diet distinctiveness using diet-related traits, one score of activity distinctiveness using traits related to time and place of activity, one score of mass distinctiveness using body mass and one mean distinctiveness score corresponding to the mean over diet distinctiveness, activity distinctiveness and mass distinctiveness. For the three first scores, we calculated distances among species using the function 'ktab.dist' from the R package ade4 (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009; Thioulouse et al., 2018) which generalizes Gower's general coefficient of distance to allow the treatment of various statistical types. For plant functional distinctiveness, we calculated a single overall score of functional distinctiveness based on the five selected traits using an in-house R function (see GitHub repository).

Overall, we had information on threat status for 32,815 species (5,813 mammals, 10,983 birds, and 16,019 plants), scores of phylogenetic distinctiveness for 369,704 species (5,424 mammals, 8,095 birds, and 356,184 plants) and calculated scores of functional distinctiveness for 225,423 species (4,798 mammals, 8,095 birds, and 212,530 plants).

Identification of conservation paradoxes

For each taxonomic group (mammals, birds and plants) and each type of cost (damage and management), we identified conservation paradoxes as the species simultaneously documented in InvaCost and falling in (at least) one of the three following categories: (i) threatened species according to the IUCN Red List *sensu lato* (i.e. belonging to the Red List categories "near threatened", "vulnerable", "endangered", "critically endangered"), (ii) species belonging to the top 25% most phylogenetically distinctive species of their taxonomic group (hereafter "most phylogenetically distinctive"), and (iii) species belonging to the top 25% most functionally distinctive species of their taxonomic group (hereafter "most functionally distinctive"). We further examined whether such conservation paradoxes occur among the top 5 costliest species for each taxonomic group and type of cost.

Results

Threat status of species documented in InvaCost

Although most species documented in InvaCost are least concern (for mammals and birds) or not assessed (for plants), seven mammals and two plants are threatened (Figure 1A-C, Table S1) and can therefore be considered as conservation paradoxes. They include two endangered (the Przewalski's horse *Equus ferus* and the European rabbit), four vulnerable (the aoudad *Ammotragus lervia*, the koala *Phascolarctos cinereus*, the reindeer *Rangifer tarandus*, and the Javan deer *Rusa timorensis*) and one near threatened (the Himalayan tahr *Hemitragus jemlahicus*) species for mammals, as well as one endangered (the Mexican hat plant *Kalanchoe daigremontiana*) and one vulnerable (the cow tree *Citharexylum gentryi*) species for plants (Table S1). Among the seven threatened mammals documented in InvaCost, two species have damage costs and six species have management costs, while the two threatened plants have management costs only (Table 1).

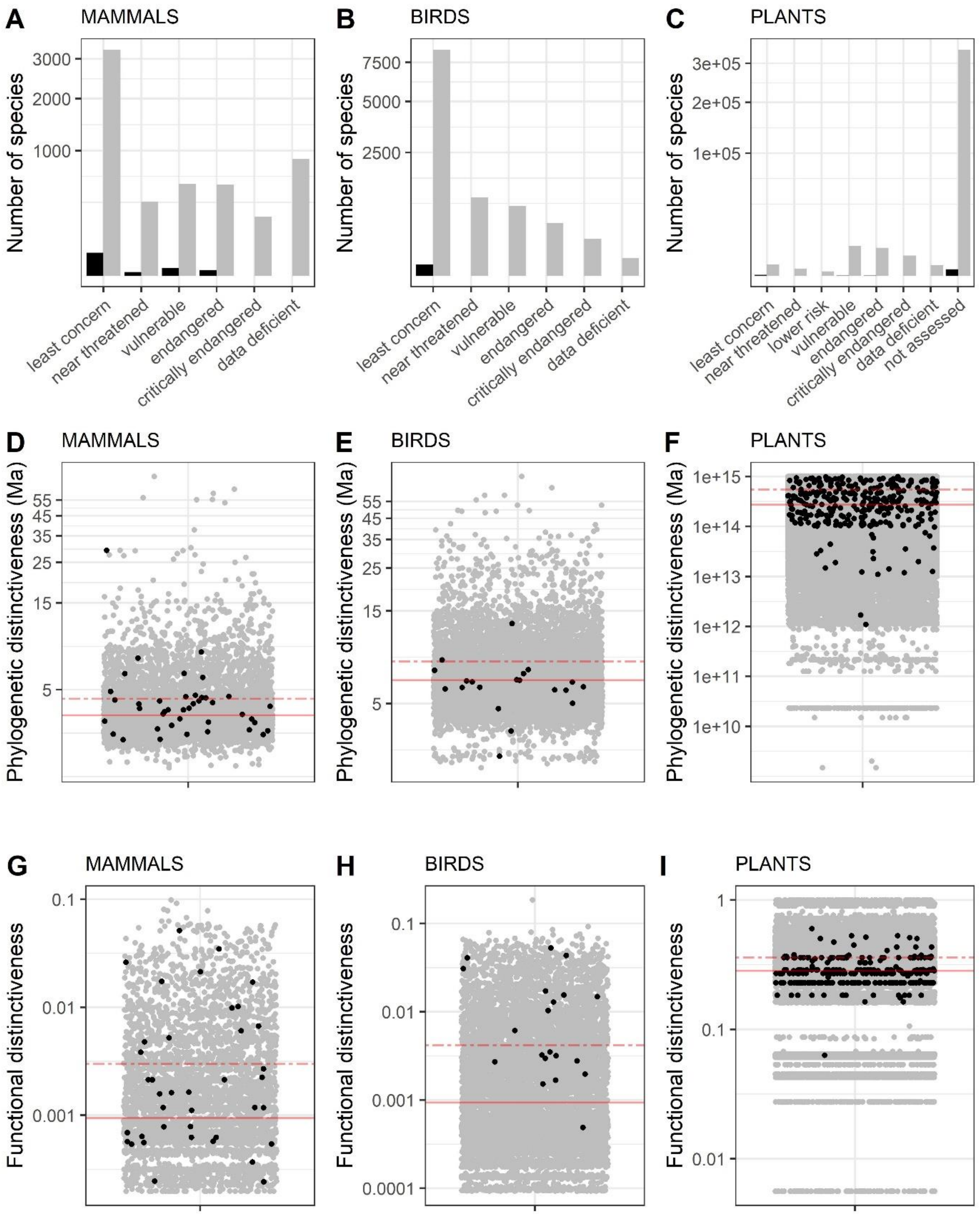

FIGURE 1. Threat status (A-C), phylogenetic distinctiveness (D-F) and functional distinctiveness (G-I) of species with costs (black bars or dots) compared to other species of their taxonomic groups (grey bars or dots) for mammals (A, D and G), birds (B, E, and H) and plants (C, F and I). Plain and dotted red lines represent respectively median and third quartile values of the taxonomic group.

TABLE 1. Number of species in InvaCost ("N InvaCost") by type of costs (total number of species with costs, number of species with damage costs, and number of species with management costs) and by taxonomic group (mammals, birds and plants), including those that are also worth-conserving because they (i) are threatened ("Threatened") and/or (ii) belong to the top 25% most phylogenetically distinctive species of their taxonomic group ("Phylogenetically distinctive") and/or (iii) belong to the top 25% most functionally distinctive species of their taxonomic group ("Functionally distinctive").

Taxonomic group	**Mammals**			**Birds**			**Plants**		
Type of costs	Total	Damage	Management	Total	Damage	Management	Total	Damage	Management
N InvaCost	44	21	36	20	13	15	333	112	287
Threatened	7	2	6	0	0	0	2	0	2
Phylogenetically distinctive	12	4	11	2	0	2	76	30	60
Functionally distinctive	13	6	11	10	6	8	22	7	18

Phylogenetic distinctiveness of species with costs in InvaCost

Although the phylogenetic distinctiveness of species with economic costs is very variable, 12 mammals, two birds and 76 plants are among the most phylogenetically distinctive species (Figure 1D-F, Table S1) and can therefore be considered as conservation paradoxes. These include the koala, the African sacred ibis *Threskiornis aethiopicus*, and the white morning-glory *Ipomoea lacunosa* (see Table S1 for their respective ranking). Among the most phylogenetically distinctive mammals, four have damage costs and 11 have management costs (Table 1). The two birds belonging to the most phylogenetically distinctive birds only have management costs (Table 1). Finally, among the 76 most phylogenetically distinctive plant species, 30 have damage costs and 60 have management costs (Table 1).

