

A global picture of biological invasion threat on islands

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Biological invasions are among the main drivers of biodiversity losses. As threats from biological invasions increase, one of the most urgent tasks is to identify areas of high vulnerability. However, the lack of comprehensive information on the impacts of invasive alien species (IAS) is a problem especially on islands, where most of the recorded extinctions associated with IAS have occurred. Here we provide a global, network-oriented analysis of IAS on islands. Using network analysis, we structured 27,081 islands and 437 threatened vertebrates into 21 clusters, based on their profiles in term of invasiveness and shared vulnerabilities. These islands are mainly located in the Southern Hemisphere and many are in biodiversity hotspots. Some of the islands share similar characteristics regarding their connectivity that could be useful for understanding their response to invasive species. The major invaders found in these clusters of islands are feral cats, feral dogs, pigs and rats. Our analyses reveal those IAS that systematically act alone or in combination, and the pattern of shared IAS among threatened species, providing new information to implement effective eradication strategies. Combined with further local, contextual information this can contribute to global strategies to deal with IAS.

Islands harbour a significant proportion of the Earth's species and have an unusually high rate of endemism¹. However, many species on islands are now recorded as threatened, and most of the recorded extinctions of vertebrate species have occurred on islands². IAS are considered the second most important driver of species extinctions on islands, and are associated with nearly 25% of birds and amphibians that are currently threatened worldwide³. Island ecosystems are particularly vulnerable to biological invasions². To date, there have been over 700 attempted eradications of invasive alien mammals⁴ that have benefited 600 local populations, leading to larger populations or increased distributional areas⁴. Specifically, 236 species have benefited from those eradication programs, including 62 species that are at risk of extinction, and four species had their extinction risk reduced as a direct result of these eradications⁴. Despite these encouraging results, the threat posed by IAS remains substantial and widespread for native species³. Therefore, prioritization of research efforts and eradication strategies needs to be more effective⁵ and there are many more opportunities to decrease extinction risk for island species by eradicating IAS.

Because the amount of funding that is allocated to conservation is limited, it is important that these interventions target those islands where the conservation benefit will be highest. Efforts to prioritize research, management and policies for IAS have traditionally relied on expert judgments, and have been limited to either single IAS⁶ or subsets of islands⁷. In the absence of a systematic analysis of IAS impacts, it is difficult to see how an efficient and comprehensive strategy can be developed. Although several recent papers have examined the threats posed by IAS globally⁸ or for entire taxonomic groups (for example, mammals⁹), all of these studies implicitly assume that the distribution of IAS reflects their impacts (for example, in terms of the decline in native species populations that they cause). However, there is a lot of evidence that the impacts of IAS are context dependent^{3,10,11}

and spatially variable. Other large-scale studies have analysed IAS impact on specific archipelagoes¹² or on a particularly problematic subset of IAS¹³. However, all of these approaches are piecemeal and cannot deliver the evidence that is needed to support an efficient approach to focus IAS research and action at a global scale.

Here we use the comprehensive data compiled by the International Union for the Conservation of Nature (IUCN) database, BirdLife International database and the Global Invasive Species Database (GISD) to extract information about vertebrates that are threatened by IAS, and the identity of the threatening IAS to address the following three questions: (i) How are the impacts of IAS distributed among islands and threatened species? (ii) Are there combinations of IAS for which targeted actions may have high conservation impacts? (iii) Within the targeted areas, what are the characteristics of the network between IAS and IAS-threatened species that can improve strategies to deal with IAS?

Some species occur on multiple islands whereas others are endemic to a single island. Moreover, some IAS are shared as threats by multiple species on the same or different groups of islands, whereas other IAS are very localized and specific. To gain insights into the structure of this complex interconnected system we apply network approaches. Many systems can be represented as networks of interconnected nodes. Networks are mathematical objects in which a node is linked (connected) to zero, one or several other nodes. The links highlight a relationship between two nodes. For instance, each inhabitant of the world can be represented as a node in a network graph and each email sent by those inhabitants to others can be represented as a link. Of course with increasing node and link number, the complexity of network graphs grows exponentially and limits our ability to identify structure. Network theory aims at extracting insightful patterns from networks.

In our study, we built two kinds of networks. In the first, the nodes are either species or islands and the links represent the presence of

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a species on a given island. We clustered this network to identify islands that are highly interconnected by the co-occurrence of many IAS-threatened species and selected the clusters with highest number and densities of IAS-threatened species. The aim of this clustering approach is to identify groups of islands that share a similar pattern of threatened species based on biogeographical knowledge. In the second set of networks, the IAS and their threatened species were linked and related to the island clusters identified in the first analysis (see Methods). This allowed us to determine the IAS that are responsible for most of the threats in those clusters of islands and we used this to provide insights to deal with IAS threat.

Results

Impact distribution of different IAS among islands and threatened species. We analysed more than 73,515 islands where the IUCN Red List has recorded IAS-threatened species. First, we selected islands for which we could expect a high return in investment for a conservation program. Specifically, we selected islands that harbour more than 1% of the total number of IAS-threatened species, and those with a high ratio of number of threatened species to area. We identified a total of 21 clusters (labelled in Supplementary Table 2) that include a total of 437 IAS-threatened species on the 27,081 islands across the world that met our criteria (Fig. 1, for the complete network see Supplementary Fig. 1). These clusters represent the groups of islands that are highly interconnected by the co-occurrence of IAS-threatened species (Fig. 1), that is, insular regions harbouring similar patterns of vertebrates threatened by IAS. Most of the islands that were detected, and which are vulnerable to invasions, are located in the Southern Hemisphere and encompass most of the Caribbean and Pacific archipelagos (including Hawaii), Madagascar and islands that are part of the southern coasts of Africa, Indonesia, the coast of America, New Zealand and Australia (Fig. 1a). The majority of the islands found in the 21 clusters are included in the insular biodiversity hotspots¹⁴.

Some clusters are fully isolated (that is, disconnected from others in terms of IAS-threatened species: for example, the Puerto Rico islands; Okinawa islands and Seychelles), because their IAS-threatened species are found nowhere else. Two of the Caribbean clusters (including Hispaniola and Jamaica islands), and Malaysia, the Philippines, and the south of the East Indies Islands are connected only to each other (Fig. 1b). Overall, the clusters that share a high number of threatened species with other clusters are Polynesia and Micronesia, North America Pacific coast islands, as well as the South American, Antarctic, sub-Antarctic and Australian islands. Our analysis revealed that most of the connections between clusters are due to bird species, but amphibians, mammals and reptiles are also responsible for connections between the southern part of New Zealand, Australia and islands in the Southern Hemisphere, Caribbean clusters, and African islands (Supplementary Fig. 1). Some clusters are particularly noticeable because of their high number of threatened species by IAS: New Caledonia, the Hawaiian islands, and Madagascar and the African southeastern coast for reptiles, birds, and amphibians, respectively. The 21 identified clusters vary in terms of the number of threatened species (see size of the taxa nodes of the outer circle in Fig. 1b), the number of islands (size of the inner circle nodes in Fig. 1b) and total area. Specifically, the number of threatened species ranges from 7 (the cut-off point that we selected that corresponds to at least 1% of the total number of insular threatened vertebrates) to 61 species, whereas the number of islands ranges from 1 (that is, Puerto Rico) to 7,460 (Table 1). Most of the threatened species found in these clusters are birds (51%), followed by reptiles (18%), amphibians (17%) and mammals (14%); this is consistent with the taxonomic groups that have been identified as threatened by IAS worldwide³.

