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Fish and macro-crustacean assemblages are relevant ecological indicators for monitoring rivers of tropical islands

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ABSTRACT

Understanding how tropical rivers change in response to human-induced disturbances represents a major challenge for management and conservation. However, monitoring networks based on ecological indicators remain scarce in oceanic islands, where freshwater indigenous fish and macro-crustacean assemblages are dominated by diadromous species. We investigated the relevance of these taxa for assessing the ecological status of rivers in two tropical islands, Reunion and Mayotte, Indian Ocean, to fulfill objectives of the European Water Framework Directive in overseas regions. Beyond providing insights on ecological responses of fish and macro-crustacean assemblages, we proposed a methodological framework to designed stressors-specific multimetric index by selecting primarily shared metrics between and within islands to improve the robustness and interpretation of this index. Numerous candidate metrics were tested to reflect the alterations induced by three stressors categories (i.e., continuity alteration, agricultural and urbanisation stresses) on the diversity, abundance, or size-structure of assemblages. Our results demonstrated that fish and macro-crustacean assemblages were sensitive to multiple stressors, but the ecological responses were more congruent when facing continuity alterations, compared to land use changes associated with agriculture or urbanization. These migratory species are understandably vulnerable to river fragmentation, but their oceanic dispersive stage favor exchanges between watersheds, which in turn can promote the resilience and persistence of local populations in degraded areas. In such insular context, we thus suggested using fish and macro-crustaceans to firstly assess the state of ecological continuity, whereas other taxa, such as diatom or macroinvertebrates, can be complementary to reflect the alteration of water quality.

1. Introduction

Tropical rivers are among the most vulnerable ecosystems to human activities (Dudgeon et al., 2006), facing numerous threats, such as water pollution, habitat degradation, and/or alien species invasion, which lead species loss and major changes in native communities (Malmqvist and Rundle, 2002; Sayer et al., 2025). Unfortunately, large knowledge gaps remain about the functioning of these ecosystems and understanding how tropical streams change in response to human-induced disturbances thus represents a major challenge for management and conservation (Boyero et al., 2009; Taniwaki et al., 2017). For several decades, monitoring networks have appeared as relevant tools to assess the ecological status of rivers and investigate the ecosystem responses to stressors, and, more importantly, to alert on the degradation of aquatic environments (Karr, 1981; Ruaro et al., 2020; Vadas et al., 2022). This viewpoint pushed the environmental authorities worldwide to manage ambitious conservation and restoration programs, such as the European Water Framework Directive (WFD; 2000/60/EC). Although numerous

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ecological indicators using on distinct biological components (e.g., diatom, invertebrate, fish, or macrophyte) have been proposed to quantify the ecological status of water bodies (e.g. Birk et al., 2012), such biomonitoring approaches still remain scarce in the context of tropical environments, and particularly in small coastal and island rivers (Ruaro et al., 2020).

Several studies highlighted the sensitivity of aquatic communities to human stressors in tropical islands, where the growing human population caused substantial land-use modifications, favoring the expansion of urban and agricultural areas while forest and wild areas declines (e.g. Jenkins et al., 2010; Lisi et al., 2018; Moody et al., 2017; Walter et al., 2012). These land-use changes are obviously related to an overall degradation of rivers in response to multiples impacts, such as the deposition of fine sediments, contaminant inputs, or increase in water temperatures (Buttermore et al., 2018; Engman and Ramírez, 2012; Ramírez et al., 2012; Vadas et al., 2022). In addition, the construction of multiple dams for communication routes and water abstraction for irrigation or human consumption causes major disruptions in the ecological functioning of insular rivers (Franklin and Gee, 2019; Holmquist et al., 1998; March et al., 2003; Storch et al., 2022). Indeed, the large majority of fish, shrimp, and decapod native to these ecosystems are diadromous, consequently, their biological cycle success depends on the integrity of ecological continuity (Joy and Death, 2001; McDowall, 2007). Therefore, the degradation of both habitat conditions and river accessibility constitutes major threats for aquatic biodiversity, as highlighted by the decline in specific diversity and changes in the composition of aquatic assemblages when river reaches are impacted by human stressors (March et al., 2003; Walter et al., 2012; Vadas et al., 2022).

Although migratory life-history makes species vulnerable to river fragmentation, the oceanic dispersive stage of native taxa can also promote stability and resilience in river populations, thanks to the repeated arrival of young individuals (Ramírez et al., 2012). Macrocrustaceans and fish of these ecosystems are amphidromous or catadromous, so that all individuals disperse in oceanic environment during larval stage, which favor exchanges across rivers and watersheds (McDowall, 2010, 2007). For these species, the genetic distinctiveness among rivers is generally low within islands (e.g., Lord et al., 2012), suggesting important exchanges and the absence of homing behavior. The post-larvae or juveniles return and settle in freshwater throughout the whole longitudinal gradient of rivers (Teichert et al., 2018), depending on the locomotor capacities of species (Cooney and Kwak, 2013; Holmquist et al., 1998; Lagarde et al., 2021b). Several species, including gobies or shrimps, have morphological features adapted to naturally flashy rivers and are able to ascend natural or man-made obstacles, such as waterfalls or dams (Cooney and Kwak, 2013; Lagarde et al., 2021a; Schoenfuss and Blob, 2003). Oceanic dispersion and colonization abilities can thus contribute to resilience to local human disturbances, as suggested by the persistence of some species in degraded environments (Engman and Ramírez, 2012; Ramírez et al., 2012, Ramírez et al., 2009). However, this buffering process can also complicate or prevent the use of fish- or macrocrustacean-based indicators to assess the ecological status of rivers, if assemblages are more constrained by regional dynamics than by local impacts.

Many indexes have been developed based on the assumption that fish or macro-crustaceans are sensitive to anthropogenic pressures (e.g. Birk et al., 2012; Pérez-Domínguez et al., 2012), but no assemblage was exclusively composed of migratory taxa, with the exception of the index developed for Hawaiian streams (Kido, 2013). Ecological indicators have become commonly used tools to assess ecosystem health, and they are generally composed of several complementary metrics to improve the stability and robustness of environmental assessments (Karr, 1981; Ruaro et al., 2020; Vadas et al., 2022). Multimetric indexes (MMIs) typically aim to assess the level of biotic integrity by quantifying the differences between the taxonomic or functional composition of assemblages and the composition expected under minimally or least-disturbed reference condition (Hering et al., 2006a; Karr, 1981; Vadas et al., 2022). MMIs generally produce scores between 0 and 1, which can be transposed into quality classes (bad, poor, moderate, good, or high) and are easily interpretable by environmental authorities. Nevertheless, the choice of metrics included in MMIs and the definition of reference values remain decisive steps to ensure that indices respond satisfactorily to one or more pressure gradients (Zucchetta et al., 2020). Hence, several algorithmic methods have been proposed to optimize the choice of metrics based on criteria maximization, such as discrimination efficiency or correlation with stressors (e.g. Mondy et al., 2012; Schoolmaster et al., 2013, Schoolmaster et al., 2012). By choosing the stressor (s), it is thus possible to develop indexes reflecting either a general alteration of ecosystem (generalist indexes) or the impact of a single pressure type (stressor-specific indexes) to reflect a specific dysfunction in the ecosystem (Hering et al., 2006a, Vadas et al., 2022). Considering the uncertainties in the responses of fish and macro-crustacean assemblages of oceanic islands, the stressor-specific approach appears preferable to ease the interpretation of MMIs and to evaluate their sensitivities to different stressor categories.