Functional distinctiveness of species with costs in InvaCost

The functional distinctiveness of species with economic costs is also very variable among species (Figure 1G-I). We found that 13 mammals, 10 birds and 22 plants in InvaCost are also among the most functionally distinctive species (Figure 1G-I, Table S1) and can therefore be considered as conservation paradoxes. These include the raccoon dog *Nyctereutes procyonoides*, the house crow *Corvus splendens*, and the wetland nightshade *Solanum tampicense* (Table S1 for their respective ranking). Among the 13 mammals, six species have damage costs and 11 species have management costs (Table 1), while among the 10 birds, six of them have damage costs and eight have management costs (Table 1). Finally, among the 22 plant species, seven species have damage costs and 18 species have management costs (Table 1).

Multi-criteria conservation paradoxes

We further analysed the nature of the conservation paradoxes among the 126 species documented in InvaCost and identified as conservation paradoxes (Figure 2). Specifically, seven species (five mammals and two plants) are considered threatened in their native ranges. Moreover, two mammals documented with costs in InvaCost are simultaneously threatened and among the most phylogenetically distinctive mammals (the Przewalski's horse and the koala). We also found that 16 species including five mammals (e.g., the raccoon dog and the wild boar *Sus scrofa*), one bird (e.g., the golden eagle *Aquila chrysaetos*) and 10 plants (e.g., the white morning-glory *I. lacunosa* and the Asiatic witchweed *Striga asiatica*) are actually conservation paradoxes based on the two conservation criteria relying on distinctiveness (Figure 2, Table S1).

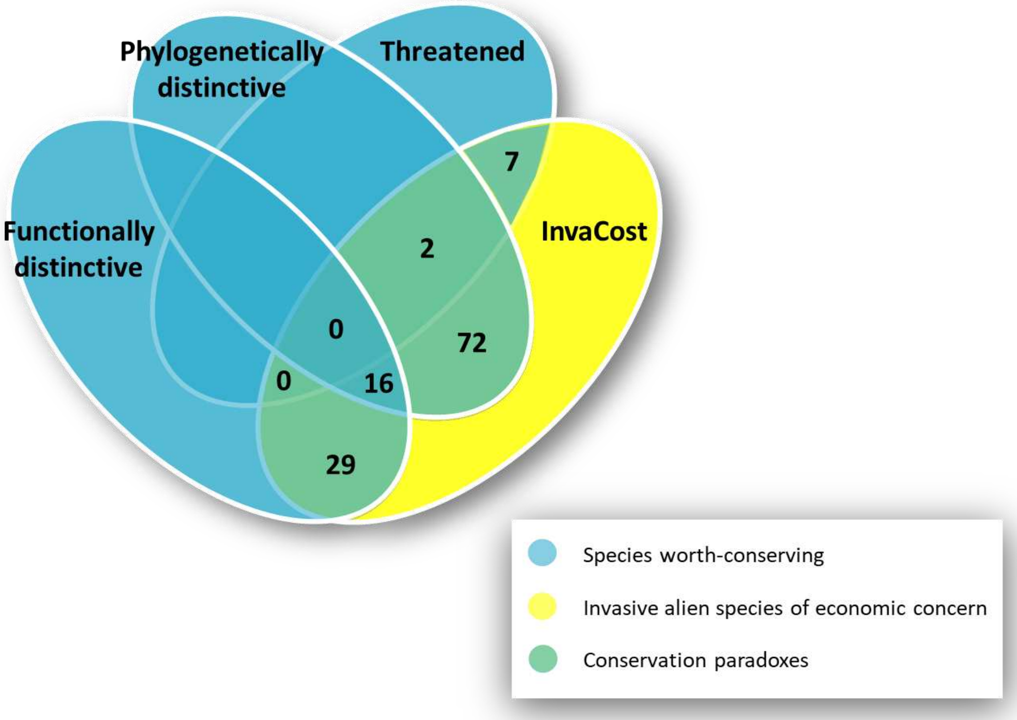

FIGURE 2. Number of mammal, bird and plant species documented in InvaCost ("InvaCost") constituting invasive alien species of economic concern that are also worth-conserving because they are threatened ("Threatened") and/or belong to the top 25% most phylogenetically distinctive species of their taxonomic group ("Phylogenetically distinctive") and/or belong to the top 25% most functionally distinctive species of their taxonomic group ("Functionally distinctive").

Conservation paradoxes within the costliest InvaCost species

We further found that, among the top 5 costliest species for each taxonomic group and for type of costs (constituting a total of 24 species), eight species represent conservation paradoxes (Figure S1, Figure 3, and Figure 4). These include one threatened species: the European rabbit, associated to an average annual cost of about 975 million US$ in terms of damage, and about 9 million US$ in terms of management (Figure S1, Table S1). These further include three of the most phylogenetically distinctive species: the wild boar (with an average annual cost of 50 million US$ in terms of damage and of 23 million US$ in terms of management), the coypu *Myocastor coypus* (with an average annual cost of 204 million US$ in terms of damage), and the common buttercup *Ranunculus acris* (with an average annual cost of 176 million US$ in terms of management) (Figure 3, Table S1). These eight conservation paradoxes within the costliest InvaCost species finally include four of the most functionally distinctive species: these are the red fox *Vulpes vulpes* (with an average annual damage cost of 9.1 million US$), the common starling *Sturnus vulgaris* (with an average annual damage cost of 40.9 million US$ and of 0.3 million US$ management cost), the rose-ringed parakeet *Psittacula krameri* (with an average annual damage cost of 1.4 million US$) and the Japanese honeysuckle *Lonicera japonica* (with an average annual damage cost of 3,512 million US$) (Figure 4, Table S1).