Targeted actions may have high conservation impacts for different IAS combinations. In a second step, we analysed the patterns of

interactions between IAS and the vertebrate species that they threaten, for the whole network and for the 21 identified clusters (Fig. 2a, for the complete network, see Supplementary Fig. 1). We built interaction networks with IAS and IAS-threatened species as nodes. The links between nodes represent the vulnerability of a given species to a known IAS (see Supplementary Fig. 2 for each IAS-threatened species) within a cluster (Fig. 2a). The global interaction network revealed that most IAS are threatening numerous species across different taxonomic groups. The top threatening IAS is the feral cat (*Felis catus*), followed by other IAS, such as rat (*Rattus* spp.), feral dog (*Canis familiaris*) and pig (*Sus scrofa*). Some IAS are more specialized, such as *Eucalyptus* spp., which predominantly threatens vertebrates located in clusters of Madagascar and African south-eastern coast islands, the little fire ant (*Wasmannia auropunctata*), which affects reptiles in the New Caledonia cluster (see also ref.¹⁴) and the Chytrid Bd (*Batrachochytrium dendrobatidis*), which mainly threatens amphibians in the Caribbean clusters.

The network approach can, in theory, help to identify the best strategies for combating IAS that maximize the number of threatened species that will benefit from any eradications. For example, eradication of feral cats and feral dogs alone would directly benefit 10 and 6 species, respectively, but targeted together the removal of these IAS could benefit up to 27 species (because 11 others species are simultaneously threatened by those two IAS). Therefore, both need to be controlled to achieve the highest overall conservation benefit. Note that other threatened species will also benefit from such eradications, because the IAS pressure on them will be reduced even if other IAS are still threatening them. The control or eradication of Chytrid Bd, feral cats and feral dogs together could fully benefit at least 41 threatened island species worldwide (Fig. 2b), assuming that no other threats are substantial for these species.

Characterizing the networks between IAS and IAS-threatened species in the targeted areas to improve IAS strategies. The characteristics of IAS and IAS-threatened species interaction networks within each cluster can also be used to focus actions to deal with the IAS threat. In each cluster, we identified the top IAS that affect the most species (that is, the highest number of links with threatened species), and the connectivity between IAS and threatened species. We also determined which IAS or combinations of IAS should be targeted, in theory, to maximize the number of threatened species that will fully benefit from IAS eradications per cluster. We found that the top IAS that threatens most of the native species is not necessarily the same as the IAS that should in theory be eradicated to maximize the number of species that fully benefit (Table 1). For most of the clusters, we found that a targeted combination of IAS would result in a better outcome for threatened species than controlling only the most important invader. For instance, the native species in the Polynesia and Micronesia cluster are highly threatened by feral cats. However, targeting only feral cats would, in theory, lead to only one species fully benefiting, because the other species threatened by cats are also threatened by others IAS. The combined control of black rat (*R. rattus*), pacific rat (*R. exulans*) and feral cats could, in theory, fully benefit 13 species of IAS (Fig. 3a). Another example is Okinawa islands cluster. This insular region might also offer good opportunities for conservation strategies, because the removal of IAS from the family Herpestidae (for example, *H. javanicus*) could directly benefit at least 6 species and decrease pressure on 6 additional species that are also threatened by other IAS (Fig. 3a). The number of links in the Okinawa cluster is quite low, so we can expect that the control of a low number of IAS would result in a high benefit for native species. In addition, most of the threatened species located in this cluster are found nowhere else (Fig. 1b), so they have a particularly high value for biodiversity. Note that neither the potential feasibility nor the cost effectiveness of such programs has been evaluated here and so our findings should be complemented with local prioritization analyses at the island and IAS level.