Here, we investigated the relevance of developing ecological indicators based on fish and macro-crustacean assemblages for assessing the ecological status of running waters in tropical islands, to fulfill the objectives of WFD monitoring in overseas regions. More specifically, we designed several MMIs by selecting metrics responding specifically to three stressors categories, i.e., continuity alteration, urbanisation stress, and agricultural stress, which are largely represented in two oceanic islands, Mayotte and Reunion, Indian Ocean (French overseas). Despite difference in species composition between islands, we hypothesized that the similarity in ecosystem functioning and pressure impacts enable us to develop mixed indicators, including both shared and specific metrics to each island and stream typology, to promote robustness and interpretation of MMIs. Beyond improving knowledge of human impacts on tropical island ecosystems, the methodological framework proposed here can be transposed for the development of indicators in other types of water body or biogeographical regions.

2. Material and methods

2.1. Study sites and biological surveys

Mayotte and Reunion are two tropical islands located in the south-western Indian Ocean (Fig. 1a). The two volcanic islands are subjected to a humid tropical climate, influenced by the ocean, and their hydrographic networks include 13 and 27 permanent rivers respectively for Reunion and Mayotte (Lagarde et al., 2021b). Indigenous fishes and macro-crustaceans of freshwater assemblages are essentially composed of diadromous species, and shared approximately 20 species between the two islands (Keith et al., 2006).

Sampling sites were distributed across all the permanent rivers of each island. From one to 14 sites were sampled per watershed depending on their areas, and sites were distributed across affluents and along the altitudinal gradient, when possible, to ensure the representativeness of heterogeneity in environmental conditions. In Reunion, 697 surveys were conducted between 2000 and 2023, in 74 sites distributed across the whole altitudinal gradient of the hydrographic network (Fig. 1a). In Mayotte, 220 surveys were performed across 73 sites between 2008 and 2023. For each survey, the composition of fish and macro-crustacean assemblages was described based on electrofishing samplings with analogous protocols in both islands (Lagarde et al., 2021b). To ensure sampling effectiveness and representativeness, two sampling procedures were applied depending on the river width. In small rivers, the whole site length (i.e., at least 10X the mean river width) was sampled with a portable electro-shocker (Deka, 3,000 or Hans Grassl, IG 200), while the sampling was stratified by hydromorphic units when the river width was over 5 m, as detailed in Lagarde et al. (2021b). This normalized protocol allowed to produce abundance estimates for each taxon based on

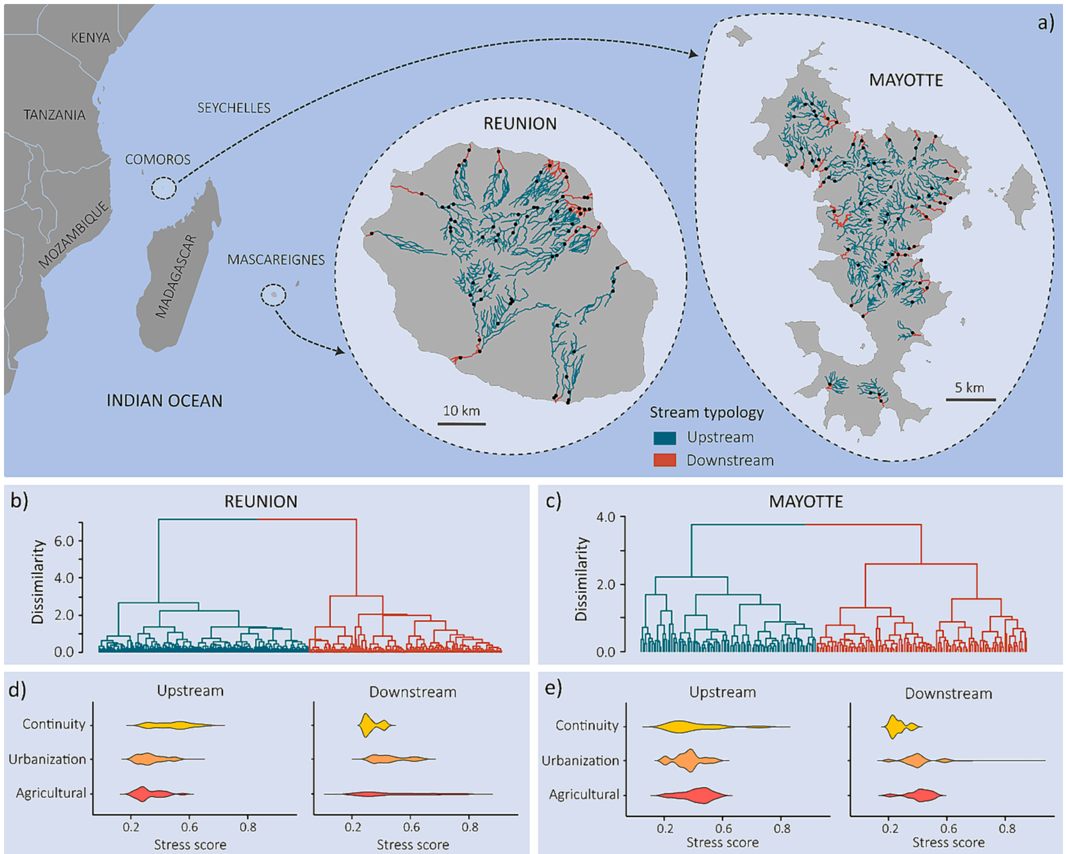

Fig. 1. Overall context of the biological surveys conducted between 2000 and 2023 in permanents rivers of Réunion and Mayotte islands, located in the southwestern Indian Ocean. a) The geographical localisations the sampling sites (black circle) within the hydrographic networks of Mayotte (n = 73) and Reunion (n = 74) are presented. The stream typology (upstream and downstream) of permanents rivers was inferred from the responses of aquatic assemblages to local hydro-morphologic features. In this purpose, the upstream and downstream assemblages of fish and macro-crustaceans were defined using hierarchical clustering based on Bray-Curtis dissimilarity index for Réunion (b) and Mayotte (c) islands. Finally, the pressure score experienced by aquatic assemblages was assessed for three stressor categories (i.e., continuity alteration, urbanisation stress and agricultural stress), by performing a TOPSIS multicriteria decision analysis in Réunion (d) and Mayotte (e) islands.

capture per effort units (CPUE, $\#/m^2$) whatever the sampling procedures.

During the surveys, 34 taxa were identified at the species level, 15 at the genus level and four at the family level (Supplementary Material, Appendix 1, Table S1 and S2). Genus or family identification mainly consisted of small individuals (post-larvae or juveniles) for which determination is complex on the basis of morphological criteria (e.g., *Agonostomus* spp, *Anguilla* spp…), species subjected to taxonomic revision during the study period (e.g., *Eleotris* spp.), or cryptic species with low occurrence (e.g., *Grapsidae* spp.). Nine species were non-natives from Réunion island (8 fishes and 1 macro-crustacean), whereas the guppy, *Poecilia reticulata*, was the only introduced species sampled in Mayotte (Appendix 1, Table S1 and S2). Overall, the occurrences of non-natives species among surveys were lower than 5 %, except for *Poecilia reticulata* (76.3 and 33.4 % in Mayotte and Réunion, respectively), *Xiphophorus helleri* (16.9 % in Réunion) and *Oreochromis* spp. (7.7 % in Réunion). Sampled individuals were measured (Total length, TL, mm) and then released in river at the end of the survey. All taxa were then assigned to functional groups (Appendix 1, Table S3) depending on their life history guild (i.e., catadromous, amphidromous, estuarine, freshwater), trophic regime (i.e., predator, omnivorous, primary consumer), habitat preference (i.e., limnophilic, rheophilic), and locomotor capacities to overcome obstacles (i.e., swimming, jumping, walking, crawling, sucking), according to Lagarde et al. (2021b) and Kreutzenberger et al. (2020).