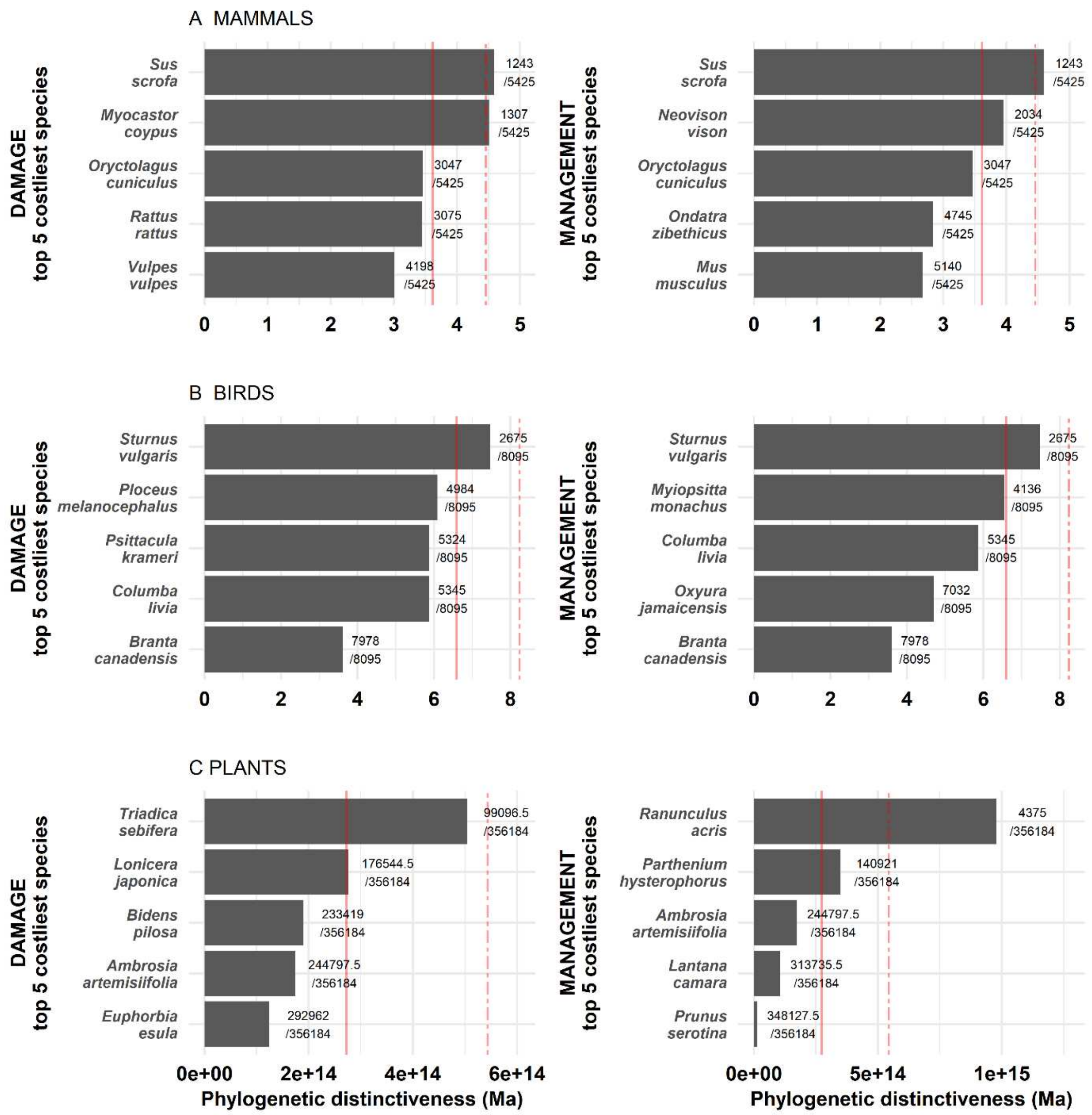

FIGURE 3. Phylogenetic distinctiveness scores (bars) and ranks (text at the right of the bars) of the top 5 costliest invasive species for mammals (A), birds (B) and plants (C) in terms of damage and management. The plain red line and the dotted red line respectively indicate the median and the third quartile of phylogenetic distinctiveness for each taxonomic group.

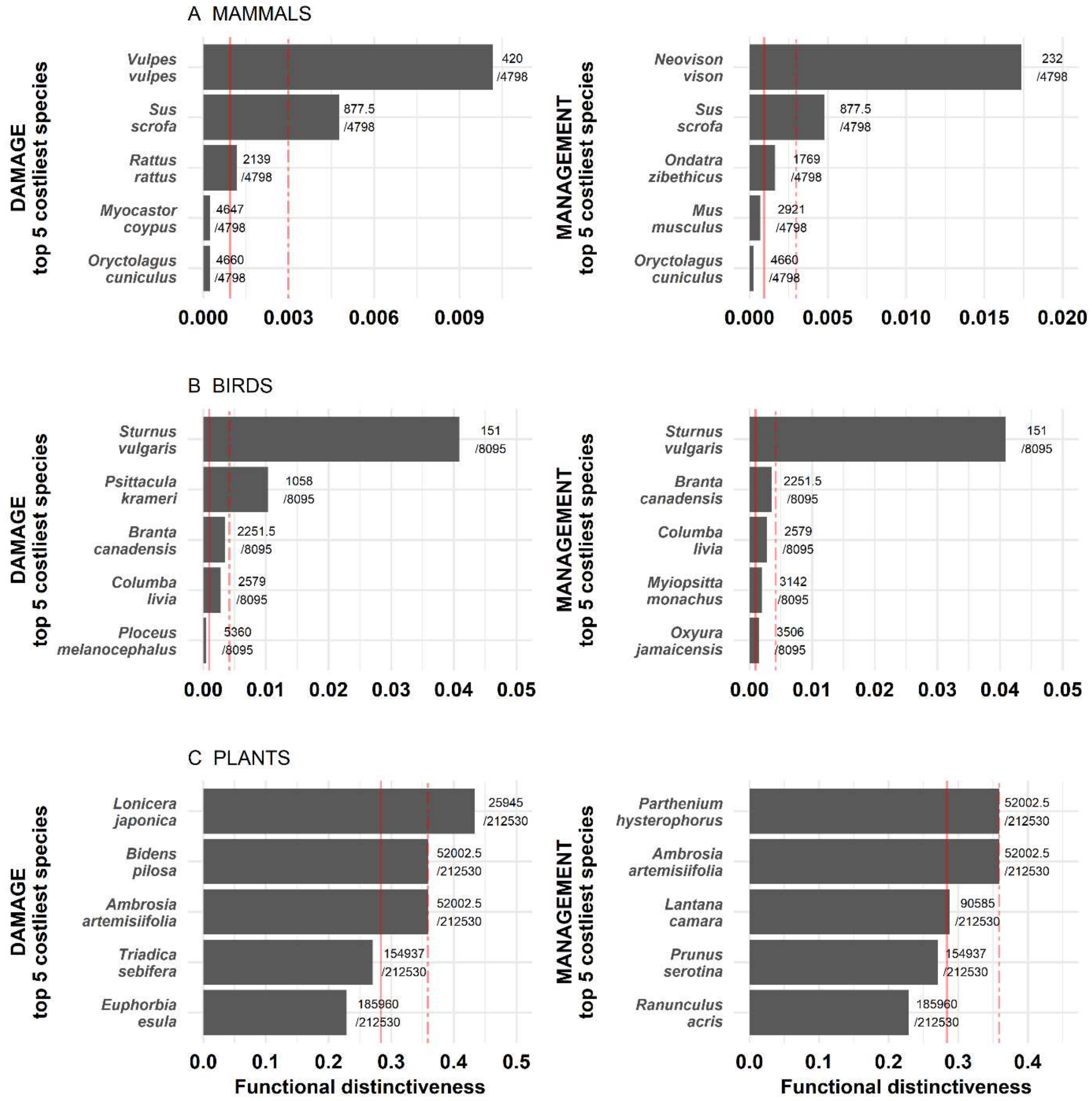

FIGURE 4. Functional distinctiveness scores (bars) and ranks (text at the right of the bars) of the top 5 costliest invasive species for mammals (A), birds (B) and plants (C) in terms of damage and management. The plain red line and the dotted red line respectively indicate the median and the third quartile of functional distinctiveness for each taxonomic group.

Discussion

Conservation paradoxes exist and are not marginal

To our knowledge, our work represents the first study investigating the number and identity of IAS of economic concern that are, paradoxically, also worth-conserving. Among the 397 species of mammals, birds and plants representing IAS of economic concern, we found that one third of them (i.e., 126 species) are worth-conserving – either because they are threatened and/or belong to the most phylogenetically or functionally distinctive species. Such conservation paradoxes further represent one third of the costliest InvaCost species: not only they exist, but they are not marginal.

We found that more species constitute a conservation paradox because they are among the most phylogenetically or functionally distinctive species than because they are threatened. On the one hand, 119 species constitute a conservation paradox because they are among the most phylogenetically or functionally distinctive species, representing 30% of the mammals, birds and plants documented in InvaCost. On the other hand, at least seven mammals and two plants are IAS in one area of the world with an economic cost but threatened in their native areas, which represents nearly 16% of mammals documented in InvaCost and 0.6% for plants, and 2.3% of all species of mammals, birds and plants (the three taxonomic groups studied here) documented in InvaCost. We also found that two species are simultaneously threatened and among the most phylogenetically distinctive mammals (i.e., the Przewalski's horse and the koala), and 16 constitute conservation paradoxes based on both phylogenetic and functional distinctiveness criteria.

Moreover, most of the conservation paradoxes have management costs. This holds true for species that are among the most phylogenetically (or functionally) distinctive species, with a total average annual cost of almost 727 million US$ of which 28% are due to the coypu (3,766 million US$, of which 93% are due to the Japanese honeysuckle). This also holds true for threatened species with a total average annual cost of almost 985 million US$ - of which admittedly, 99% are due the European rabbit.

Management implications of conservation paradoxes

The 126 IAS of economic concern identified as conservation paradoxes all have, by definition, negative ecological impacts, in turn supporting the need for management efforts for protecting the invaded ecosystems. However, the nature of management measures needed may differ between conservation paradoxes that are threatened and those identified on distinctiveness criteria.

