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Raphaël Lagarde, Nils Teichert, Pierre Valade, Dominique Ponton

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Structure of small tropical island freshwater fish and crustacean communities: A niche- or dispersal- based process?

Lagarde Raphael [1, 2, *] , Teichert Nils [3], Valade Pierre [4], Ponton Dominique [5]

[1] Centre de Formation et de Recherche sur les Environnements Méditerranéens UMR 5110 Université de Perpignan Via Domitia Perpignan ,France
[2] Centre de Formation et de Recherche sur les Environnements Méditerranéens UMR 5110 CNRS Perpignan ,France
[3] UMR 7208 BOREA (Biologie des Organismes et Ecosystèmes Aquatiques) Sorbonne Université MNHN CNRS UMPC Université Caen IRD – Station Marine de Dinard – CRESCO University of Antilles Guadeloupe ,France
[4] OCEA Consult' La Réunion, France
[5] ENTROPIE IRD Université de La Réunion CNRS Université de la Nouvelle-Calédonie – Ifremer c/o Institut Halieutique et des Sciences Marines (IH.SM) Université de Toliara Toliara, Madagascar

* Corresponding author : Raphael Lagarde, email address : raphael.lagarde@univ-perp.fr

Abstract :

Determining the relative importance of niche- and dispersal-based processes in the structuring of animal communities is central in ecology. Freshwater fish and crustacean communities of small tropical islands can bring new insights for understanding these processes as all their species present a pelagic larval stage which gives them important dispersal capacities. Consequently, we hypothesized that dispersal-based process may be preponderant for structuring these communities from the regional to the local, that is, survey site, scales. Gradient forest analyses allowed us to model the effect of 12 environmental variables on freshwater taxa abundances in two southwestern Indian Ocean islands: Mayotte (26 taxa) and Reunion (21). A total of 153 surveys in Mayotte and 266 in Reunion were used for building the models. Despite the strong heterogeneity of environmental conditions between the two islands, the main factors structuring freshwater fish and crustacean communities in both islands were the elevation and the slope of the sites. The observed structure appeared more pronounced for predatory species than for primary consumers and omnivores. As predators generally have limited locomotor capacities, it is concluded that dispersal-based process structures these communities not only at large geographical scales but also at the intra-watershed scale, by limiting the inland penetration (or dispersion) of species in relation to their locomotor capacities. However, more knowledge concerning ecological traits and taxonomic status of many species is needed to confirm this assumption. Abstract in French is available with online material

Keywords : abundances, diadromy, environmental gradients, migration, taxonomic richness, western Indian Ocean

1. INTRODUCTION

Investigating the mechanisms which drive communities structure is a central task in community ecology (Menge and Olson, 1990). Niche- and dispersal-based processes are among the most influential mechanisms structuring animal communities. Niche-based process suggests that environmental habitat conditions and biotic interactions (i.e. competition and/or predation) generate a spatial segregation of species depending on their ecological requirements (Legendre et al., 2005). On the other hand, dispersal-based process advocates the existence of dispersal limitations between habitat patches due to geographical or physical barriers. In this context, dissimilarities in species compositions can occur between habitat patches due to speciation-extinction events (Barton et al., 2013). Nevertheless, the relative importance of niche- and dispersal-based processes are generally hard to disentangle, and depend on the geographic scale of the studies (Chase and Myers, 2011). At large geographic scales, dispersion of propagules may play a preponderant role in community structure by limiting the connectivity between populations present in distant localities (Leprieur et al., 2009). Oppositely, at smaller geographic scales, niche-based processes related to biotic and abiotic habitat preferences may dominate when habitat conditions strongly differ between localities. Indeed, dispersal opportunities are rarely limited when localities are close to each other, but the local environmental conditions may reduce the capacity of propagules to settle in new areas. Beyond the geographical scale, the relative importance of niche- and dispersal-based processes are also influenced by species-specific traits (Soininen, 2010). For example, some fish species have developed specific behaviors adapted to their physiological and anatomical traits that allow them to pass barriers swimmers cannot get beyond (Carvajal-Quintero et al., 2015; Schoenfuss and Blob 2003). Consequently, these species have enhanced active dispersal abilities (Jenkins et al., 2007) which limit the importance of dispersal-based process in structuring their populations.