2.2. *Stream typology*

Despite heterogeneity in environmental conditions between the two islands, the main factor structuring freshwater fish and macro-crustacean assemblages remains the local topography, which affects the accessibility of stream reaches depending on the locomotor capacities of organisms (Lagarde et al., 2021b). We thus proposed an objective typology for insular streams inferred from available data, that reflect changes in aquatic assemblages induced by stream hydro-morphologic features. In this purpose, fish and macro-crustacean abundances were log-transformed before performing a hierarchical clustering based on Bray-Curtis dissimilarity, which revealed two distinct clusters for Reunion (Fig. 1b) and Mayotte (Fig. 1c). Two clusters were selected to limit the number of typologies per island and because preliminary analyses revealed spatial inconsistencies (i.e., irregular typology successions along the altitudinal gradient) when the number of clusters was larger. Moreover, a finer partition of riverine assemblages could reflect the impact of anthropogenic stresses inducing changes in occurrence and abundance of species. Here, the two clusters reflect modifications in taxonomic composition of assemblages between up- and down-stream reaches, due to species turnover, but mainly related to lower richness in the upper river sites (Supplementary Material, Appendix 1, Fig. S1). For each island, we then adjusted a logistic generalised-linear model (GLM) to predict assemblage clusters as a function of six hydro-morphologic features: altitude (m), slope (%), relative distance from the source (value between 0 and 1), length of the upstream hydrographic network (km), area of the catchment (km^2), and cumulative height of downstream waterfalls (m). A variable selection was conducted based on the Akaike information criterion (AIC) to select the most parsimonious models (Venables and Ripley, 2013), which were fitted with 70 % of the data while the remaining 30 % data were used to evaluate the models' performances. In Reunion, all hydro-morphologic features were retained by the AIC selection process, with the exception of the relative distance from the source. The model accurately predicted changes in assemblage clusters (94.6 and 91.8 % of correct classification for training and independent data respectively). In Mayotte, only altitude and slope were retained by the selection process, but the model also provided high classification performances for both training (81.4 %) and independent (80.0 %) datasets. Finally, the models were used to predict what type of assemblages was expected along the river network, resulting in two typological groups (i.e., down- and upstream) for each island (Fig. 1a). This stream typology was thereafter used in analysis to account for the influence of environmental constrains, as advocated for the development of biological indicators through the WFD (Hering et al., 2010).

2.3. Assessing stressors gradients

The level of anthropogenic pressure experienced by aquatic assemblages was assessed for each survey based on tree stressor categories (i.e., continuity alteration, urbanisation and agricultural stresses), following a similar methodological approach in both islands. For each category, several criteria were determined to reflect different aspects of the disturbance or different spatial scales (all criteria are detailed in Supplementary Material, Appendix 2). The criteria were selected based on previous knowledges on stressor impacts to reflect the cumulative effect of dams on the colonization of upstream areas (Kreutzenberger et al. 2020; Lagarde et al., 2021a,b) or to assess diffuse sources of stress caused by urban and agricultural surfaces (Chen and Olden, 2020; Walter et al. 2012). Then, the criteria were combined to obtain a synthetic pressure score for each category by performing a TOPSIS multi-criteria decision analysis (Technique for Order of Preference by Similarity to Ideal Solution; Hwang and Yoon, 1981). Briefly, this method is based on a scoring process, bounded between 0 and 1, of a series of alternatives according to their relative distance from extreme favourable and unfavourable conditions, reflected by the maximum or minimum values of criteria. Here, the TOPSIS approach was used to produce a pressure score for each stressor category by combining several criteria, among which some must be maximized (e.g., vegetated surface), but others must be minimized (e.g., urbanized surface). In such case, a maximum pressure score (of 1) is expected when the criteria reflect unfavourable conditions for aquatic organisms (e.g., high proportion of urbanized surface and low cover of vegetated surface), whereas a minimum score (of 0) is obtained when the criteria have a minimal impact (e.g., low anthropized areas with highly vegetated surface).

The pressure scores were calculated for the three stressor categories in Reunion (Fig. 1d) and Mayotte (Fig. 1e), and were subsequently used for identifying biological metrics sensitive to anthropogenic alterations of river ecological quality.

2.4. Developing stressor-specific indexes

Instead of a general approach, we attempted to develop three multimetric indexes (MMI) specific to stressor categories (i.e., continuity alteration, urbanisation stress, and agricultural stress) in order to improve their interpretability (Hering et al., 2006a). As a first step, a large panel of candidate metrics was computed to reflect composition and structure of fish and macro-crustacean assemblages (Fig. 2). For each stressor category, the responses of metrics were then described to identify which ones were impacted in similar direction whatever the typology. Finally, a correlative approach helped to determine the best combination of metrics, by maximizing the occurrence of common metrics between typologies to improve robustness and comparability across stream types.

Metric calculation

A total of 161 metrics reflecting the composition and functional structure of native assemblages were initially calculated, either by considering conjointly fish and macro-crustacean taxa, or by focussing on the two phyla separately (see Supplementary Material for a detailed list, Appendix 3, Table S1). Non-native species were excluded from the analyses to produce metrics representative of the local indigenous assemblages and their sensitivity to ecological alterations. To complement assemblage metrics, some metrics were calculated using functional groups or high-occurring taxa to reflect changes in abundance and size-structure of index species. As the metrics were calculated at different taxonomic level (i.e., species, genus, phylum, functional group), some metrics cannot be calculated for each typology due to dissimilarity in species distribution along rivers (Lagarde et al., 2021b). Accordingly, metrics were selected as candidates for a given typology when they can be calculated for at least 95 % surveys and included over 25 % zero values to have a wide range. Otherwise, the metric was excluded from analyses for this river type. Finally, the total dataset was divided in two subsets for each typology. The first subset gathers 70 % of the data and

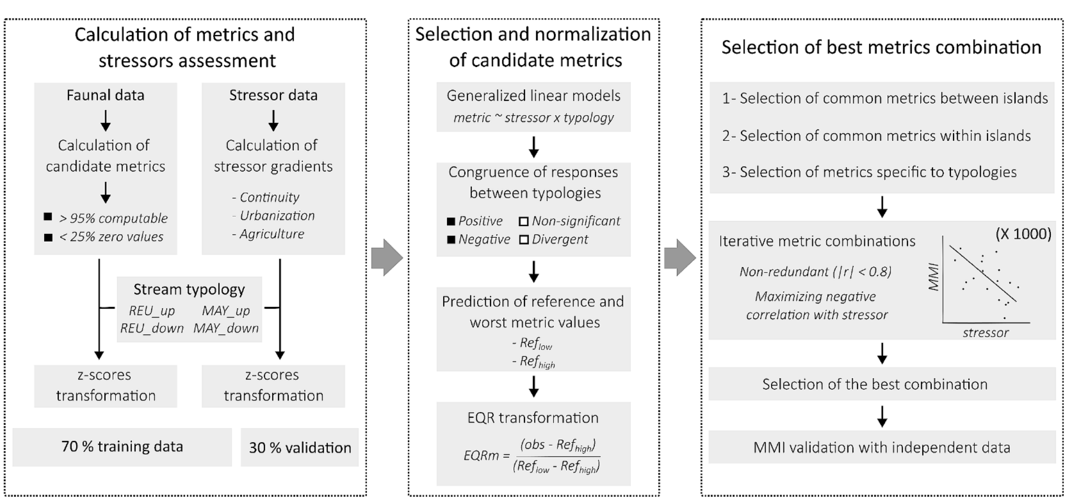

Fig. 2. Schematic overview of the steps conducted to construct the three stressor-specific multimetric indexes (MMI), while maximising the congruence of metrics between typologies. Four typologies were considered to construct the MMIs, upstream (up) and downstream (down) areas of Réunion (REU) and Mayotte (MAY) islands. For each metric, Ref_{low} value represents the best condition when the pressure level is the lowest and oppositely for the Ref_{high} value. Finally, the EQR transformation for a given metric (EQRm) is a normalization between the observed value (obs), the Ref_{low} and Ref_{high} to standardize the EQRm between 0 and 1.

was used to construct the ecological indicators (i.e., training data), whereas the remaining 30 % data were used as independent data to validate the indicators proposed for the four typologies (i.e. validation data).