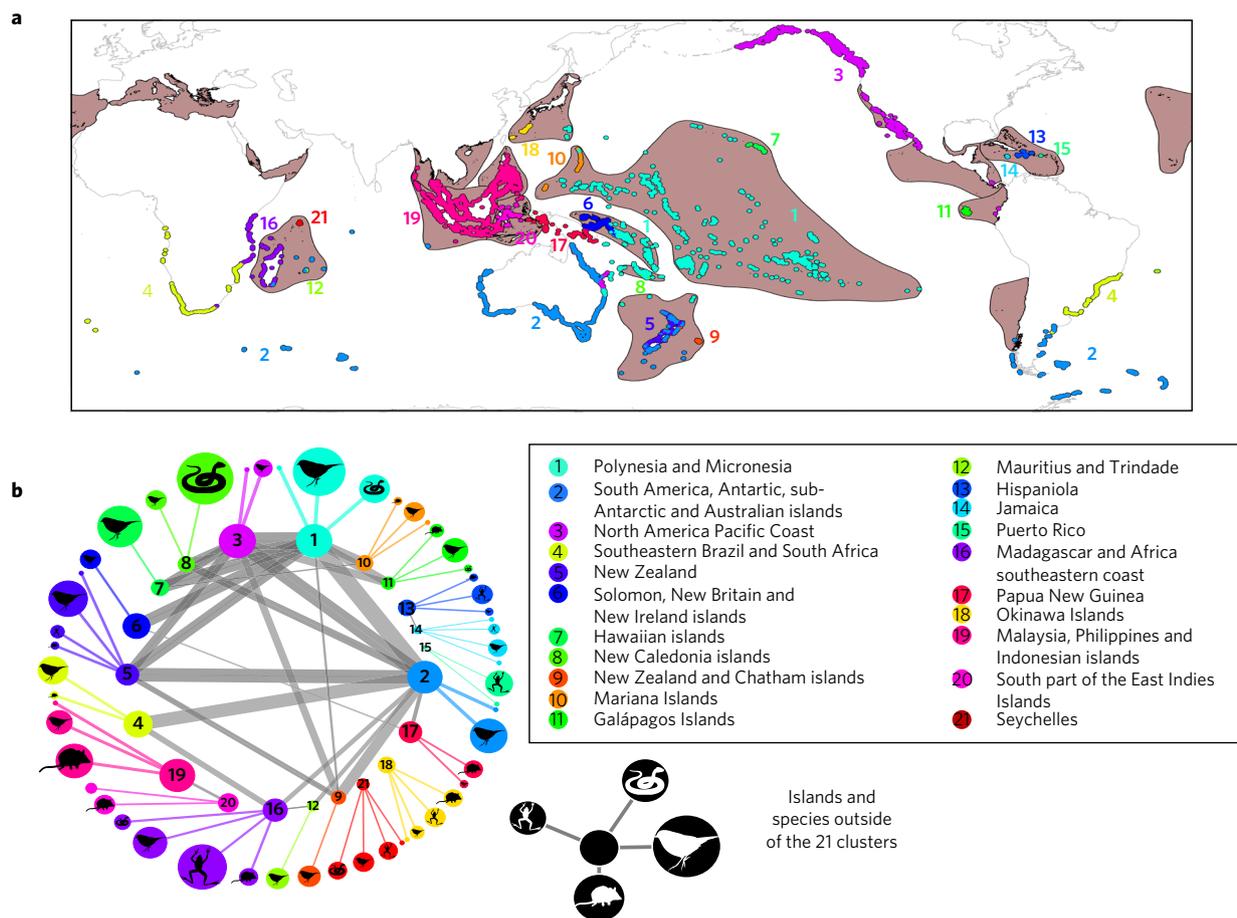


Fig. 1 | Bipartite IAS-threatened species and islands network. a, The map represents the location of the 27,081 islands that were included in the 21 clusters coded using ID number and colour. Brown areas show the location of biodiversity hotspots originally defined in ref.¹⁵ and then updated to 35 hotspots⁴⁸. **b**, Graphical summary of the 21 clusters; each cluster is defined by islands and IAS-threatened species, and distinguished using the same colour as in **a** with the ID numbers shown. The size of the nodes in the inner circle is log-proportional to the number of islands in the cluster, and the size of the nodes in the outer circle is log-proportional to the number of species of each taxon in a cluster. Shapes representing the higher taxa are shown in the circle when possible. The width of the grey links is log-proportional to the number of species that are located in two given clusters. Nodes (islands and IAS-threatened species) represented in black show the species and islands that were not included the analysis (see Methods).

We also identified some clusters where the networks share similar properties that could be helpful in understanding their response to IAS. For example, two clusters (that is, the Papua New Guinea cluster and the South of the East Indies Islands cluster) share both a high-density value (a high ratio of the number of links per node to the number of possible links) and a relatively low number of IAS in their clusters (Fig. 3b). This means that the threatened species within these two clusters are threatened by few IAS, but these few IAS threaten most of the species in this cluster. Therefore, the control or eradication of this small number of IAS may offer a great opportunity for conservation, especially because the number of IAS-threatened species is important (Fig. 3a). Because these two clusters are also highly disconnected from other clusters (Fig. 1b), protecting their species might be particularly important globally. We observed similar characteristics for Solomon, New Britain and New Ireland islands that may also offer substantial opportunities for conservation (Table 1). We also observed that the Hispaniola, Jamaica and Puerto Rico clusters share similar characteristics in terms of the average number of links and density values. Some other interaction networks are particularly distinctive and should be studied individually. For instance, Madagascar and the Africa southeastern coast clusters harbour a larger number of IAS-threatened species and the New Caledonia cluster has more interconnections than any other clusters.

Discussion

We have identified 21 clusters of islands harbouring threatened vertebrates species that are highly important sites of IAS threat and where focusing resources, for both research and conservation action, should be most efficient. The spatial distribution of the 21 identified clusters overlaps with the majority of global biodiversity hotspots (except some coastal islands, see brown polygons represented in Fig. 1a) that are priorities in terms of endemic plants threatened by habitat loss¹⁵. Over US\$1 billion has been spent on the protection of the remaining natural vegetation of these biodiversity hotspots¹⁶. We identified other areas important for conservation, including many small islands and island groups that may offer a high return on investment. Specifically, we were able to identify clusters that harbour a unique part of vertebrate species diversity threatened by IAS. These island clusters include Caribbean, Okinawa and Seychelles islands, and Malaysia, the Philippines, some of the Indonesian islands and South of East Indies Islands, and would qualify as priorities on their own, whereas clusters that are interconnected (that is, where IAS-threatened species are shared) will require also trans-national efforts for conservation to be fully effective.

We also reaffirm here the role of major invaders, such as rats, cats and the Chytrid Bd, that are already known to cause widespread threats to species on islands^{17–19}. Feral cats are well-known to drive

Table 1 | Characteristics of the 21 clusters based on the two types of network: the network of IAS-threatened species and islands, and the interaction network between IAS and their threatened species

ID	Number of IAS-threatened species	Number of islands	Area (km ²)	Top 1 IAS	Percentage of IAS	Mean number of links per IAS-threatened species	Mean number of links per IAS	Density	Combination of IAS to target	Number of full benefitting species
1	54	6,011	52,488	<i>F. catus</i>	42.3	3.3	4.5	0.1	<i>R. rattus</i> + <i>F. catus</i> + <i>R. exulans</i>	13
2	20	4,836	106,070	<i>F. catus</i>	67.2	3.9	1.9	0.1	<i>F. catus</i> + <i>R. norvegicus</i>	3
3	7	7,460	124,150	<i>F. catus</i>	60.0	2.8	1.9	0.31	<i>R. rattus</i>	1
4	15	1,034	3,004	<i>Rattus</i> spp.	46.1	2.0	2.3	0.17	<i>F. catus</i>	2
5	28	263	266,420	<i>M. erminea</i>	62.2	5.3	3.2	0.12	Chytrid Bd	1
6	7	741	48,737	<i>F. catus</i>	36.4	1.9	3.2	0.46	<i>C. familiaris</i> + <i>F. catus</i> + <i>Rattus</i> spp.	6
7	28	70	16,891	<i>P. relictum</i>	63.2	8.1	4.7	0.17	-	-
8	55	56	16,700	Family Rodentia	24.7	3.7	11.4	0.21	-	-
9	8	31	983	<i>F. catus</i>	61.9	4.0	2.5	0.31	-	-
10	10	56	1,523	<i>B. irregularis</i>	64.0	3.8	2.1	0.24	<i>B. irregularis</i>	1
11	16	24	8,081	<i>R. rattus</i>	62.5	4.7	2.8	0.19	<i>M. musculus</i> + <i>R. rattus</i>	4
12	8	13	1,894	<i>L. robustum</i>	74.2	6.25	2.2	0.27	-	-
13	11	63	74,555	Chytrid Bd	41.2	1.6	2.3	0.23	Chytrid Bd	6
14	11	5	11,028	<i>Rattus</i> spp. + others	54.2	1.7	1.5	0.13	-	-
15	12	1	8,761	Chytrid Bd	36.9	1.6	2.7	0.23	Chytrid Bd	7
16	61	387	598,629	<i>Eucalyptus</i> spp.	30.9	2.1	4.7	0.08	-	-
17	8	256	823,053	<i>R. rattus</i> + others	40.0	1.2	1.7	0.29	<i>C. familiaris</i>	2
18	18	64	3,091	<i>F. catus</i>	54.2	1.9	3.6	0.21	Family Herpestidae	6
19	30	5,566	1,656,400	<i>F. catus</i>	40.0	1.6	2.4	0.10	<i>Rattus</i> spp.	4
20	10	126	196,869	<i>C. familiaris</i>	36.4	1.7	3.0	0.43	<i>C. familiaris</i> + <i>F. catus</i>	5
21	20	18	250	<i>F. catus</i>	53.9	2.9	2.5	0.21	<i>T. ecaudatus</i>	2