While riverine fish and crustacean communities of small tropical islands remain poorly examined, processes structuring these communities can bring new insights on the relative importance of niche- and dispersal-based processes across nested geographic scales. Indeed, small oceanic islands are discrete entities, presenting contrasted geomorphology, which are separated from continents, or other islands, by variable distances (Fitzsimons et al., 2002). Within each island, the watersheds present major environmental gradients. Indeed, streams flow from several thousand meters of elevation to the sea in a few kilometers (Strauch et al., 2017). Consequently, very lotic- (i.e. cascades, rapids) and lentic- (i.e. pools, shoals) habitats successively occur within several meters of river length. Finally, indigenous fish and crustacean species of insular streams are diadromous species, or estuarine species with a strong tolerance to salinity variations (Keith et al., 2006). Among the diadromous species, some are catadromous, adults reproduce in sea and their juvenile grow and mature in rivers, whereas others are amphidromous, adults reproduce in rivers, larvae grow in sea and juvenile return to rivers to grow and mature (McDowall, 1988). For all these species, connectivity between islands, and between different watersheds within an island, mainly occurs during the marine larval stage. Therefore, the occurrence of a species at a given location within a watershed first depends on its capacity to disperse and reach this watershed on an island, and secondly on the presence of suitable habitat conditions to settle in the newly colonized environment. Because of the marine larval phase, the colonization of river systems by juveniles necessarily starts from the estuary at each generation. As a result, the distribution of fish and crustacean species along the watersheds not only depends on local habitat conditions but also on the capacity of individuals to reach upstream sections. The active migration from the estuary thus represents a second dispersal step. This migration shapes the local distribution of species as a function of rivers morphology and individuals locomotor capacities (i.e. swimming, leaping, crawling …) that allow their upstream progression. Therefore, the structure of freshwater fish and crustacean assemblages in oceanic islands are expected to be controlled by successive dispersal- and niche-based processes taking place at the inter-island (i.e. regional), island (i.e. inter-watershed), and watershed scales. Finally, niche-based processes related to biotic and abiotic habitat conditions are probably the most influential drivers of these assemblages at the local scale (i.e. river site) in small tropical islands.

In small tropical islands, life traits of many fish and crustacean species, particularly their trophic position, are related to their dispersion capacity and habitat preferences. Indeed, spatial segregation of fish and crustacean species depending on their trophic levels have been observed within watersheds (Fitzsimons et al., 2002, Schoenfuss and Blob, 2007; Cooney and Kwak, 2013) as well as at the sites, or micro-habitats, scales (McRae et al., 2013; Donaldson et al., 2013). Generally, species of lower trophic level tend to be able to migrate higher upstream and to inhabit faster-flowing areas compared to predators. These capabilities probably evolved as predation avoidance strategies (Hein and Crowl, 2010; Diamond et al., 2016; 2019). Lower trophic level species, such as gobies or shrimps, tend to present better locomotor capacities compared to predators (Fitzsimons et al., 1997). They can resist faster flow conditions and/or climb-up more important barriers than most predator species (Blob et al., 2010; Hein and Crowl, 2010). These differences suggest that the relative contribution of niche- and dispersal-based processes may differ between trophic groups due to their different locomotor capacities. For example, the capacity of low trophic level species to climb-up waterfalls may enhance their dispersion capacities and, consequently, reduce the importance of dispersal-based process in structuring the communities observed locally.

In this context, the present study investigated the relative importance of niche- and dispersal-based processes for explaining the structure of freshwater fish and crustacean communities of two oceanic islands, Mayotte and Reunion, Indian Ocean. While the regional scale was examined qualitatively based on assemblage comparisons, an extensive dataset of 153 surveys in Mayotte and 266 in Reunion was analyzed to investigate processes shaping stream communities at the island, the watershed, and the site scales. More particularly, we hypothesized that:

(a) at the regional scale, the importance of dispersal-based process for explaining freshwater fish and crustacean species richness is promoted by extended distances between the islands;

(b) more locally, dispersal-based processes also greatly influence freshwater fish and crustacean communities because the colonization occurs from the river mouths at each generation;

(c) and the relative importance of dispersal- compared to niche-based processes is greater for predators compared to lower trophic groups in relation to their lower locomotor capacities.

2. METHODS

1. Study areas and field sampling

Mayotte and Reunion are two small tropical islands in the southwestern Indian Ocean (Figure 1a). Indigenous fishes and crustaceans communities inhabiting freshwaters are similar with approximately 20 species shared between the two islands (Keith et al., 2006). In Mayotte, Eberschweiler (1987) enumerated 27 permanent rivers joining the sea, their watershed areas ranging from two to 23 km². In Reunion, only 13 permanent rivers join the sea, their watershed areas ranging from 28 to 154 km² (Robert, 1986).

A total of 86 and 61 sites were sampled from 2004 to 2017 along the downstream-upstream gradient of the main rivers of Mayotte (Figure 1b) and Reunion (Figure 1c), respectively. In Mayotte, sampling was repeated between one and seven years at each site (Figure 1b). As a result, 161 surveys were conducted with 12 to 23 surveys each year from 2008 to 2012, in 2014, 2015 and 2017, six in 2013 and 40 in 2016. In Reunion sampling was performed from one to 12 different years at each site (Figure 1c) resulting in 366 surveys (i.e. 29 to 35 surveys each year from 2004 to 2014, four in 2015 and 22 in 2016).