Selection of responsive metrics

As a first step, we used Generalized linear models (GLMs) to identify the candidate metrics that responded significantly to each stressor category (i.e., continuity alteration, urbanisation stress, and agricultural stress) and the signs of model coefficients were extracted to select metrics that responded in a similar direction whatever the typology of the rivers. Indeed, we assumed that when the pressure directions were different between river typologies, the impacts were too variable and lacked stability to be integrated into an indicator. Conversely, we selected pressures when their responses (positive or negative) remained common between typologies and thus transferable from one river type to another.

In this purpose, all metric values were transformed in z-score, i.e., centred to 0 and variance standardized to 1, for each typology. This normalization approximate normality and expresses all metrics in a common scale across typologies, allowing us to directly compare metric values obtained from different stream types (Mondy et al., 2012). GLMs where then used to identify which metrics responded significantly to the stressors with similar effect across typologies. The impact of the three stressors was analysed separately by adjusting a GLM with the metric as response variable, whereas the typology and pressure scores were used as explanatory variables. Deviance reduction tests were then conducted to assess the significance of model parameters, including the interaction between stressor and typology. When the stressor impact was significant, its direction (i.e., positive or negative effect) on metric was determined for each stream type, based on the signs of model coefficients. Finally, we only selected the responsive metrics showing congruence in responses between river types within each stressor categories (i.e., continuity alteration, urbanisation stress, and agricultural stress).

Metric normalization

Following the WFD requirements, ecological indicators have to be expressed as Ecological Quality Ratio (EQR), which represents the deviation between the value of the observed biological parameter and the expected value under reference conditions (Hering et al., 2006a). Its range is 0–1, with high ecological status represented by values close to one and bad ecological status by values close to zero. Whereas reference conditions can be defined from historical data or relatively pristine areas of low human impact (Vadas et al., 2022), the references values can also be extrapolated based on expert judgements or predicted from modelling approaches (Borja et al., 2012; Hering et al., 2006a). Such approach was preferred for the streams of Reunion and Mayotte, where pristine sites remain scarce. More precisely, we used quantile regressions to simulate metric values reflecting in the lowest (Ref_{low}, reference conditions) and highest (Ref_{high}, worst conditions) pressure conditions depending on river typology (Delpech et al., 2010; Zucchetta et al., 2020).

For each stressor category, two quantile regressions were adjusted for the 10th and 90th conditional quantiles (i.e. τ parameter = 0.1 and 0.9) using the candidate metric as response variable and the pressure scores as explanatory variable. The typology was also included as explanatory co-variable when it influenced significantly the response metric (see previous paragraph). The models were then used to predict reference and worst metric values, by setting the stressor scores either to the 0.01 or 0.99 quantiles, respectively. When the stressor had a negative impact on the response metric, the Ref_{low} and Ref_{high} values were inferred from the 0.9 and 0.1 quantile regression models, respectively, whereas the reverse models were used when the stressor impact was positive. This approach allows us to estimate expected values for the metrics under the best and worst conditions, by assuming that anthropogenic pressures affect the upper and lower bound of metric distribution, rather than the average values (Cade and Noon, 2003; Zucchetta et al., 2020).

Following Hering et al. (2006), the references values were then used as upper and lower anchors to normalize metrics between 0 and 1. The upper anchor corresponds to the upper limit of the metric's value under best conditions (Ref_{low}), whereas the lower anchor corresponds to the lower limit of the metric's value under worst conditions (Ref_{high}). Each candidate metric (EQR_m) was thus normalised using the following formula: $EQR_m = (obs - Ref_{high}) / (Ref_{low} - Ref_{high})$. As some observed values can be out of the '$Ref_{low} - Ref_{high}$' interval, the EQR_m values above 1 or below 0 were fixed as 1 or 0, respectively.

Selecting best metrics combination

For each stressor category (i.e., continuity alteration, urbanisation stress, and agricultural stress), we attempted to develop a specific multimetric index (MMI) from the aggregation of several candidate metrics retained during the previous steps. As suggested by Schoolmaster et al. (2012), a correlative approach was used to select a combination of metrics maximising the strength of the negative correlation between the MMI and stressor scores. Although all metrics were standardized and can be conjointly analysed between stream typologies, some candidate metrics remained specific to certain river types (e.g., specific to an island or an altitudinal level). Therefore, we implemented an iterative process allowing us to maximize the number of common metrics among typologies, by selecting primarily the metrics common to the four typologies, then those common within the islands, and finally the metrics that maximize the negative correlation for a single river type. Such an approach eases the comparison of metrics among river types, while taking into account specificities of local assemblages.

For each stressor category, we firstly selected the metrics common to the four typologies based on an iterative process (Schoolmaster et al., 2012), including a bootstrap sub-sampling of the training dataset (Mondy et al., 2012), so that the following procedure was repeated 1000 times:

1. 70 % of the training data were randomly selected.
2. One candidate metric common of the four typologies was selected as the first metric in the MMI, m_1, and its correlation with stressor scores was calculated.
3. Candidate metrics correlated ($|r| > 0.8$) with m_1 were excluded.
4. m_1 was averaged (i.e., arithmetic mean) with each of the other uncorrelated metrics and the combination, m_j, providing the strongest negative correlation with stressor score was selected.
5. The combination m_j was retained when its correlation with stressor was improved by at least 5 %, otherwise m_1 was kept.
6. Candidate metrics correlated ($|r| > 0.8$) with pre-selected metric(s) are excluded.
7. The combination was averaged with each of the remaining uncorrelated metrics, and the combination with the strongest negative correlation with stressor was selected. It was retained when the improvement was over 5 %.
8. Steps 6–7 were repeated until the stopping criterion was satisfied (i.e., <5 % increase in correlation strength).
9. Steps 2–8 were repeated until each metric has been used as first metric, m_1. The combination with the maximal correlation strength with stressor score was retained, as the best selection of metrics common for the four typologies.

For each stressor, the best combination of common metrics was selected by calculating a score, taking into account the frequency of the combination and its metrics among the 1000 iterations, such as: $\sum P_{met} \times N_{com}$, where P_{met} is the occurrence frequency of the metrics and N_{com} is the number of occurrences of the combination. After identifying the common metrics between the islands, a second bootstrap sub-sampling was conducted based on the steps 6–8, using data separately for each island to increment MMI with the non-selected metrics and the specific metrics of Mayotte and Reunion islands. Finally, the steps 6–8 were repeated one last time, separately for each typology, to increment MMI with the non-selected metrics and the specific metrics of typologies.

Such bootstrap sub-sampling allowed us to reduce the potential bias of the training dataset composition in metric selection (Mondy et al., 2012). The three proposed indices were thus specific to the continuity alteration (MMI_{CONT}), urbanisation stress (MMI_{URB}), and agricultural stress (MMI_{AGRI}), and included common cores metrics within and between islands, but they remained specific to each type of river. Finally, the relevance of MMIs were validated by assessing the significance of the relationship between the MMI and stressor scores across each typology, based on Pearson corelation tests using the validation data.

Determining class boundaries

The final MMIs provide scores from 0 to 1, with values near 1 reflecting high ecological quality and values near 0 for fish and macro-crustacean assemblages strongly affected by human disturbances. As recommended by the WFD, we defined ecological quality class boundaries with equal ranges (i.e., 0.80, 0.60, 0.40, and 0.20) to provide five ordinal rating categories (i.e., delimiting 'high', 'good', 'moderate', 'poor', and 'bad' classes), based on the EQR scores (Hering et al., 2006a).