On the one hand, threatened IAS of economic concern constitute real conservation paradoxes, as the control and/or eradication of invasive populations may jeopardise the survival of the species at global scale (Marchetti & Engstrom, 2016). Examples of such cases in our study include the European rabbit (endangered in its native range and among the costliest invasive mammal species with a total average annual cost of 984 million US$), the aoudad (vulnerable in its native range and an IAS of economic concern threatening at least 8 native species - Global Invasive Species Database, 2022), the koala (vulnerable in its native range and an IAS of economic concern) and the cow tree (vulnerable in its native range and an IAS of economic concern). In such cases, particular attention should be paid to coordinate management between invasive and native ranges, so that control and/or eradication of invasive populations do not contribute to precipitate the global extinction of the species. Specifically, while control and/or eradication measures should be taken for invasive populations, conservation actions are needed to protect or restore native, threatened populations. In this context, we argue that relocate alien individuals to reinforce native populations and/or for *ex-situ* conservation while respecting codes of conduct to avoid transport of contaminants appears as a strong coordinated management solution. This could be coordinated by fine-tuning existing intergovernmental instruments to that aim (e.g. the Convention on International Trade in Endangered Species of Wild Fauna and Flora) or by developing new, dedicated ones. Currently, while some threatened IAS such as the European rabbit, the aoudad and the koala are controlled in their invasive ranges and also benefit from intensive conservation efforts in their native ranges (Cassinello et al., 2021; Lees & Bell, 2008; Villafuerte & Delibes-Mateos, 2019; Woinarski & Burbidge, 2020), other threatened IAS such as the cow tree are only controlled in their invasive ranges without any recorded conservation effort in their native ranges (Santiana & Pitman, 2004).

On the other hand, conservation paradoxes identified on distinctiveness criteria only might not necessarily be conservation paradoxes *sensu stricto*, as control and/or eradication actions of invasive populations are fully compatible with preventive conservation actions for native, not-yet threatened populations. Examples of such cases in our study include the wild boar, the golden eagle and the white morning-glory - the three of them being both among the most phylogenetically and functionally distinctive species. Even if these distinctive IAS of economic concern are not threatened yet, relocating alien individuals to reinforce native populations and/or for *ex-situ* conservation could be relevant as an insurance strategy to ensure the long-term persistence of those distinctive species at global scale. Such strategy may become more relevant, with species in their native area that may be at risk of local extinctions with ongoing and future climate change and habitat losses, as it has been predicted for some important IAS such as *Miconia calvescens* (González-Muñoz, Bellard, Leclerc, Meyer, & Courchamp, 2015).

Here, we demonstrated the existence and quantified the number of conservation paradoxes defined as IAS of economic concern both damaging in some areas of the world and of conservation need in others. Since most of those IAS have management costs, the situation is even more paradoxical: on one side, governments and non governmental organisations spent money to limit the number of individuals and potential spread of the species, while on the other side, they spent money to protect and strengthen population size. In such highly paradoxical situations, two options are possible: refrain from controlling IAS in invaded areas, or intensify their conservation in native areas. Clearly, we do not argue for the first of these options. We forcefully maintain that biological invasions are among the most dramatic drivers of biodiversity loss worldwide (Bellard, Marino, & Courchamp, 2022) and that they need to be managed in invaded areas and, when possible, entirely removed from them. The remaining option is therefore that conservation of those paradoxical species is reinforced in native areas, and if relevant the control is adapted (e.g. considering translocation) in invaded areas. This also includes cost-benefit actions across the whole range of the IAS and optimisation of human resources and costs across the range of the species. An international platform or organism to manage IAS worldwide could contribute to fill this gap and avoid waste of money and other resources.

Limits and perspectives

Our work focused on mammals, birds and plants because these are the groups with the most available data over the four variables: threat status, phylogeny, functional traits and economic costs. However, we did not have a full taxonomic coverage for any of these variables, which may bias some of our results. First, regarding threat status, while we have a good taxonomic coverage for mammals (96.9% of the mammal species estimated by Upham et al., 2019) and birds (99.8% out of the ca. bird species estimated by BirdLife in 2021), only 0.04% of the estimated seed plant species (Govaerts, 2001) have a threat status. This implies that we possibly underestimated the number of plant conservation paradoxes based on the threat criterion. Phylogenetic distinctiveness is probably the less biased variable, since we have phylogenetic distinctiveness scores for 91.4% of mammals, 73.6% of birds, and 89.9% of plants. We also have a good taxonomic coverage for functional distinctiveness scores: 80.0%

of mammals, 73.6% of birds, and 53.1% of plants. However, concerning phylogenetic or functional distinctiveness, the lack of a complete taxonomic coverage leads to an overestimation of distinctiveness (Robuchon et al., 2019). Finally, the economic costs represent the variable with the largest gap in terms of taxonomic coverage, since InvaCost does not represent all costs of IAS but only those that have been reported. Typically, less than 10% of IAS have economic costs recorded, while the >90% without data are certainly not all without cost (Haubrock et al., 2021 and references therein).

Finally, while we defined conservation paradoxes as those IAS of economic concern that are also globally threatened and/or are among the most phylogenetically or functionally distinctive species, we argue that other definitions may apply resulting in the identification of more conservation paradoxes. For instance, we focused here on IAS with economic impacts, completely ignoring their ecological impacts. Further, we only considered globally threatened species, while some IAS are only regionally threatened, such as the popular bony fish (*Arapaima gigas*), invasive in Indonesia, not assessed globally because of a lack of data (World Conservation Monitoring Centre, 1996), but endangered in Brazil (Marková et al., 2020).

Conclusion

In this study, we highlighted that as many as one third of mammal, bird, and plant IAS of economic concern are also worth-conserving. In the context of global changes, with the increasing pressure of habitat loss, climate change, and overexploitation, the biodiversity crisis is such that the potential number of IAS that are also worth-conserving is probably much higher. This stresses to an unprecedented level that some species simultaneously need to be controlled and/or eradicated in their invasive ranges and conserved in their native ranges. The management of such species needs to be tightly coordinated between alien and native ranges to optimise cost-effective actions and maximise conservation benefits.

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Data archiving statement

The sources of the data used in this study are mentioned in the Material and Methods section. The data generated within this study (distinctiveness scores and figures) will be made publicly accessible in a GitHub repository together with the code to generate them upon acceptance of the manuscript.

Authors' contributions

MR, FC, ACV and CBel designed the study, which was initially discussed in a workshop with all co-authors. MR, CBer, CAKMD, GH, SP, VR and CBel ran the analyses. MR led the writing of the manuscript with substantial contributions of CBel. All authors revised the manuscript.

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Conflict of interest statement

The authors have no competing interests to declare.

Annexe 8 : Matériel supplémentaire de la partie « Perspectives » de la discussion générale

Table S1 : Description des hypothèses liées à chaque variable utilisée

Variable	**Type de variable**	**Hypothèse : Lien avec le nombre d'espèces exotiques**	**Références**
Nombre d'espèces de poissons d'eau douce natives	Biotique	(+) Le nombre d'espèces natives est lié à une plus grande redondance fonctionnelle, une plus forte compétition et à un faible nombre de niches écologiques inoccupées. (-) Au contraire, le nombre d'espèces natives peut être positivement corrélée au nombre d'exotiques selon l'hypothèse *rich-get-richer.*	Yonekura *et al.*, 2004; Ruesink, 2005; Jeschke and Heger, 2018.
Indice d'empreinte humaine *(Human footprint index)*	Anthropique	(+) Une forte anthropisation est liée a de fortes perturbations anthropiques qui augmentent la susceptibilité aux invasions	Clavero *et al.*, 2013; Su *et al.*, 2021
Nombre de barrages par bassin	Anthropique		
Amplitude de températures Amplitude de précipitations	Abiotique	(+) Une grande amplitude de températures et/ou de précipitations augmente la susceptibilité aux invasions	
Aire des bassins versants	Abiotique	(+) Les grands bassins versants seraient plus accessibles aux humains. Sur les îles, l'aire est associée positivement à la richesse en espèces exotiques.	Clavero *et al.*, 2013; Blackburn *et al.*, 2016
Différence d'élévation au sein des bassins	Abiotique	(+) Une grande différence peut aussi être liée à une grande taille de colonne d'eau à exploiter, augmentant le nombre de niches écologiques à occuper. (-) Une grande différence d'élévation peut être liée à un débit fluvial rapide, rendant difficile l'expansion des espèces exotiques.	

Table S2 : Résultats des text de Wilcoxon pour chaque variable testée.