The cluster identification number (ID), the number of IAS-threatened species, the number of islands, the total area in km², the top invader, the percentage of IAS included in the network, the average number of links per IAS-threatened species and per IAS, the density of the network, the combination of IAS the removal of which could in theory benefit the highest number of vertebrate species, and the number of vertebrate species free of IAS are reported. The last is defined as the number of threatened species for which all known IAS in the cluster are eradicated based on the stated combination of IAS. Note that when the ratio between the number of targeted IAS and the number of vertebrates free of IAS is less than 1, we did not include it in the table, as indicated by a dash. The full species names of the IAS mentioned in the table are *Felis catus*, *Rattus rattus*, *Rattus exulans*, *Rattus norvegicus*, *Mustela ermina*, *Plasmodium relictum*, *Boiga irregularis*, *Mus musculus*, *Ligustrum robustum*, *Canis familiaris* and *Tenrec ecaudatus*.

numerous extinctions of endemic vertebrates (>175)⁶. However, our analysis quantifies their roles whether they are the only invader responsible for the population decline in islands or if they act in combination with other IAS on islands.

Most of the current eradication programs focus on a single species, which may be ineffective when multiple IAS are involved²⁰. On the basis of our results, we suggest that targeting multiple IAS simultaneously would be a more efficient strategy for species conservation²⁰ and should be achievable as eradication programs increase in coverage and complexity²¹.

In our analyses we have identified the co-occurrences of IAS threats on islands and quantified the potential number of species that could, in theory, benefit from the eradication of these IAS. However, we do not account for any predator release effects that could further threaten species^{22,23} or other unanticipated events (for example, changes in vegetation or trophic webs that could occur after IAS eradication). In addition, we assume that all IAS have the same effect on threatened species, which may not be a safe assumption, but there is currently too little information with which to improve this aspect of the analysis. Moreover, we

did not assess the potential for reintroductions or the feasibility of eradication events.

The eradication of Chytrid Bd could, for example, be quite challenging. Indeed, we lack efficient methods to systematically eradicate Chytrid Bd, although two recent advances have greatly improved our understanding of amphibian–chytridiomycosis dynamics²⁴. First, the recognition that Bd is not one species, but distinct lineages that vary in distribution and virulence and, second, that species have been infected for much longer than was initially thought with some species co-evolving without any impact (see ref. ²⁴ for a review). Therefore, preventing measures to avoid further propagation of Chytrid Bd in nearby clusters should be a priority. By contrast, eradication attempts for vertebrates have been quite efficient for cats or rats with failure rates of only 12%^{6,25}, as well as for invasive ants²⁶.

In general, we argue that network approaches should complement local prioritization schemes, including eradication feasibility information to target regions and IAS for which actions should be undertaken^{6,25}. For example, a recent study analysed conservation opportunities for seabird populations in most of the 800 small, uninhabited and islands of high- or middle-income countries²⁷.

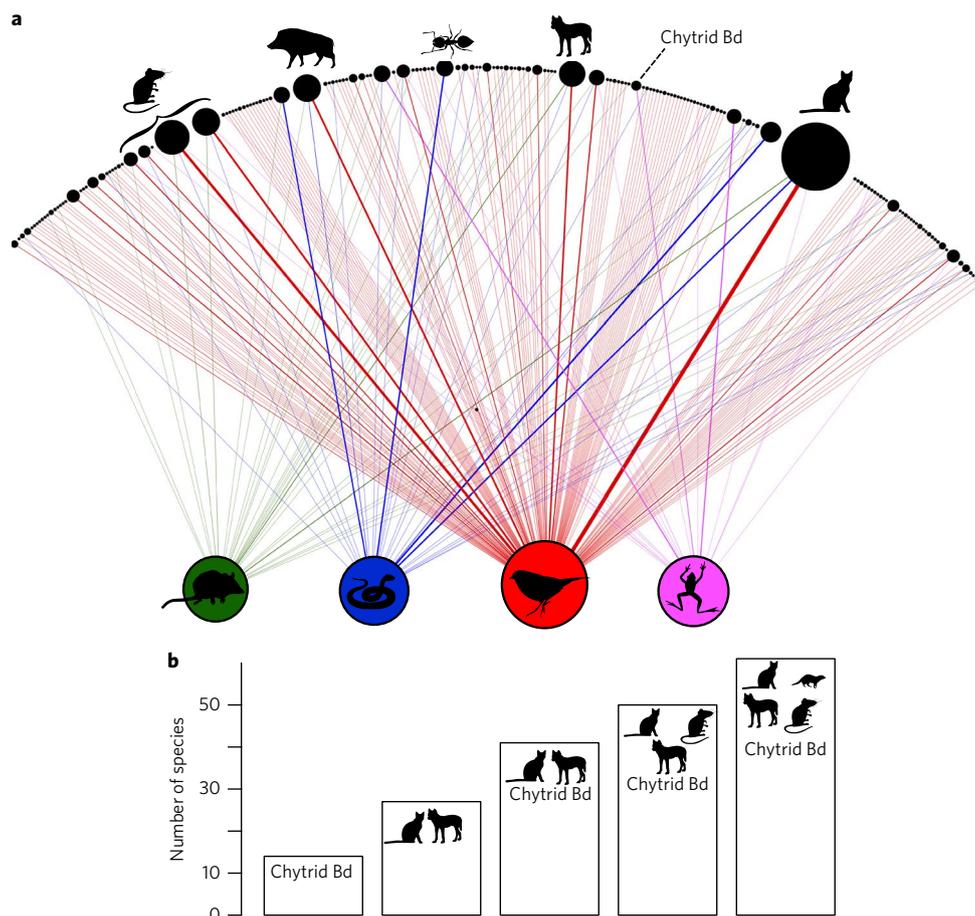


Fig. 2 | Interaction network between IAS and threatened species and number of species that could benefit from removal of IAS. a, Global interaction network between IAS in black ($n = 169$) and individual threatened species ($n = 397$; green, mammals; red, birds; purple, amphibians; blue, reptiles). Node size of the IAS is proportional to the number of species that it is reported to threaten, whereas the node size for higher taxa is log-proportional to the number of species threatened by IAS. Some IAS shapes are represented: rats (including *R. exulans*, *R. norvegicus*, *R. rattus* and unspecified *Rattus* spp.), pig (*Sus scrofa*), ant (*Wasmannia auropunctata*), feral dogs (*Canis familiaris*), Chytrid Bd and feral cat (*Felis catus*). **b**, Bar graph of the theoretical number of vertebrate species that would fully benefit from the removal of the top (Chytrid Bd) to top 5 IAS in the network.