All statistical analyses were performed in the R environment v. 4.0.5 (R Core Team, 2018).

3. Results

3.1. Identification of responsive metrics

Among the 161 initial metrics, 37 were excluded because they could not be calculated on a minimum of 95 % of the surveys and/or included over 25 % zero values within the four typologies. For the other 124 metrics, 47 and 51 were used as potential metrics for up- and downstream rivers of Mayotte, and 72 and 120 as metrics for up- and downstream rivers of Reunion, respectively (Appendix 3, Table S2). The GLMs analyses emphasized that 66.1 % (n = 82) of the metrics were significantly influenced by the alteration of continuity, whereas 46.8 % (n = 58) and 54.8 % (n = 68) were impacted by urbanisation and agricultural stresses, respectively. Overall, the effects of each stressor were similar across river types (i.e., same signs of GLM coefficients), with the exception of 11 metrics showing divergent responses between typologies for agricultural stress (Fig. 3). Most of the metrics were negatively affected by the alteration of stream continuity, including richness and abundance-based metrics for fish and macro-crustacean. However, size-based and evenness metrics (based on taxa or functional group proportions) increased significantly with continuity disturbance, suggesting that individual body sizes increased when stream accessibility was disrupted. For the two others stressor categories, the metric responses were more balanced between positive and negative effects (Fig. 3). For agricultural stress, the size-based metrics were generally negatively impacted, whereas the responses were mixed for the other metric categories. For urbanisation stress, the abundance-based metrics were positively influenced, whereas other metrics revealed decreasing trends, which suggested the occurrence of some dominant taxa in the presence of urban pressure.

3.2. Selection of metrics combination

The iterative metric selection process provided MMIs composed of 4–9 metrics, depending on the stressor categories and the stream typologies (Fig. 4). In each MMI, both fish-based and macrocrustacean-based metrics were included, which emphasises the complementarity of the two phyla for assessing river alteration. In accordance with the composition of local assemblages, the relative proportion of fish-based metrics was larger in the MMI of Reunion than for Mayotte, where macro-crustacean were more frequent whatever the typology.

For the continuity alteration, the MMI_{CONT} was composed of four core metrics common to the four typologies, including abundance-based and richness-based metrics, which were all negatively related to the disturbance of ecological continuity. The addition of one (Reunion) or two (Mayotte) metrics specific to an island also helped improve the correlation strength with the stressor scores, as well as the inclusion of typology-specific metrics for three river types (Fig. 4). Interestingly, size-based metrics (i.e., q10_fish and q90_index_SIC) were included for MMI of Reunion Island, which revealed an overall increase in individual fish lengths when the river continuity was altered.

For the agricultural stress, only two metrics common to the four typologies were included in the MMI_{AGRI}, whereas metrics specific to islands or typologies were mostly represented, especially for Reunion Island (Fig. 4). Overall, the selected metrics reflecting richness and abundance in fish assemblages trended to be positively related to agricultural fingerprint, whereas macrocrustacean-based metrics were mostly negatively impacted. Similarly, agricultural stress tended to affect evenness in fish sizes, with a negative impact on body lengths, especially for *S. lagocephalus* in Reunion Island, reflecting a lower proportion of adults.

For the urbanisation stress, five metrics common to both islands were selected in the MMI_{URB}, including three metrics jointly based on fishes and macro-crustaceans (Fig. 4). Similar to agricultural stress, the responses of abundance-based metrics were mostly positively affected by urban stress, whereas the diversity and size-based metrics tended to be negatively impacted. Accordingly, the MMI_{URB} reflects an overall

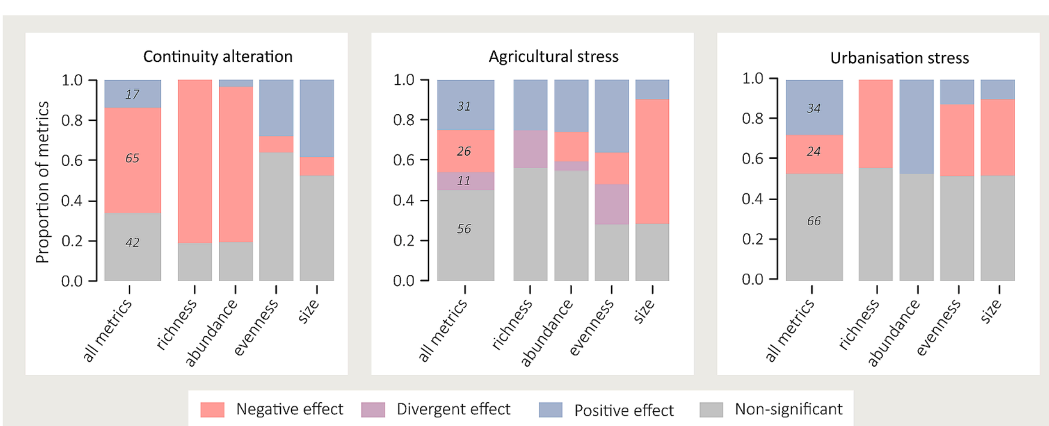

Fig. 3. Responses of the candidate metrics used to assess the impact of continuity alteration, agricultural stress and urbanisation stress on the composition and structure of fish and macro-crustacean assemblages, in Mayotte and Reunion islands. The proportion of non-significant, divergent, negative or positive responses across typologies is provided for each stressor category for the 124 pre-selected metrics, and then detailed according to the type of metric (i.e., richness, abundance, evenness, and size-based metrics).

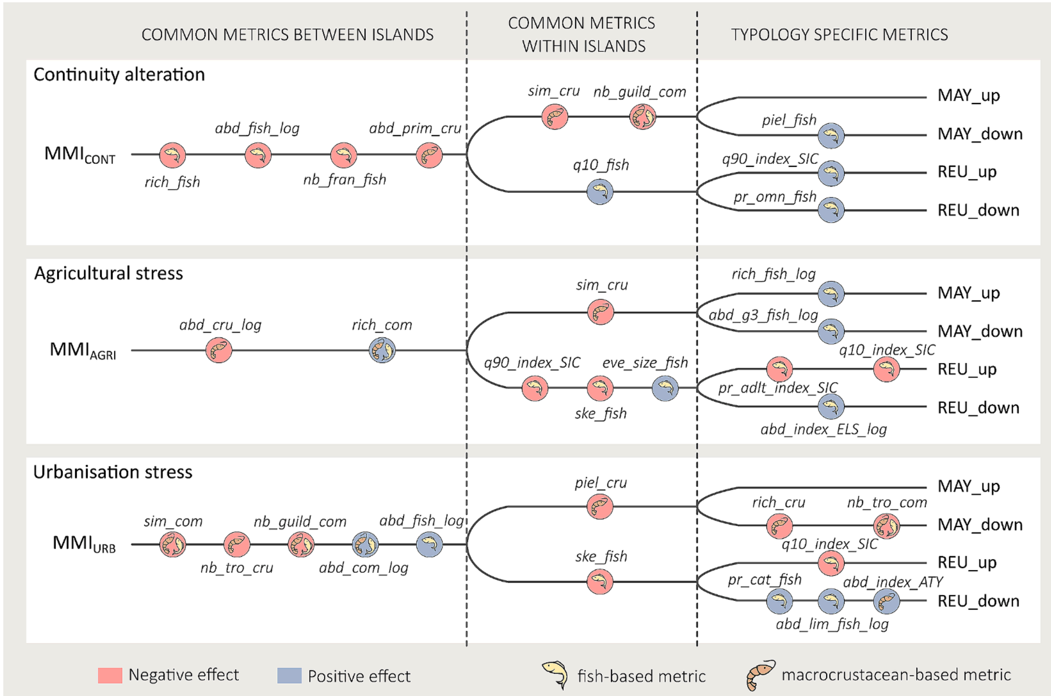

Fig. 4. Schematic representation of the metrics aggregated for constructing the three multimetric indexes specific to continuity alteration (MMI_{CONT}), agricultural stress (MMI_{AGRI}) and urbanisation stress (MMI_{URB}) in Mayotte and Reunion islands. The trees discriminate common metrics between and within islands, as well as metrics specific to each river type. MAY_up: Mayotte upstream, MAY_down: Mayotte downstream, REU_up: Reunion upstream, REU_down: Reunion downstream. The metrics are defined in Supplementary Material, Appendix 3.

decline in fish and macro-crustacean diversity (taxonomic and functional), as related to an increase in abundance of some dominant taxa, and also suggested by changes in evenness indices (e.g., sim_com or piel_cru).