Variables explicative	**p-value**	**W**
Nombre d'espèces natives	1.412e-08	146407
Nombre de barrages	<2.2e-16	167876
Amplitude de précipitations	0.013	109772
Amplitude d'élévation	3.650e-04	136279
Human footprint index	0.010	132490
Aire des bassins	1.832e-11	151127
Amplitude de température	0.163	127235

Matériel et méthodes :

Variables à expliquer

Statut envahi des bassins versants : Nous avons utilisé la base de données de Tedesco et al. (2017) afin de compiler les bassins versants ayant au moins une espèce de poisson d'eau douce exotique établie, et les bassins ne comportant aucune espèce de poisson exotique établie. Pour chaque bassin, nous avons considéré comme établies les espèces ayant un statut d'occurrence *« valid »* dans la base de données de Tedesco et al. (2017). Ainsi, nous avons identifié 415 bassins comme comportant au moins une espèce de poisson d'eau douce exotique établie (*i.e.*, bassins dits envahis), et 583 bassins comme ne comportant aucune espèce de poisson d'eau douce exotique.

Variables explicatives

Nous avons considéré sept variables explicatives au statut envahi des bassins versants. Ces variables peuvent être regroupées en trois groupes : les variables biotiques, abiotiques et anthropiques.

Variable biotique – nombre d'espèces de poissons d'eau douce natives : Nous avons utilisé la base de données de Tedesco et al. (2017) afin de compiler le nombre d'espèces de poissons d'eau douce natives par bassin versant. Nous n'avons considéré comme présentes dans un bassin donné que les espèces ayant un statut d'occurrence « *valid* ».

Variable anthropique – nombre de barrages par bassin : Nous avons utilisé la base de données GOODD (GlObal geOreferenced Database of Dams) (Mulligan *et al.*, 2020) qui répertorie plus de 38 000 barrages géo-référencés. En utilisant les délimitations de bassins de Tedesco et al. (2017), nous avons pu compter le nombre de barrages par bassin versant.

Variable anthropique – Indice d'empreinte humaine (Human footprint index) : Nous avons utilisé la deuxième version de la base de données de Venter et al. (2016). Cet indice prend en compte sept types de données mondiales sur la période 2000-2013 concernant la densité de population, l'utilisation humaine des terres (terres cultivées et pâturages), les infrastructures électriques, les environnements bâtis, l'accès humain (routes, voies ferrées, voies navigables). Nous avons calculé pour chaque bassin la médiane de l'indice d'empreinte humaine, en utilisant les délimitations de bassins versants de Tedesco et al. (2017).

Variables abiotiques – Amplitudes de température et de précipitation : Pour chaque bassin, nous avons récupéré la température minimale du mois le plus froid et la température maximale du mois le plus chaud dans les bassins d'origine des espèces à partir de Worldclim (Fick and Hijmans, 2017). Nous n'avons considéré que le quantile 0.95 de la température maximale du mois le plus chaud et le quantile 0.05 de la température minimale du mois le plus froid pour éviter les valeurs aberrantes extrêmes. Nous avons ensuite calculé l'amplitude de températures dans chaque bassin en soustrayant le quantile 0.05 de la température du mois le plus froid au quantile 0.95 du mois le plus chaud. Nous avons procédé de la même manière pour l'amplitude de précipitations, en utilisant les précipitations du mois le plus sec et du mois le plus humide.

Variable abiotique – Différence d'élévation au sein du bassin : Nous avons utilisé la base de données ETOPO5 (*World digital elevation model)* (National Geophysical Data Center. 1988). Nous avons calculé la différence d'élévation par bassin en soustrayant la valeur d'élévation la plus haute à la valeur la plus basse dans chaque bassin.

Variable abiotique – Aire du bassin : Nous avons utilisé l'aire des bassins renseignée dans Tedesco et al. (2017).

Analyse statistique : Comparaison entre bassins envahis et bassin non-envahis – Nous avons tout d'abord procédé à une analyse des corrélations sur le logiciel R entre chaque variable grâce à la fonction *cor()* du package *stats* (R Core Team 2021). Toutes les variables étant des variables quantitatives, nous avons utilisé des tests de wilcoxon (*wilcox.test()*) afin de comparer les bassins envahis aux bassins non-envahis pour chaque variable. Ces analyses ne sont que des analyses préliminaires, le but à terme étant de faire des modèles linéaires généralisés en utilisant le nombre d'espèces de poissons établis dans chaque bassin en tant que variable à expliquer.

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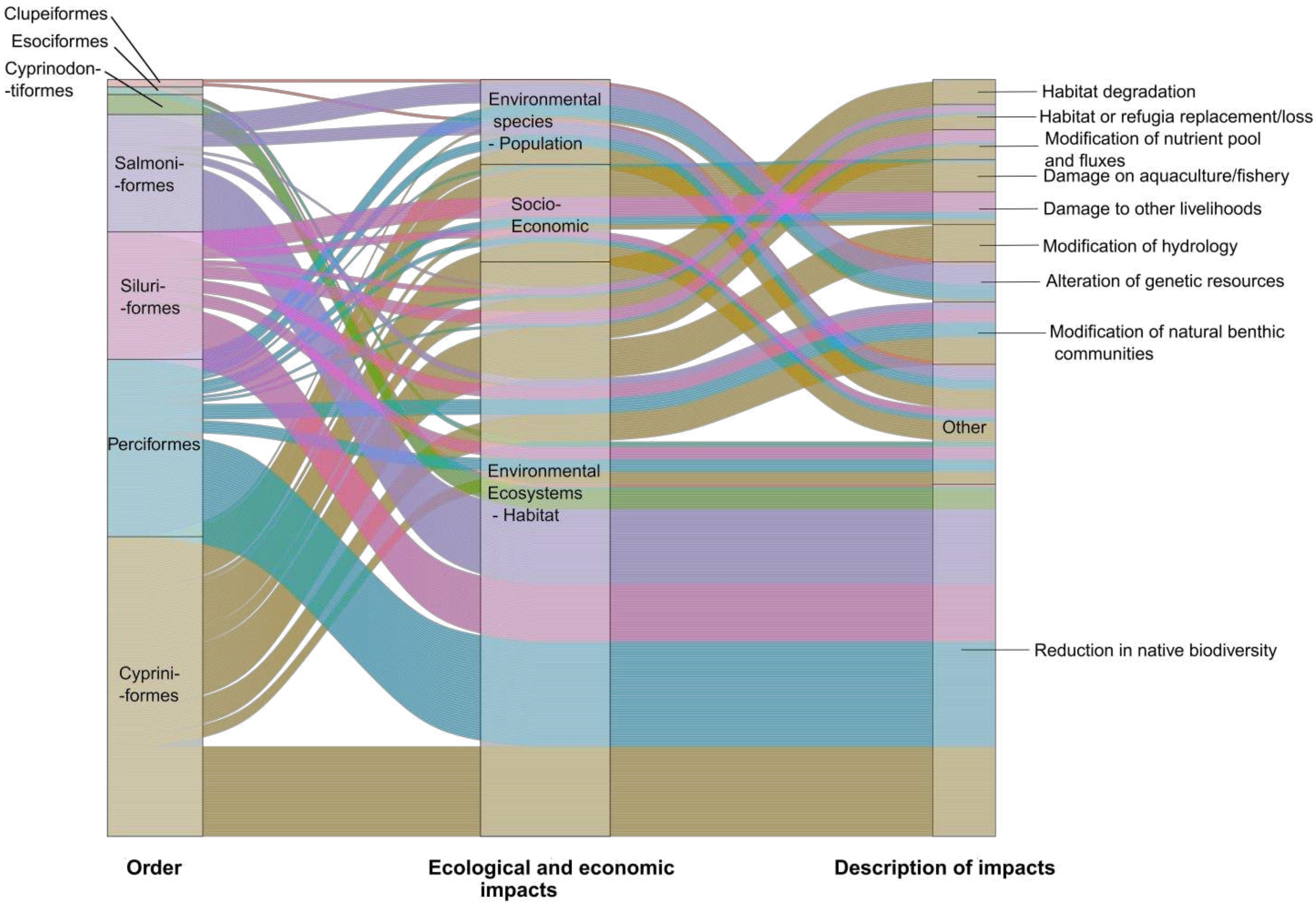
Annexe 9 : Matériel supplémentaire de la partie « Limites » de la discussion générale



Impacts of non-native freshwater fish species per order. Each line represents a species-location association. The data used come from the GISD dataset (GISD, 2015, http://www.iucngisd.org/gisd/). 303 species-locations associations are considered for impacts.