Our analyses also revealed that in some clusters it might be quite challenging to protect native species from extinctions, because of the high number of IAS combinations that threaten native species, as was shown by their high values of connectivity. However, local removal of IAS could prevent local extirpations of native populations and therefore benefit biodiversity. This is particularly the case in the Polynesia and Micronesia cluster.

There are some limitations to our approach that are discussed here. First, we considered the impacts of IAS as a reduction in population size or distribution range determined by the IUCN Red List of threatened species, but other type of impacts on functional or genetic diversity through hybridization or ecosystem services might also be important. Our network-based analyses only accounted for the existence of an impact between IAS and IAS-threatened species, but neither the types of impact (predation, competition, habitat modification) nor the population abundance of IAS-threatened species were investigated. Moreover, we focused on IAS threat, but many IAS threatened species are also affected by habitat loss or overexploitation, and these threats might prevent full recovery of populations even if IAS are controlled or eradicated²⁸. Our work considered only IAS-threatened vertebrate species, for which data are most comprehensively available, but invertebrate species are also known to be particularly affected by IAS. In addition, IUCN and BirdLife provide comprehensive data for some regions and taxa, but are

far from being comprehensive in some regions (for example, Africa). Regarding these limitations, the analyses here should be considered a first step to inform about the combination of IAS that, in theory, might offer high return for species conservation. Despite these limitations, our results have the potential to help to mitigate the impacts of invasive species in insular habitats known for their remarkably rich biodiversity.

Concluding remarks

Our network-oriented analysis of threats posed by IAS on islands allowed us (1) to structure 27,081 islands and 437 threatened vertebrates into 21 clusters that could be used to define priorities for conservation research and actions to address threats from biological invasion; and (2) to identify the major invaders that threaten a large number of vertebrate species. We suggest that an approach based on networks that takes into account islands, IAS and their impacts has been largely missing from biological invasion studies, despite its potential to guide effective responses. The clusters of islands with similar profiles in terms of IAS impacts represents an efficient and innovative way to determine priorities for both areas and species and then to better understand and mitigate the IAS threat. Continuous investment to understand, eradicate, control or prevent new invasions in islands could benefit a high number of endemic species that are predicted to be extirpated

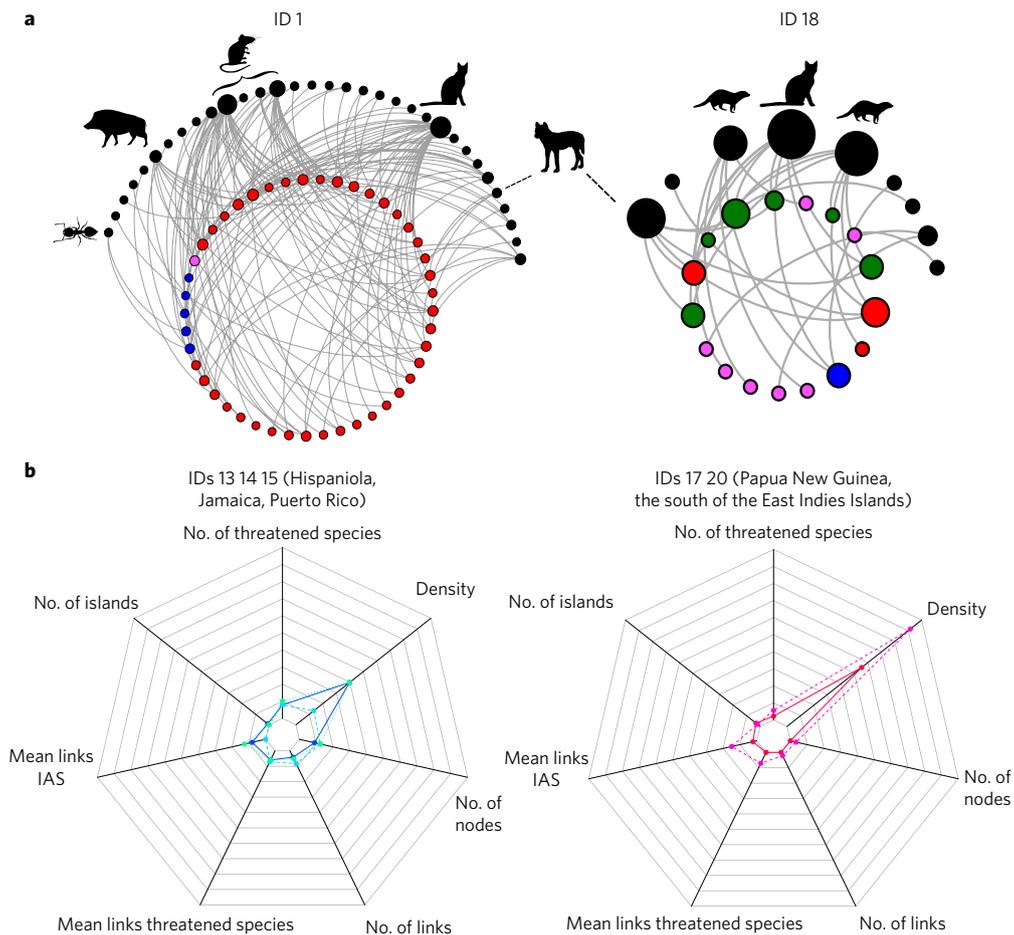


Fig. 3 | Examples of network characteristics. **a**, Representation of two networks between IAS (in black) and IAS-threatened species (in colour: green, mammals; red, birds; purple, amphibians; blue, reptiles) for ID 1 and 18. Some IAS shapes are represented: ant, pig, rats and feral cat for ID 1, the Herpestidae family and cat for ID 18. Note that *Herpestes* spp. appear twice, because one node represents the whole Herpestidae family and the other represents the species identified as *H. javanicus*. **b**, Radarplot showing the network characteristics of the Caribbean clusters (IDs 13, 14, 15), and the Indonesian region clusters (IDs 17, 20). All of the variables (number of threatened species, total number of nodes, total number of links, density, average number of links per threatened species, average number of links per IAS and number of islands) have been normalized for comparison.

(for example, see ref.⁹), and the high phylogenetic and functional richness located on those islands offers a unique opportunity to mitigate the loss of biodiversity and contribute to achieve international conservation commitments such as the Aichi Targets 9.