3.3. Validation of multimetric indices

The distributions of the MMI values calculated from assemblages of the training and validation datasets did not significantly differ for MMI_{CONT} (Kolmogorov–Smirnov test: D = 0.055, p = 0.606; Fig. 5), MMI_{AGRI} (D = 0.055, p = 0.606) and MMI_{URB} (D = 0.084, p = 0.135). All MMIs were significantly correlated with the pressure scores based on the training dataset, with coefficients of −0.305 to −0.670 (Table 1). Although the coefficients remained negative, the correlations calculated from the validation data were not significant for the MMI_{AGRI} in Mayotte and the MMI_{URB} in upstream rivers of Mayotte. For the other indices, the correlations were significant based on validation data, and their relationships with stressors were very close to those established with the training data for each typology (Fig. 6).

The correlation coefficients of MMI were always higher with the target stressors than with other pressure categories, though often still significant. Indeed, the MMI_{URB} was not related to continuity alteration (n = 917, r = 0.01, p = 0.662), but was negatively correlated with agricultural stress (n = 917, r = -0.26, p < 0.001). Similarly, the MMI_{AGRI} was negatively correlated with urbanisation stress (n = 917, r = -0.21, p < 0.001), but positively with continuity alteration (n = 917, r = 0.14, p < 0.001). Finally, the MMI_{CONT} was positively correlated with urbanisation stress (n = 917, r = 0.07, p = 0.029) and agricultural stress

Fig. 5. Frequency distribution of the three multimetric indexes specific to continuity alteration (MMI_{CONT}), agricultural stress (MMI_{AGRI}) and urbanisation stress (MMI_{URB}) in Mayotte and Réunion islands, calculated based on training and validation datasets.

Table 1
Summary of the Pearson correlation tests between the pressure scores the three multimetric indexes specific to continuity alteration (MMI_{CONT}), agricultural stress (MMI_{AGRI}) and urbanisation stress (MMI_{URB}) in Mayotte (MAY) and Reunion (REU) islands. Results are detailed for each stream typology, as well as from both training and validation datasets. P-values < 0.05 are identified in bold.

	Training data			Validation data		
Multimetric indices	n	Correlation	p-value	n	Correlation	p-value
MMI_{AGRI}						
– all stream types	649	−0.468	**<0.001**	268	−0.368	**<0.001**
– REU upstream	263	−0.437	**<0.001**	93	−0.354	**<0.001**
– REU downstream	225	−0.670	**<0.001**	116	−0.552	**<0.001**
– MAY upstream	85	−0.339	**0.001**	28	−0.093	0.637
– MAY downstream	76	−0.305	**0.007**	31	−0.196	0.292
MMI_{CONT}						
– all stream types	649	−0.457	**<0.001**	268	−0.498	**<0.001**
– REU upstream	263	−0.504	**<0.001**	93	−0.505	**<0.001**
– REU downstream	225	−0.555	**<0.001**	116	−0.588	**<0.001**
– MAY upstream	85	−0.478	**<0.001**	28	−0.590	**<0.001**
– MAY downstream	76	−0.303	**0.008**	31	−0.379	**0.036**
MMI_{URB}						
– all stream types	649	−0.424	**<0.001**	268	−0.394	**<0.001**
– REU upstream	263	−0.599	**<0.001**	93	−0.649	**<0.001**
– REU downstream	225	−0.359	**<0.001**	116	−0.228	**0.014**
– MAY upstream	85	−0.362	**<0.001**	28	−0.187	0.341
– MAY downstream	76	−0.341	**0.003**	31	−0.499	**0.004**

($n = 917$, $r = 0.10$, $p = 0.002$).

4. Discussion

4.1. Ecological responses of fish and macro-crustacean assemblages

Given the limited understanding of anthropogenic impacts on tropical rivers (Ramírez et al., 2012; Sundar et al., 2020), investigating the ecological responses of assemblages appeared a crucial issue to guide conservation and management practices (Taniwaki et al., 2017) and provide a critical view on the metrics integrated into ecological indicators (Birk et al., 2012; Martínez-Fernández et al., 2019). Here, we focused our analyses on native species, but the presence of introduced species can contribute to modify the local assemblages, through resource competition, predation or diseases (Kido 2013; Walter et al. 2012). Further investigations are thus required to quantify the impact of non-native species on the functioning of the tropical island ecosystems. Overall, our analyses demonstrated that both fish and macro-crustacean metrics were sensitives to the three studied stressor categories, which confirm that native fauna of island streams are suitable indicators of the river ecological status (Kido, 2013). However, a larger number of metrics were more impacted by the alteration of ecological continuity than by agricultural or urban stresses. Furthermore, the direction of ecological responses was generally consensual, indicating that the impacts of habitat fragmentation were congruent and consistent, whatever the river type. Overall, the disturbance of ecological continuity positively affected evenness- or size-based metrics, whereas richness- and abundance-based metrics tended to decrease. Such decline in richness and abundance has been previously described in several islands (Franklin and Bartels, 2012; Joy and Death, 2001; Katano et al., 2006), where the accumulation of obstacles downstream of watersheds represents one of the major pressures on native riverine assemblages (Franklin and Gee, 2019; Greathouse et al., 2006; March et al., 2003). However, the impact also depends on the morpho-ecological traits of species (Kreutzenberger et al., 2020; Lagarde et al., 2021a), which can have morphological adaptations facilitating the crossing of obstacles, whereas other species remain blocked downstream of the first obstacles encountered (Cooney and Kwak, 2013; Fièvet et al., 2001). Interspecific differences can also contribute to explain why most metrics based on evenness and proportions responded positively to continuity alterations. For example, the proportion of omnivorous taxa, often indicative of human impacts (Vadas et al., 2022), tended to increase in fish assemblages when the continuity is altered, probably in response to hydromorphological changes and altered food webs in fragmented environments (Cooney and Kwak, 2013; Frotté et al., 2020; Greathouse et al., 2006). Similarly, our results demonstrated a strong impact of continuity alteration on size-based metrics, as similarly demonstrated in other studies (Frotté et al., 2020; Lagarde et al., 2015). In Reunion Island, fish body sizes, and in particular those of eels and *Sicyopterus lagocephalus*, were significantly larger when continuity was disrupted, indicating that young individuals were not able to freely reach watershed headwaters (Lagarde et al., 2020, Lagarde et al., 2015). Thus, river fragmentation appeared to be a limiting factor for population turnover upstream of obstacles, which in turn contributes to weakening local populations (Franklin and Gee, 2019; Holmquist et al., 1998; Storch et al., 2022).