Annexe 10

C. Bernery*, L. Lusardi*, C. Marino*, M. Philippe*, E. Angulo, E. Bonnaud, L. Guéry, E. Manfrini, A. Turbelin, C. Albert, U. Arbieu, F. Courchamp (2022). The PhD student experience: highlighting the positive aspects (2022). *eLife, **11**:e81075.*

*Co-premiers auteurs

eLife

FEATURE ARTICLE

RESEARCH CULTURE

Highlighting the positive aspects of being a PhD student

Articles about doing a PhD tend to focus on the difficulties faced by research students. Here we argue that the scientific community should also highlight the positive elements of the PhD experience.

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Introduction

Doing a PhD can be both demanding and rewarding. In addition to overcoming the scientific and intellectual challenges involved in doing original research, a PhD student may also have to deal with financial difficulties, an unhealthy work-life balance, or resulting concerns about their mental health (***Woolston, 2017***; ***Auerbach et al., 2018***; ***Oswalt et al., 2020***; ***Evans et al., 2018***). Despite all this, most PhD students seem satisfied with their decision to do a PhD, mostly because they work in stimulating environments with a high degree of independence and good supervision (***Pommier et al., 2022***; ***Woolston, 2017***).

Paradoxically, however, the fact that most PhD students are positive about doing a PhD is not always apparent to the outside world. For example, the present authors recently analysed more than 90,000 tweets about the PhD experience: almost half of the tweets were positive, and less than a sixth were negative, yet the negative tweets received more likes and retweets (***Figure 1***). What can be done to counter such misleading and negative impressions? In this article we – a group of PhD students, postdocs and permanent academics – highlight the positive elements of doing a PhD in order to present a more balanced view of the whole PhD experience. We also make recommendations to maintain a positive momentum throughout the PhD. Although these ideas and recommendations are based on our experiences as researchers in ecology working in Europe, we feel that most of the points we make also apply in other disciplines and places.

Three benefits of doing a PhD

There are two primary outputs from a PhD: new skills and expertise for the graduate, and new knowledge for the wider world. In this article we focus on the former and discuss the three main benefits of doing a PhD for the individual: (i) the development of specific skills to become an expert; (ii) the ability to work in a collaborative environment; (iii) improved communication skills while sharing knowledge (***Figure 2***). For each of these benefits we discuss both general aspects that apply to most doctoral students, and specific aspects that depend on the student's supervisor, field of research, location and other factors.

Becoming an expert

Throughout a doctoral project, a PhD student will develop many of the skills needed to grow into an independent researcher, while also developing

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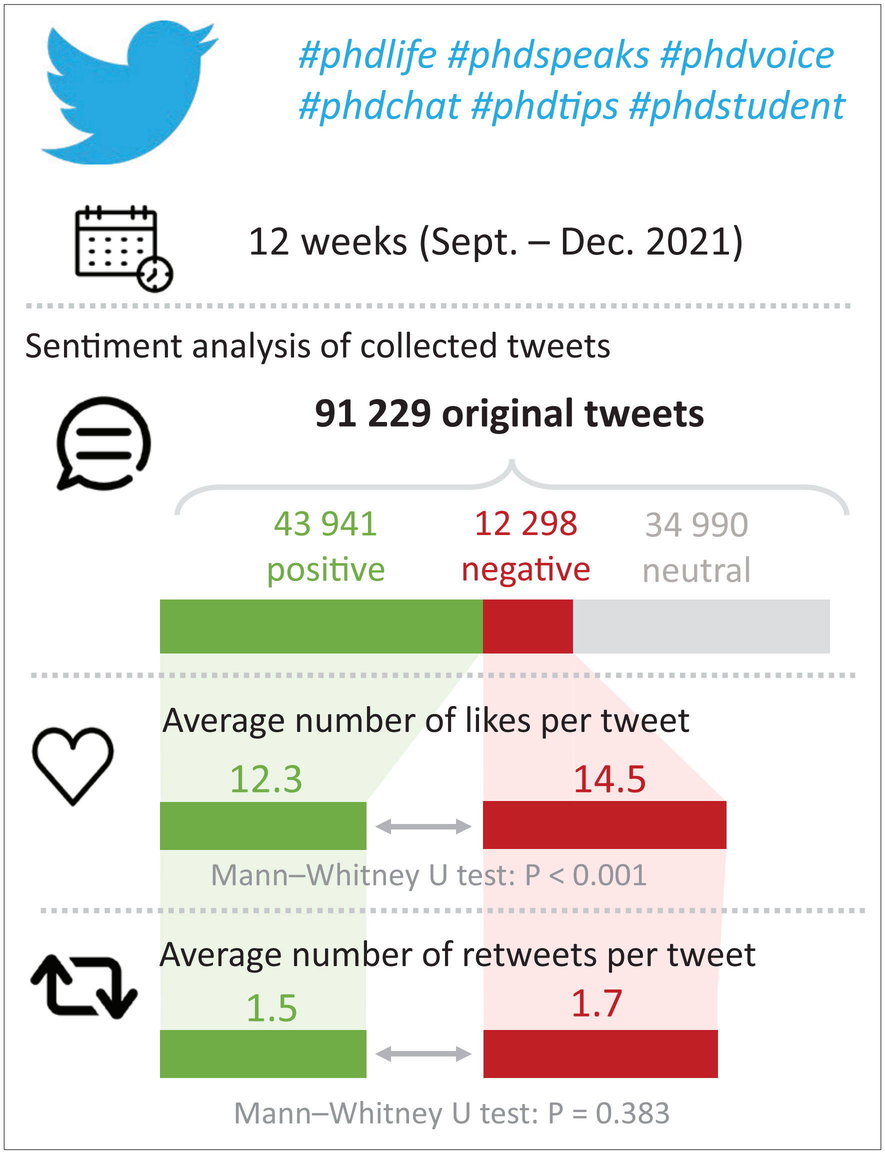

Figure 1. Sentiment analysis of tweets about the PhD experience. We retrieved all tweets posted in the English language during 12 consecutive weeks, from September to December 2021, that contained any of the following six hashtags: #phdlife, #phdspeaks, #phdvoice, #phdchat, #phdtips, #phdstudent. We then measured the sentiment (positive, negative or neutral) associated with each original tweet (excluding retweets). Of the 91 229 tweets we retrieved, 43,941 were positive, 12,298 were negative, and 34,990 were neutral. Mann-Whitney U tests were performed to compare the average number of likes and retweets of positive versus negative tweets. Negative tweets received significantly more likes than positive tweets (14.5 vs 12.3; $P<0.001$); negative tweets were also retweeted more than positive tweets but the difference was not significant (1.7 vs 1.5; $P=0.383$). The Twitter API and the "rtweet" R package (cran.r-project.org/web/packages/rtweet/vignettes/intro.html) were used to retrieve the tweets; the "syuzhet" R package (rdrr.io/cran/syuzhet/) and the Bing lexicon (***Liu, 2012***) were used for the sentiment analysis; all analyses were performed with R software (***R Development Core Team, 2021***).

expertise in a given field. In addition to learning a great deal about their own field – and adding knowledge to it – a PhD student will learn how to perform a variety of tasks, and thus acquire new transferable skills. These will include autonomy, critical thinking, organization and planning, resilience, and the ability to design, lead and carry out projects. Furthermore, unlike postdocs and principal investigators, who have to carry out various management and administrative tasks, PhD students are usually free to dedicate their working hours almost exclusively to academic pursuits that they are (or can become) passionate about. This freedom is one of the aspects that make the PhD experience unique, and it should not be overlooked or taken for granted. Unfortunately, not all PhD students benefit from or are aware of such autonomy, but this ought to be an objective for all PhDs.

A PhD does not consist of a number of uneventful years that culminate in a single success. Rather, there are many steps along the way – such as mastering a technique, completing a series of experiments or activities in the field, or finishing the first draft of a manuscript – and the feeling of accomplishment that comes with each completed milestone should be a source of pride to the student.