Methods

Data. Information about vertebrate species threatened by invasive species was extracted from the International Union for the Conservation of Nature (IUCN Red List²⁹), and the BirdLife International database³⁰. We used the Global Invasive Species Database (GISD³¹) for information on the identity of IAS that are responsible for the threat and the Global Islands Database from the IUCN²⁹ website to obtain spatial data on islands worldwide.

Vertebrates threatened by IAS. The species assessments of the IUCN Red List classify the risk of species extinction into one of the following categories: extinct (EX), extinct in the wild (EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC) and data deficient (DD). These categories are based on quantitative criteria that indicate the extinction risk, including the rate of population decline (criterion A), the size and decline of the geographical range (criterion B), the population size, its fragmentation and decline rate (criteria C and D) or quantitative analyses (criterion E)³². Prior to 2001, Red List assessments were based on expert opinion, but now all assessments use the standard quantitative Red List Categories and Criteria, so that they are objective, transparent and repeatable. As part of the species assessment process, factors associated with decline are collated for each species³³. Specifically, the IUCN and BirdLife International have classified these factors into 11 main threat categories (that is, the IUCN threat classification scheme v.3.0). These threats are: (1) residential and

commercial development; (2) agriculture and aquaculture; (3) energy production and mining; (4) transportation and service corridors; (5) biological resource use; (6) human intrusion and disturbance; (7) natural system modifications; (8) invasive and other problematic species, genes and diseases; (9) pollution; (10) geological events; and (11) climate change and severe weather³³. We extracted information for terrestrial vertebrates (that is, mammals, reptiles, amphibians and birds) that are classified under category 8 and identified those threatened by IAS, and these are included our analysis.

We selected vertebrates that were classified into one of the threatened categories (that is, CR, EN and VU; $n = 1,324$) and extracted their spatial distributions (spatial polygons) from IUCN spatial data for mammals, amphibians and reptiles, and from the BirdLife database³⁰ for birds (resulting in a total $n = 1,291$). Spatial data were missing for 4 mammals and 29 reptiles. Note that in our analyses any IAS-threat associated with a species is a binary response—either an invasive alien species does impact a species or it does not; we do not consider different intensities of invasive species impact (but see Supplementary Figs. 3, 4). In this way, we were able to identify those vertebrates that are threatened by any IAS among islands.

Information about invasive alien species. We used the GISD, which interlinks the IUCN Red List with IAS information³¹. The information in the GISD has been compiled from many sources, including scientific papers and regional databases that have been reviewed by international expert contributors. Specifically, for vertebrate species identified as threatened by IAS, we collected information about the identity of IAS responsible.

Island data. We used the Global Islands Database from the IUCN website (<http://www.iucnredlist.org/technical-documents/red-list-training/iucnspatialresources>), a spatial dataset of more than 180,488 islands²⁹.

We overlaid the spatial polygon of islands and the polygon of vertebrate species distributions to derive a set of 73,515 islands where vertebrate species are threatened by IAS (see Supplementary Methods for more details). When an overlap between an island and the polygon of species distribution was indistinct, we visually checked the species distribution. In order to restrict the analysis to insular vertebrates (persisting only on islands), we excluded species that were both on continental coastal areas and islands. The resulting dataset includes 97 amphibians threatened by IAS on 903 islands, 120 reptiles on 2,340 islands, 336 birds on 72,433 islands and 110 mammals on 9,709 islands.

Bipartite networks. We first built an island and IAS-threatened species network that we clustered into groups of islands on the basis of shared IAS-threatened species. Then, for each of the clusters, we conducted analyses of IAS and IAS-threatened species interaction networks.

Analyses of the island–IAS-threatened species network. Recently, geographical relationships between species and localities have been abstracted as a bipartite association network, where links are the occurrences of species within geographical locations³⁴. Similarly, the occurrence of species on islands worldwide can be represented as a network for which nodes are either species or islands. When a species is present on a given island, a connection between this species and the island is established in the network. Because species never connect to species, and islands never connect to islands (that is, links only connect species to island in the network), such a network is called a bipartite network. This network provides information on co-occurrences of species on islands, the number of times species co-occur and the number of species shared by particular groups of islands. Here, we built a network with all vertebrate species threatened by IAS on islands. We chose a biogeographical approach to represent connections between islands, IAS-threatened species and invasive species without any a priori knowledge of political jurisdiction or geographical proximity. Indeed, native and invasive species do not respect political boundaries, but are mostly bound by environmental boundaries. Therefore, it makes more biological sense to use biogeography of species (spatial distribution of species) to delimit the impact of IAS across islands, because it will better reflect the processes of dispersion among islands than other types of boundaries.

Because such an interconnected network has a high degree of complexity (663 species, 73,515 islands), numerous techniques have been developed to synthesize information by clustering nodes (for example, the map equation minimization approach³⁵ and the modularity maximization approach³⁶). Among these techniques, the map equation algorithm³⁷ has been proven to be particularly well-suited for cluster networks in comparative studies^{37–39}. This technique allowed us to extract a meaningful ecological structure composed of islands and species that are similar. Specifically, this technique allowed us to cluster our bipartite network based on biogeographical knowledge (species distribution) and to detect common patterns of threatened species among islands.

The map equation algorithm is iterative: first it chooses a random node, and then randomly selects a second node that is connected to the first one. This process is repeated a random number of times. Then another node is chosen randomly and the same process repeated. If some nodes are strongly interconnected, this process tends to frequently select the same nodes, which are then attached to a cluster. In groups of islands with marked structure (high connectivity), the algorithm will focus mostly within clusters, crossing only when a cross-cluster species is selected. Once the algorithm goes through all the nodes of the system, it will provide the list of clusters where it spent more time³⁵. This technique allowed us to extract meaningful ecological structure composed of islands and species that are connected.

We expected a hierarchical structure in the dataset—because of the nested nature of species distribution—because species may be located on specific islands, which are encompassed in archipelagos, and in larger regions. Consequently, we applied the multiple-level implementation of the map equation, which produces hierarchically nested groups of clusters. Thus, the algorithm hierarchically partitions the groups of nodes into clusters^{39,40}.

In this study, a three-step approach was used to identify clusters of islands and species that are of high interest for conservation.

- (1) We applied the map equation algorithm to define hierarchical clusters of island based on IAS-threatened species co-occurrences. Each cluster corresponds to a subset of the original network in which species and islands are strongly interconnected to each other, but weakly linked to species and islands outside of the subset⁴¹.
- (2) We selected clusters with high conservation interest defined as those that harbour at least 1% of all IAS-threatened species (>6 IAS-threatened species, see Supplementary Fig. 6 for sensitivity analyses of this parameter).
- (3) We then selected, for each branch in the hierarchy, clusters that maximize the ratio of the number of IAS threatened species to the total area. In this way, we identify islands with a high density of threatened species. Specifically, we chose to maximize the ratio between number of threatened species and total area for a given unit area (km² here), so the eradication events could benefit a high number of species. Indeed, eradications outcome are more likely to succeed in a small area⁴² than in large ones. We made assumptions here that all species

have the same value and interest for conservation, without any distinctions of their originality or role in the community or ecosystem. Therefore, we used this criterion to consider eradication opportunities that attempt to protect as many species as possible.