As reported in other topical islands (e.g. Lisi et al., 2018; Walter et al., 2012), our results revealed that about half of the candidate metrics were also impacted by land-use stresses, but ecological responses appeared more heterogeneous than for the continuity alteration. Although the decline of richness in native aquatic assemblages was expected along an urban gradient (Lisi et al., 2018; Moi and Teixeira-de-Mello, 2022), we also highlighted that abundance of some fishes and macro-crustaceans significantly increased. Similar results have been reported in other oceanic islands, where some native amphidromous taxa can persist and prosper in degraded streams despite intensive urbanisation (Engman and Ramírez, 2012; Jenkins et al., 2010; Ramírez et al., 2012). In such context, the opportunistic life-history strategy (Labeille et al., 2024; Teichert et al., 2014) and the trophic flexibility of some species (Vadas et al., 2022) can contribute to improve resilience against environmental degradation and food-web changes, whereas other sensitive taxa decline with urbanisation (Lisi et al., 2018). For agricultural stress, our results also highlighted an increase in both richness and abundance of fish assemblages, whereas the macro-crustacean abundances tended to decrease. This suggests higher sensitivity of macro-crustaceans, which was featured by a drop in abundance and proportion of rheophilic macro-crustaceans, probably due to changes in substrate and flow patterns in agricultural landscapes (Burdon et al., 2020). The positive influence on fish richness and abundance metrics was more unexpected, but it can be related to the confounding effect of nutriment enrichment, which often increase

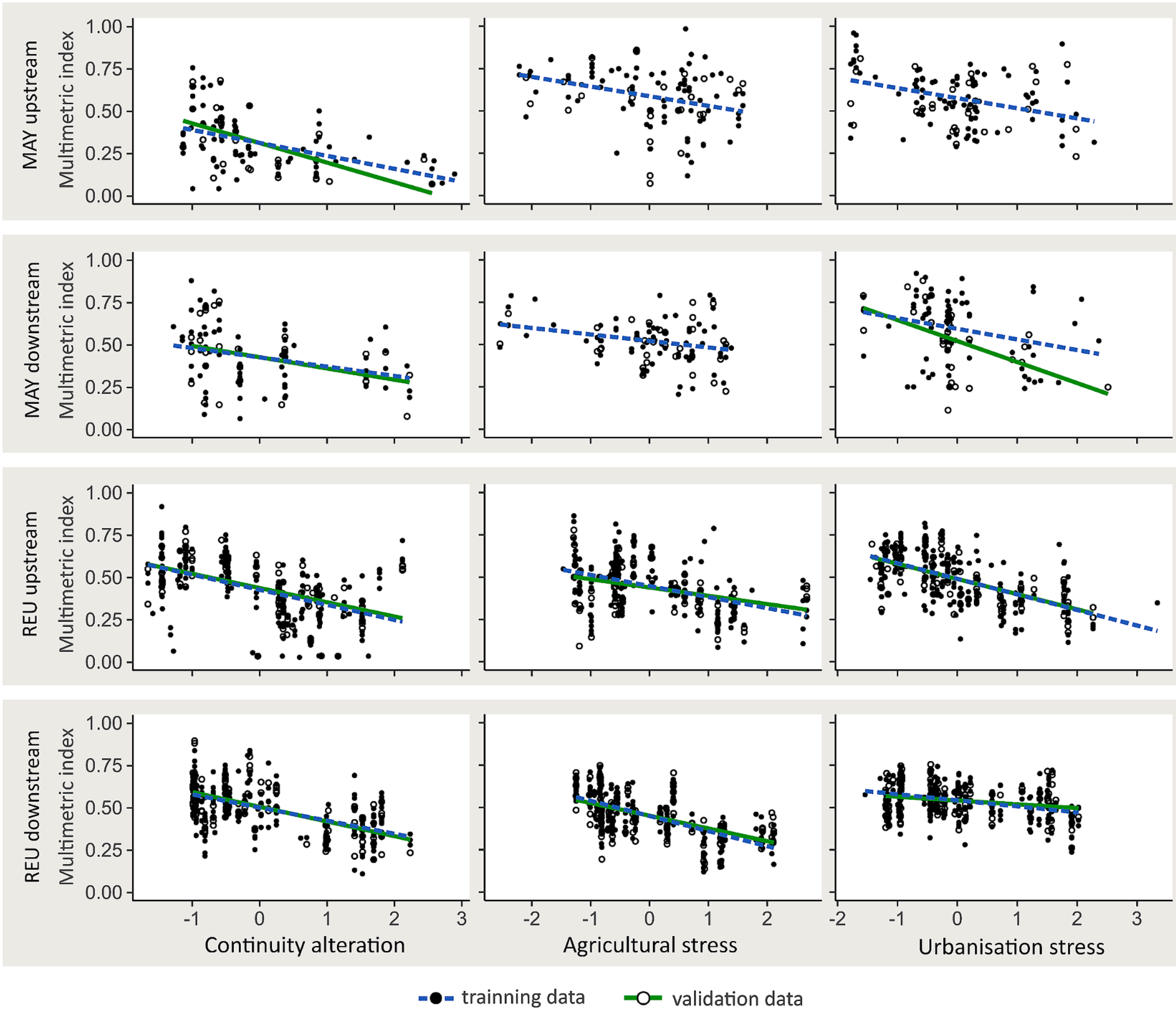

Fig. 6. Linear relationships between the stressor-specific multimetric indexes and the pressure scores for continuity alteration, urbanisation stress and agricultural stress in Mayotte (MAY) and Réunion (REU) islands. Regression lines are presented when correlations are significant from the training (blue dotted line) or validation (green continuous line) datasets. Details of corelation tests are provided in the Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ecosystem productivity and total-taxa richness (Vadas et al., 2022). Moreover, these effects are associated with changes in habitat preference or trophic regime guilds, which indicate modifications in local habitat conditions and trophic functioning. Indeed, marked modifications in assemblage composition can occur because of difference in species sensitivity to land-use change, whereas impact on local richness can remain limited (Chen and Olden, 2020). In oceanic islands, previous studies have highlighted that the modification of riparian forest can have serious consequences on the distribution of native fauna, through changes in the quantity and quality of trophic resources (Frotté et al., 2020; Jenkins et al., 2010; Vadas et al., 2022). Furthermore, the predominance of negative effects on fish size-based metrics suggested an important turnover in populations subjected to agricultural and urban stresses, and probably a disruption of settlement, survival and/or growth processes. Hence, even if juveniles recruit repeatedly to impacted areas, adults do not settle or have limited life expectancy. Indeed, beyond the modification of riparian habitats and river-bed, the contamination of water by agricultural or urban inputs can sometimes limit fish growth, functional performances, and/or survival (de Albuquerque et al., 2020; Diamond et al., 2022), which mechanically cause a drop in body size.

Land-use reflects diffuse pressures and thus an indirect assessment of impacts on aquatic assemblages, whereas the continuity alteration reflects a physical impact directly affecting the mobility of individuals across river reaches. Likely, the weakness of the responses from urban and agricultural stresses is partly related to the migratory life-history of native taxa, which can lead to unexpected responses compared to temperate continental assemblages (Engman and Ramírez, 2012; Ramírez et al., 2009). Even if individuals remain sensitive to land-use disturbances, the recurrent arrival of juveniles in rivers can buffer and compensate for local losses due to human activity (Walter et al., 2012). In this sense, the demographic turnover induced by the recruitment of young diadromous individuals plays a decisive role in the resilience of river populations when facing anthropogenic impacts, even if settlement process and adult survival are disturbed to potentially impact reproductive success. Such functioning pattern has been suggested for tropical rivers of Puerto Rico, where fish and shrimp assemblages can remain diverse and abundant despite river urbanization (Ramírez et al., 2012). However, the buffering effect on assemblages in impacted areas (population sinks) remains only possible if pristine watersheds (population sources) allow the maintenance and demographic growth of the *meta*-population at the regional scale (McDowall, 2010; McRae, 2007). This observation emphasises the importance of monitoring networks based on ecological indicators to identify source watersheds that should be conserved, but also to assess the temporal trends in stocks, which contribute to the resilience of local populations.