Working in a collaborative environment

Learning how to work with other researchers is an important part of getting a PhD. The PhD student's most important working relationship is with their supervisor (or, in some cases, supervisors), but most PhD students will also have the opportunity to collaborate with other members of their research group or lab, or even with researchers from the wider community. Working on other projects from time to time can help the student's own project through increased productivity and creativity; moreover, it can strengthen lab cohesion, and might even lead to the student being a co-author on a paper. Additionally, supervising undergraduate students – or even new graduate students – is a good way of acquiring management skills.

Conferences are another way to meet and interact with other researchers. In particular, they are an opportunity to discover, discuss and be inspired by the work of other scientists. Conversations at conferences can generate new research questions or ideas for new and improved ways to tackle existing questions. Moreover, presenting results at a conference gives students a chance to receive feedback, to be recognized as active researchers by their peers, and to build a professional network.

Collaboration also can happen through the many virtual communities that PhD students can join for technical, scientific or moral support. For example, the Global PhD Server enables doctoral students

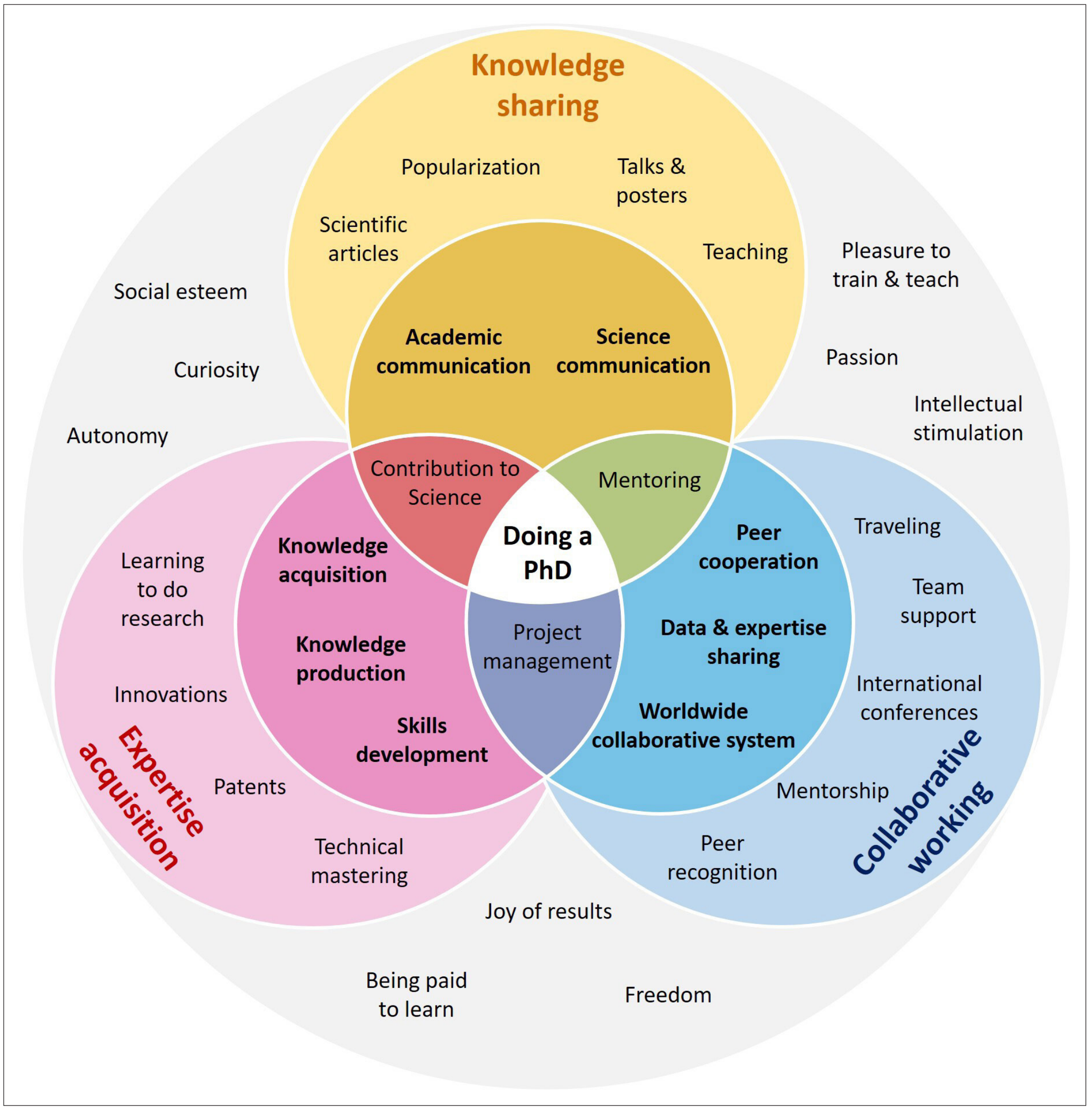

Figure 2. The positive aspects of doing a PhD. The three primary benefits of doing a PhD are acquiring expertise (pink circle), learning to work in a collaborative environment (blue), and developing communication skills for sharing knowledge (yellow). For each benefit, general aspects that apply to almost all doctoral students are shown in bold type in the small circle, and specific aspects that depend on, for example, the student's supervisor or field of research are shown in plain type in the large circle. The large grey area contains more abstract and subjective ideas that are not discussed in the main text. It should be noted that this figure is conceptual, and that the aspects and ideas in it could be grouped in other, equally valid, ways.

to discuss their experience, exchange anecdotes, and offer or seek help. The @PhDForum supports a variety of activities, such as writing sessions for PhD students working on papers or chapters of their thesis, while Stack Overflow is a good place to offer/seek help with coding and statistics.

Developing communication skills

The ability to communicate results is a crucial skill for any researcher. A PhD student will, for example, be required to present their work to other scientists as talks or posters at meetings and conferences. The student will also start learning how to write a scientific article. Moreover, there are many opportunities for PhD students to share their passion and knowledge about their field, such as teaching and mentoring undergraduates and other graduate students. They can also get involved in public outreach, and contribute to awakening new passions or educating citizens on certain topics.

Recommendations

Along the PhD journey, neither the doctoral student nor the supervisor will have full control over what will happen. Some things will go wrong, which is why it is important to remain positive and try to make the most of what is a unique opportunity. Ways for the student to remain positive include going back to old pages in their laboratory notebook to see how much progress has been made, and keeping a note of all the positive feedback from different people. It is also important to remember that one does not become a PhD student by chance – being accepted to do a PhD is an achievement in itself. Additionally, sharing preliminary results with other members of the group and attending social events of a lab can build a supportive working atmosphere and help students to stay positive.

Focusing only on research can sometimes be exhausting, so spending time on other activities – such as supervising students, teaching, or working on outreach – can break the monotony and generate a sense of progress. Finally, it is important to celebrate achievements, such as a first draft, an accepted paper, a conference presentation or the submission of a grant proposal (and, obviously, a successful grant proposal). These achievements can be celebrated in the real world, on social media – or both! By regularly highlighting positive outcomes, it is easier to recognise that past difficulties have been overcome, that progress has been made, and that expertise, skills and knowledge have been gained.

In parallel, it is important to try to limit the impact of the negative aspects of the PhD experience, for they are real and various, and can be crushing if left unchecked. First, it is essential to contextualize them. For example, bear in mind that failure is an integral part of progress, and is often just a temporary setback as opposed to a defeat. This is especially true when a manuscript is rejected by a journal: viewing the rejection as an opportunity to improve the manuscript, and acknowledging that the reviewer reports are about the science, not the authors, can help reframe rejections in a positive light. After all, even the most distinguished researchers have experienced rejection many times. Moreover, as highlighted above, science is a collective adventure, and one is rarely alone when help is sought out. In this regard, talking about the challenges one encounters during a PhD with other students or researchers can also help put these challenges into perspective and to see the positive aspects.

The relationship between the PhD student and their supervisor will likely have a big influence on the PhD experience. However, it is important to recognize that this relationship works both ways, and both stand to benefit if it works well. Among other things, the PhD students can help their own cause by being clear on the type of feedback they want, or by scheduling regular meetings focused on their PhD – and persisting even if their supervisor is busy (***Kearns and Gardiner, 2011***).

We would also encourage supervisors to be positive in their interactions with their PhD students, and to build a global productive environment that could benefit the PhD student (***Andreev et al., 2022***). Supervisors could, for example, praise PhD students when the opportunity arises, and ensure that criticism is always constructive – and also encourage other members of their lab to do the same.