The application of those criteria results in the exclusion of 226 species (24 amphibians, 111 birds, 50 mammals and 41 reptiles) (black nodes in Fig. 1b) as they did not meet the criteria detailed above. Note that 14 of the excluded IAS-threatened species could offer particular opportunities for research and eradication programs as 4 birds, 5 reptiles and 5 amphibians are both located on single islands and are threatened by only one identified IAS (see list in the Supplementary Table 1).

From these three steps we obtained 21 clusters that correspond to groups of strongly interconnected species and islands with a high density of IAS-threatened species (see Supplementary Fig. 5 for illustration of the three-step approach). For each cluster, we document the number of IAS-threatened species, number of islands, total area (km²) and identities of IAS-threatened species (Table 1).

IAS–IAS-threatened species interaction network. Thereafter, for each of the 21 clusters, we constructed an interaction network between IAS-threatened species and their associated IAS. This relationship is based on the IUCN GISD information that identified which IAS threatens which species. The majority of IAS-threatened species are threatened by several IAS. Using a network to describe the relationships between IAS-threatened species and IAS provides a means to list all species threatened by a given IAS and how they are linked with other IAS.

For each of the 21 interaction networks we identified (1) the top IAS per cluster (that is, the IAS with the highest number of links to threatened species), (2) the number of nodes (total number of IAS and threatened vertebrates included in the cluster), (3) the number of links (total number of interactions between IAS and threatened vertebrates), (4) the connectivity of IAS and their threatened species nodes (that is, the average number of links (interactions) per IAS and their threatened species) and (5) graph density: a ratio of the number of links per node to the number of possible links. Knowing a network's property regarding connectivity is important here for two reasons. First, it will help to identify whether control of certain IAS in the network will have positive effects on a number of threatened species. Conversely, knowing the number of connections of IAS-threatened species will help to determine which IAS should primarily be controlled or eradicated. Indeed, the connectivity of IAS and their threatened species nodes will help to identify how IAS and threatened species are connected. It can be used to identify which IAS threaten a large number of species and if those threatened species share the same IAS or not. This can indicate how eradication of any IAS will benefit different threatened species. We also measured whether the network is close to saturation (density value close to 1, indicating that all the possible interactions have been achieved). In a saturated network, where the threatened species are threatened by many IAS, it will be very difficult to release sufficient pressure from threatened species, as most IAS would have to be removed to release sufficient pressure from threatened species. Yet, in a saturated network, where the threatened species are threatened by a low number of IAS, it will be highly beneficial to conduct eradication campaigns, especially if the number of threatened species is high.

Maximizing the number of IAS-threatened species that may benefit from IAS eradication. Finally, we calculated, for the whole network ($n=21$ clusters), the combination of IAS for which control or eradication programs could theoretically benefit the largest number of threatened species. Specifically, for each potential combination of invasive species (from 1 to 5 IAS), we calculated the number of species that would be IAS-free after eradication of that combination of IAS. We found the best strategy by testing every possible eradication scenario (see Fig. 2b). Any IAS-threatened species could benefit from the eradication of one or several of its associated IAS, but the highest conservation benefit would require all of its known IAS (according to the IUCN–GISD data) to be eradicated. For this analysis, we assume that a threatened species only benefits from the eradication, if all invasive species that affect it are eradicated. Obviously, this assumption does not necessarily reflect real ecological situations, because other native species might also benefit from such eradications. But, it is not possible to predict the effect of eradication for species that would partially benefit from eradication (such data do not exist at the global scale). In addition, it is worth noting that many other factors, such as Allee effects or the existence of other threats may limit recovery, even if all invasive species are eradicated. Consequently, for the purposes of the analyses, we define conservation success as the eradication of all of known IAS threatening a given species. Note that eradicating any IAS may also benefit others species by releasing pressure on them, even if other IAS are still threatening them. For example if a species_A is threatened only by IAS_B, the eradication of this IAS_B from the cluster will theoretically allow species_A to recover. But, if species_A is threatened by IAS_B, IAS_C, IAS_D, the removal of IAS_B would not be sufficient to permit the full recovery of species_A, it will only release some pressure. We report the top 5 IAS whose eradication would most benefit IAS-threatened species across the whole network.

We conducted the same analysis for each cluster. We kept the identity of the IAS or the combination of IAS that maximized the ratio of the number of invasive-free species to the number of necessary eradicated IAS per cluster. All analyses were carried out with R version 3.2.4 using ggplot2⁴³ maptools⁴⁴, igraph⁴⁵,

infomap version 0.18.2³⁹ and dplyr⁴⁶ packages, and gephi⁴⁷ software using a Debian–Linux operating system.

Life Sciences Reporting Summary. Further information on experimental design and reagents is available in the Life Sciences Reporting Summary.

Code availability. The code to create the network is available upon request from the corresponding author.

Data availability. The dataset of the co-occurrence of species on islands is available in the Zenodo data repository (<https://doi.org/10.5281/zenodo.884886>).