4.2. Proposal of stressor-specific multimetric indexes

Although correlative approaches are classically used to develop ecological status indicators (Schoolmaster et al., 2012), we proposed an original method to maximize the number of common metrics between and within islands, while keeping a component specific to river types. To ensure compliance with the WFD, the definition of a stream typology is a prerequisite of indicator construction because it allows to take into account the natural variability in assemblages related to biogeographic regions or local characteristics of rivers (Hering et al., 2010; Jupke et al., 2023). Thus, we proposed a typology based on the dissimilarity in fauna composition along the fluvial continuum, resulting in two stream types for each island. The topographic bounds separating the up- and downstream types were defined on the basis of a predictive modelling approach to account for the differences in accessibility between the watersheds (e.g., slope, waterfall downstream), which significantly constrain the assemblage types (Lagarde et al., 2021b). Subsequently, the typology characteristics were directly accounted when the candidate metrics were normalized into EQRs, as suggested by Mondy et al. (2012). Although the normalization allows us to investigate the metrics of all typologies conjointly, we chose to implement a hierarchical selection procedure with the aim to maximize the number of common metrics. This original approach appeared as a compromise between type-specific indicators where the selected metrics can differ between rivers and generic indicators where a single set of metrics is used for all typologies (e.g. Gabriels et al., 2010; Mondy et al., 2012; Pont et al., 2007). The advantage of our approach was to take into account local specificities through the integration of type-specific metrics, while improving the robustness and comparability of indices between typologies because they share numerous common metrics.

Rather than a general indicator, we chose to favour a stressor-specific approach to facilitate the interpretation of indices and to discriminate the sources of alteration (Hering et al., 2006a; Lemm et al., 2019). Stressor-specific MMIs were also relevant because we have demonstrated that the assemblage responses were different depending on the pressure categories, and can even display antagonistic effects on the candidate metrics (Schinegger et al., 2016). In this context, the construction of distinct indicators offers the choice to calculate the indices independently from each other, and subsequently gathering them (or not) by averaging the values or by keeping the worst quality class (Hering et al., 2006a). In such case, the 'one out, all out' principle is commonly used in the Water Framework Directive to combine the assessment of multiple ecological indicators, by selecting the worst ecological status, which provides a conservative assessment in comparison to other aggregating approaches, such as mean or median (Caroni et al., 2013).

Overall, the metrics selected in the MMIs properly reflected the impacts of the three stressors on the composition and functional structure of assemblages, as detailed previously. For each indicator, the number of metrics retained varied between four and nine, which was comparable to the number of metrics classically used for the calculation of other fish-based indicators (Birk et al., 2012; Pérez-Domínguez et al., 2012). Indeed, the number of metrics included in the MMIs can influence the stability of the relationship between the indicator and the pressure score (Zucchetta et al., 2020). Here, the selection procedure enabled to automatically identify sets of non-redundant (correlation < 0.8) and complementary metrics, which improved the correlation strength between indicator and targeted stressor (Schoolmaster et al., 2013, 2012). For each MMI, metrics based on richness, abundance, evenness, or size were included so that different aspects of the diversity, functioning, and size-structure of assemblages were represented in accordance with the WFD recommendations (Reyjol et al., 2014). In addition, metrics based on fish and macro-crustaceans were selected. We have previously demonstrated that sensitivity of the two phyla differed according to stress factors, which suggests a complementarity in reflecting anthropogenic impacts. Furthermore, these two phyla have already been used jointly in the calculation of several indices, as for assessing the ecological quality of Basque estuaries (Uriarte and Borja, 2009). In tropical island rivers, the similarity in life cycles and the co-occurrence of fish and macro-crustaceans justifies the joint use of these taxa in ecological indicators (Fièvet et al., 2001; Kido, 2013; Lagarde et al., 2021b). Moreover, these taxa have relatively high abundances in tropical streams and can be sampled concurrently with similar methods, such as electrofishing (Pottier et al., 2022).

Although the three MMIs were consistently correlated with stressor scores using the training datasets, some relationships became not significant using the validation data, particularly for the Mayotte rivers. This result highlights the importance of independent dataset to validate the indicators (Birk et al., 2012), even if resampling procedures are implemented to limit the dependence on training datasets (Mondy et al., 2012). The lack of significant correlations between the MMI_{AGRI} and MMI_{URB} and land-use scores in Mayotte reinforce the statement that assemblages are less sensitive to these categories of pressure. Indeed, the heterogeneous and sometimes unexpected ecological responses of the metrics for urban or agricultural gradients suggest considering with carefulness the indices developed, because they might be less robust and transferable to other biogeographic zones. Consequently, we suggest preferentially using the MMI_{CONT}, which revealed a strong correlation with continuity alteration scores, whatever the river type. Although this indicator was slightly correlated with the two land-use stressors, it essentially reflected the disturbance of ecological continuity, which represents a major threat for the functioning of island aquatic ecosystems (Franklin and Gee, 2019; Holmquist et al., 1998; March et al., 2003). Indeed, we have already emphasized the determining role of the regular arrival of diadromous juveniles to ensure stability and resilience of local assemblages, particularly against urbanization and agricultural constraints (Engman and Ramírez, 2012; Ramírez et al., 2012). The WFD recommends monitoring inland waters based on several biological quality elements, whose ecological responses could provide additional and complementary information on the ecological status of water bodies (Birk et al., 2012; Marzin et al., 2012). Tropical island rivers therefore appear as a typical case where fish and macro-crustaceans can be used to assess the state of ecological continuity, whereas diatoms and invertebrates appear more sensitive to changes in water quality (Jannel et al., 2024; Tapolczai et al., 2017; Touron-Poncet et al., 2014), as also reported in continental rivers (Hering et al., 2006b; Vadas et al., 2022; Sullivân et al., 2025).

To conclude, our results demonstrated that the composition and functional structure of fish and macro-crustacean assemblages in island environments were significantly impacted by anthropogenic pressures. This observation highlights the relevance of using these taxa as indicators of the ecological status of insular running waters, provided that the local specificities of assemblages across typologies are accounted. We proposed an iterative approach to identify the best combination of metrics aggregated in multimeric indexes, while selecting primarily shared metrics between and within islands to promote the cross-interpretation of indices. Considering three different stressor categories, a stressor-specific method was favored to adopt a diagnostic approach, allowing us to identify the origin of ecological dysfunctions. Although fish and macro-crustacean assemblages were sensitive to multiple anthropogenic pressures, our results revealed that ecological impacts were more congruent in response to alterations of continuity, regardless of typology, compared to stresses induced by agriculture or urbanization. Accordingly, we suggest using chiefly the continuity-specific indicator (MMI_{CONT}) to maximize the complementarity between the biological components used in the WFD. The vulnerability of native migratory species to river fragmentation is thus a distinctive feature of island assemblages, which can be used to develop stressor-specific indicators allowing to assess the state of ecological continuity and to evaluate the improvements induced by the restoration measures. Although indices were developed for Reunion and Mayotte, the conclusions can largely be extended to other tropical island rivers, and the methodological framework can be transposed for the development of indicators in other types of water body or biogeographical regions.

CRediT authorship contribution statement

Nils Teichert: Writing – original draft, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Raphaël Lagarde:** Writing – review & editing, Methodology, Funding acquisition, Data curation. **Laëtitia Faivre:** Writing – review & editing, Methodology, Funding acquisition, Data curation. **Pierre Valade:** Writing – review & editing, Methodology, Funding acquisition, Data curation. **Henri Grondin:** Data curation. **Marion Labeille:** Writing – review & editing, Methodology, Funding acquisition, Data curation. **Philippe Keith:** Writing – review & editing, Supervision. **Eric Feunteun:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113585.

Data availability

Data will be made available on request.

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