PhD students may also face challenges that cannot be overcome with positive thinking. Abusive behaviours such as bullying, harassment or discrimination should be reported to the relevant authorities immediately.

Some PhD students will also be anxious about their future job prospects, especially if they hope to remain in academic research. One way to help reduce such anxiety is to clarify life/career goals and identify the steps needed to reach them. For example, if the student makes a list of all potential funding opportunities (including deadlines) at the start of their last year, it will help them plan for the future and relieve some of the pressure that will build up towards the end of their PhD. Building a professional network can also help with career planning, and attending conferences and establishing collaborations are crucial in this regard.

Finally, if needed, it is entirely acceptable for a PhD student to take a break during their PhD, to refocus on what they really want in life, or to even leave their PhD without finishing it if they realize that it is not for them. However, before making such a decision, we would encourage the student to ask themselves if the doubts they are experiencing are due to a momentary difficulty that will pass, or if a PhD is not really the right career path for them.

Doing a PhD is a unique experience that typically occupies three or more years of someone's life. Through this experience the student will be enriched by acquiring a range of professional and personal skills, and by gaining a prestigious qualification. In the end, it is in the interest of everyone – the PhD student, the supervisor, their colleagues, their institutions, and academia in general – to make this experience as positive as possible.

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Competing interests: The authors declare that no competing interests exist.

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Data availability

All data generated or analysed during this study came from Twitter API and cannot be shared.

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université PARIS-SACLAY

ÉCOLE DOCTORALE
Sciences du végétal :
du gène à l'écosystème
(SEVE)

Titre : Synthèse globale des invasions de poissons d'eau douce, et identification des facteurs influençant leur succès

Mots clés : Invasions biologiques, macro-écologie, biologie de la conservation

Résumé : Les invasions biologiques sont l'une des principales causes de perte de diversité dans les écosystèmes d'eau douce. Parmi les espèces envahissantes en eau douce, les poissons sont parmi les taxons les plus introduits et sont à l'origine de nombreux impacts écologiques et socio-économiques. Dans ce cadre, cette thèse a deux objectifs principaux : 1. Fournir une synthèse globale des connaissances actuelles sur les invasions biologiques de poissons d'eau douce et 2. Étudier les facteurs expliquant le succès de ces invasions, en s'appuyant sur le travail de synthèse fait en amont. Pour répondre au premier objectif, nous avons synthétisé les principaux aspects des invasions de poissons d'eau douce, depuis leurs voies d'introduction, jusqu'aux méthodes de gestion mises en place, en passant par les facteurs expliquant la réussite de l'invasion et leurs impacts. Nous avons également mis en avant les biais de recherche actuels et ceux des bases de données disponibles et le manque de compréhension de plusieurs aspects de ces invasions. En particulier, nous avons souligné l'absence d'évaluation globale des coûts économiques des poissons, malgré des coûts connus pourtant importants de certaines espèces. Ainsi, grâce à la base InvaCost, nous avons synthétisé les coûts économiques connus des poissons envahissants : une perte économique d'au moins 37,08 milliards de dollars (valeur 2017) à l'échelle mondiale depuis 1960, pour seulement 27 espèces répertoriées. Plusieurs facteurs, régissent le succès des invasions de poissons d'eau douce. Toutefois, malgré leur importance, aucune étude n'a encore déterminé ces facteurs à l'échelle globale, ni pris en compte les différents types de facteurs existant aux différentes étapes de l'invasion. Ainsi, pour répondre au deuxième objectif de la thèse, nous avons identifié les caractéristiques des poissons exotiques à chaque étape de l'invasion et à l'échelle mondiale, en analysant 20 caractéristiques spécifiques, écologiques et socio-économiques de 307 espèces de poissons d'eau douce. Plus précisément, grâce à des modèles linéaires généralisés, nous avons analysé le nombre de pays dans lesquels chaque espèce a été introduite, s'est établie et a eu des impacts écologiques, comme un indicateur du succès de chaque étape d'invasion. Nous avons déterminé que les facteurs favorisant les invasions diffèrent selon l'étape d'invasion. Par exemple, les poissons ayant un régime alimentaire varié, prodiguant des soins parentaux et étant introduits par de multiples voies sont les plus largement introduits et établis dans le monde. L'impact, quant à lui, s'explique mieux par le type de voie d'introduction. Au sein même de l'étape d'établissement, nous avons aussi démontré que différents profils d'espèces peuvent se démarquer suivant un gradient d'établissement décrit par le nombre de bassins versants et le lieu d'établissement. Pour ce faire, nous avons compilé et analysé 13 traits morphologiques, écologiques et comportementaux de 222 espèces de poissons exotiques d'eau douce. Nous avons constaté que les poissons ayant de faibles capacités d'établissement étaient regroupés dans l'espace fonctionnel, ne se chevauchant pas avec d'autres groupes. Les poissons super-établis (établis dans de nombreux bassins versant et en dehors de leurs biorégions) englobaient un éventail plus large de stratégies fonctionnelles, avec des espèces ayant différents régimes alimentaires et un niveau élevé de soins parentaux. L'ensemble des résultats de cette thèse constitue une vision synthétique des invasions de poissons d'eau douce, ce qui permettra de guider plus efficacement à la fois les futures études et les approches de gestion, notamment proactives. Cette thèse met aussi en avant l'importance de considérer simultanément un large panel de facteurs et de voies d'introduction, et d'explorer les variations au sein des étapes de l'invasion, par une approche macro-écologique quantitative.

Title : Global synthesis of freshwater fish invasions, and identification of factors influencing their success

Keywords : Biological invasions, macro-ecology, conservation biology

Abstract : Biological invasions one of the main causes of diversity loss in freshwater ecosystems. Among the invasive freshwater species, fishes are among the most introduced taxa and are the cause of numerous ecological and socio-economic impacts. In this context, this thesis has two main objectives: 1. to provide a global synthesis of the main aspects of biological invasions of freshwater fishes and 2. to study the factors explaining the occurrence of biological invasions of fishes, based on the above synthesis. To answer the first objective, we synthesized the main aspects of freshwater fish invasions: the introduction pathways, the characteristics of the exotic species and the invaded ecosystems, their impacts and the management methods implemented. We have also highlighted current research biases including those of available databases and the fundamental lack of understanding of several aspects of these freshwater fish invasions. In particular, we have highlighted the lack of a comprehensive assessment of the economic costs of freshwater fishes, despite the known significant costs of some species. Thus, thanks to the InvaCost database, we have synthesized the economic costs known in the literature of invasive fish: an economic loss of at least US$37.08 billion (2017 value) globally since 1960, for only 27 species listed. Several factors, highlighted in the global literature review, govern the success of freshwater fish invasions. However, despite their importance, no study has yet determined these factors on a global scale, nor taken into account the different types of factors existing, or the different steps of the invasion. Thus, to address the second objective of the thesis, we identified the characteristics of invasive freshwater fishes at each stage of the invasion process, and at the global scale, by analyzing 20 specific, ecological, and socioeconomic characteristics of 307 freshwater fish species. Specifically, using generalized linear models, we analyzed the number of countries in which each species was introduced, became established and had ecological impacts, as an indicator of the success of each invasion steps. In this way, we determined that the factors driving invasions differed by invasion steps. For example, exotic freshwater fishes with diverse diets, parental care, and multiple pathways were the most widely introduced and established in the world. Impact, in turn, was best explained by the type of introduction pathway. Within the establishment step, we also demonstrated that different species profiles can be distinguished along an establishment gradient described by the number of drainage basins and the location of establishment of these species. To do so, we compiled and analyzed 13 morphological, ecological and behavioral traits of 222 species of exotic freshwater fishes. We found that fishes with low establishment abilities were clustered in the functional space, with little functional overlap with other groups. Super-established fish (i.e., established in more than 4 drainage basins and outside their bioregions) encompassed a broader range of functional strategies, with species having different diets and a high level of parental care. Taken together, the results of this thesis provide a synthetic view of freshwater fish invasions, which will more effectively guide both future studies and management approaches, including proactive management, of these invasions of freshwater ecosystems. This thesis also highlights the importance of simultaneously considering a wide range of different factors, pathways of introduction, and exploring variation within successive stages of invasion through a quantitative macro-ecological approach.