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References

- Kier, G. et al. Global patterns of plant diversity and floristic knowledge. *J. Biogeogr.* **32**, 1107–1116 (2005).
- Bellard, C., Cassey, P. & Blackburn, T. M. Alien species as a driver of recent extinctions. *Biol. Lett.* **12**, 20150623 (2016).
- Bellard, C., Genovesi, P. & Jeschke, J. M. Global patterns in threats to vertebrates by biological invasions. *Proc. R. Soc. B* **283**, 20152454 (2016).
- Jones, H. P. et al. Invasive mammal eradication on islands results in substantial conservation gains. *Proc. Natl Acad. Sci. USA* **113**, 4033–4038 (2016).
- Nogales, M. et al. Feral cats and biodiversity conservation: the urgent prioritization of island management. *Bioscience* **63**, 804–810 (2013).
- Helmstedt, K. J. et al. Prioritizing eradication actions on islands: it's not all or nothing. *J. Appl. Ecol.* **53**, 733–741 (2016).
- Dawson, J. et al. Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom overseas territories. *Conserv. Biol.* **29**, 143–153 (2015).
- Early, R. et al. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat. Commun.* **7**, 12485 (2016).
- McCrealess, E. E. et al. Past and estimated future impact of invasive alien mammals on insular threatened vertebrate populations. *Nat. Commun.* **7**, 12488 (2016).
- Gallardo, B., Clavero, M., Sánchez, M. I. & Vilà, M. Global ecological impacts of invasive species in aquatic ecosystems. *Glob. Change Biol.* **22**, 151–163 (2016).
- Kumschick, S. et al. Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *Bioscience* **65**, 55–63 (2015).
- Carrión, V., Donlan, C. J., Campbell, K. J., Lavoie, C. & Cruz, F. Archipelago-wide island restoration in the Galápagos Islands: reducing costs of invasive mammal eradication programs and reinvasion risk. *PLoS ONE* **6**, e18835 (2011).
- Courchamp, F., Chapuis, J.-L. & Pascal, M. Mammal invaders on islands: impact, control and control impact. *Biol. Rev. Camb. Philos. Soc.* **78**, 347–383 (2003).
- Berman, M. et al. Overview of the distribution, habitat association and impact of exotic ants on native ant communities in New Caledonia. *PLoS ONE* **8**, e67245 (2013).
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
- Sloan, S., Jenkins, C. N., Joppa, L. N., Gaveau, D. L. A. & Laurance, W. F. Remaining natural vegetation in the global biodiversity hotspots. *Biol. Conserv.* **177**, 12–24 (2014).
- Bonnaud, E. et al. The diet of feral cats on islands: a review and a call for more studies. *Biol. Invasions* **13**, 581–603 (2011).
- Medina, L. I. X. M., Bonnaud, E., Vidal, E. & Tershy, B. R. A global review of the impacts of invasive cats on island endangered vertebrates. *Glob. Change Biol.* **17**, 3503–3510 (2011).
- Jones, H. P. et al. Severity of the effects of invasive rats on seabirds: a global review. *Conserv. Biol.* **22**, 16–26 (2008).
- Glen, A. S. et al. Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? *Biol. Invasions* **15**, 2589–2603 (2013).
- Keitt, B. et al. Best practice guidelines for rat eradication on tropical islands. *Biol. Conserv.* **185**, 17–26 (2015).
- Bergstrom, D. M. et al. Indirect effects of invasive species removal devastate World Heritage Island. *J. Appl. Ecol.* **46**, 73–81 (2009).
- Rayner, M. J., Hauber, M. E., Imber, M. J., Stamp, R. K. & Clout, M. N. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proc. Natl Acad. Sci. USA* **104**, 20862–20865 (2007).
- Lips, K. R. Overview of chytrid emergence and impacts on amphibians. *Phil. Trans. R. Soc. Lond. B* **371**, 20150465 (2016).
- B. Keitt et al. in *Island Invasives: Eradication and Management* (eds Veitch, C. R., Clout, M. N. & Towns, D. R.) 74–77 (IUCN, Gland, 2011).
- Hoffmann, B. D., Luque, G. M., Bellard, C., Holmes, N. D. & Donlan, J. Improving invasive ant eradication as a conservation tool: a review. *Biol. Conserv.* **198**, 37–49 (2016).
- Spatz, D. R. et al. The biogeography of globally threatened seabirds and island conservation opportunities. *Conserv. Biol.* **28**, 1282–1290 (2014).
- Doherty, T. S., Dickman, C. R., Nimmo, D. G. & Ritchie, E. G. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biol. Conserv.* **190**, 60–68 (2015).
- The IUCN Red List of Threatened Species*. (IUCN, Gland, 2015); <http://www.iucnredlist.org/>
- Bird Species Distribution Maps of the World*. Version 4.0. (BirdLife International, Cambridge and NatureServe, Arlington, 2014); <http://www.birdlife.org/datazone/info/spcdownload>
- Global Invasive Species Database* (IUCN/SSC Invasive Species Specialist Group, 2016); <http://www.issg.org/database>
- Mace, G. M. et al. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* **22**, 1424–1442 (2008).
- Salafsky, N. et al. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conserv. Biol.* **22**, 897–911 (2008).
- Vilhena, D. & Antonelli, A. A network approach for identifying and delimiting biomes. *Nat. Commun.* **6**, 6848 (2014).
- Rosvall, M. & Bergstrom, C. T. Multilevel compression of random walks on networks reveals hierarchical organization in large integrated systems. *PLoS ONE* **6**, e18209 (2011).
- Graham, J. I. M. et al. Vision of a cyberinfrastructure for nonnative, invasive species management. *Bioscience* **58**, 263–268 (2008).
- Lancichinetti, A. & Fortunato, S. Community detection algorithms: a comparative analysis. *Phys. Rev. E* **80**, 056117 (2009).
- Aldecoa, R. et al. Exploring the limits of community detection strategies in complex networks. *Sci. Rep.* **3**, 2216 (2013).
- Rosvall, M., Axelsson, D. & Bergstrom, C. T. The map equation. *Eur. Phys. J. Spec. Top.* **178**, 13–23 (2009).
- Rosvall, M. & Bergstrom, C. T. Maps of random walks on complex networks reveal community structure. *Proc. Natl Acad. Sci. USA* **105**, 1118–1123 (2008).
- Tylianakis, J. M., Laliberté, E., Nielsen, A. & Bascompte, J. Conservation of species interaction networks. *Biol. Conserv.* **143**, 2270–2279 (2010).
- Pluess, T. et al. When are eradication campaigns successful? A test of common assumptions. *Biol. Invasions* **14**, 1365–1378 (2012).
- Wickham, H. *ggplot2: Elegant Graphics for Data Analysis* (Springer, New York, 2009); <http://ggplot2.org>.
- Bivand, R. & Lewin-Koh, N. *mapproj: Tools for Reading and Handling Spatial Objects*. R package version 0.9-2 (2016); <https://cran.r-project.org/package=mapproj>
- Csárdi, G. & Nepusz, T. *The igraph Software Package for Complex Network Research* (InterJournal, 2006); <http://igraph.org/>
- Wickham, H. & Francois, R., Henry, L. & Müller, K. *dplyr: A Grammar of Data Manipulation*. R package version 0.5.0 (2015); <https://cran.r-project.org/package=dplyr>
- Bastian, M. & Heymann, S. *gephi: An Open Source Software for Exploring and Manipulating Networks* (2009); <http://www.aiai.org/ocs/index.php/ICWSM/09/paper/view/154>
- Mittermeier, R. A. A. et al. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions* (CEMEX, Mexico City, 2004).

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Author contributions

C.B. and J.-F.R. conceived and designed the study with contributions by G.M.M. J.-F.R. and C.B. carried out the analyses, B.L. provided the initial version of the computing code. C.B. and J.-F.R. wrote the first draft of the manuscript and all authors substantially contributed to interpreting and writing the manuscript.

Competing interests

The authors declare no competing financial interests.

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1. Sample size

Describe how sample size was determined.

Sample size is determined by the number of species recorded on islands as threatened by invasive species by the IUCN Red List

2. Data exclusions

Describe any data exclusions.

No exclusion

3. Replication

Describe whether the experimental findings were reliably reproduced.

-

4. Randomization

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-

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