Fish and crustaceans were sampled using a portable electro-shocker (Deka, 3000 or Hans Grassl, IG 200). The sampled river length was at least ten time the mean river width. The upstream and downstream limits of the sites were blocked by a net or a physical barrier (i.e. waterfall, weir …) to limit fish and crustacean emigration and immigration. To ensure sampling effectiveness and representativeness, two sampling procedures were applied depending on the river width (Olivier et al., 2004). When the river width was less than five meters, the whole area of the river site was prospected by fishermen moving upstream (i.e. complete sampling). When the river width was greater than five meters, the sampling was stratified by hydromorphic units (i.e. cascade, rapid, riffle, run, shoal and pool). In this case, the hydromorphic units were firstly identified based on mean water velocity and depth following Malavoi and Souchon (2002), and their surfaces were estimated using a laser meter (Leica DISTO D5). Then several sampling units ranging from 10 to 25 m² were distributed within each hydromorphic unit proportionally to its surface, ensuring that a minimum of 200 m² was sampled across the whole site. Finally, each sampling unit was prospected by moving upstream using the electro-shocker. For both sampling procedures, fish and crustacean were captured by a minimum of three operators equipped with hand nets (width 50 cm, maximum mesh size four mm) and positioned immediately downstream to the operator manipulating the electro-shocker.

2. Estimate of taxa abundances

Captured fish and crustaceans were identified at the species level using the identification keys provided by Keith et al. (2006) except individuals for which identification to the species level is doubtful: small-sized *Eleotris* and *Anguilla* spp., all specimens of the *Ambassis*, *Glossogobius*, *Kuhlia* and *Microphis* genus, as well as Carangidae and Mugilidae. Each taxon was assigned to one of three different trophic levels (i.e. primary consumers, omnivores and predators) based on published data (Table S1). For simplification purpose, herbivorous and saprophagous species were considered as primary consumers when insectivorous and piscivorous species were considered as predators.

The abundance of each taxon was estimated based on capture per effort units (CPUE, ind.m^{-2}) whatever the fishing procedures. For the complete sampling procedure, the abundance of one taxon was the number of individuals divided by the fished area (m^2). For the stratified sampling procedure, the abundance of each taxon was first calculated within each hydromorphic unit by averaging the number of individuals captured in each sampling unit divided by its area. Then, the abundance of one taxon in a sampling site was obtained by the mean of the abundance in all hydromorphic units weighted by their relative surface proportion in the river site. Non-natives species were not considered in the analyses as their abundance in a given site depends both on ecological process and on (re)stocking events.

3. Environmental descriptors

A total of 17 environmental variables describing the river sites from the island to the site scale were either recorded in the field or estimated based on GIS data (Table 1). Ten environmental factors reflecting local physicochemical conditions and habitat characteristics were measured during each survey. The local physicochemical conditions were the water temperature (°C), pH, conductivity (µS.cm^{-1}) and the dissolved oxygen (O_2, mg.l^{-1}) measured using a multi-parametric probe (YSI, Professional Plus). The local habitat conditions were described as the relative proportion of hydromorphic units in the site. Six environmental variables describing the location and accessibility of each site at the watershed scale were recorded. The GPS coordinates of river site were used to determine: the distance from the river mouth (km), the elevation (m) and the slope (%), i.e. the difference between the altitude of the lower and upper limits of the site divided by its length (m). Three descriptors were used to reflect the accessibility of each site from the estuary: the number, the maximum height (m) and the cumulative height (m) of migration barriers such as waterfalls, dams, weirs, etc. located downstream. The location and height of migration barriers were based on previous studies (DEAL, 2011, 2017) complemented by field observations. Finally, the length of the main river (km) within each watershed was estimated using GIS. All GIS analyses were made with the open source Qgis v.2.18.6 software (QGIS Development Team, 2017).

4. Data analyses

In order to identify redundant parameters, a correlation analysis of all environmental variables was performed based on the Kendal correlation coefficient (τ). When τ value between two or more parameters was greater than 0.70, only one parameter was included in the following analyses. The selected parameter was either the one providing the strongest effect on species abundances based on visual inspection of univariate plots, or the parameter that best summarized the others. The distance from the river mouth was correlated with elevation in Reunion ($\tau = 0.74$) and the number, the maximum height and the cumulative height of migration barriers were inter-correlated for the two islands ($\tau \geq 0.78$). The elevation was kept for the subsequent analyses as it showed a greater influence on species abundances variation than distance from the river mouth. The cumulative migration barriers height was also kept as it synthetizes the number of migration barriers and their maximum height. In addition, the water temperature and pH were removed from subsequent analysis as the water temperature is higher in Mayotte's rivers due to the proximity of the island to the equator and because pH values were missing in approximately 30% of the Reunionese dataset. Consequently, further analyses were performed on a total of 12 environmental variables: eight collected at the site scale (i.e. the percentages of cascades, rapids, riffles, runs, shoals and pools in the river site, along with conductivity and dissolved oxygen concentration), three representing the watershed scale (i.e. the site elevation and slope and the cumulative migration barriers height) and one, the main river length, representing the island scale.

In a first step, the habitat conditions were compared between the two islands using a between class PCA of environmental variables based on sites. This between class PCA was useful to limit the influence of the sites sampled several times compared to the sites sampled only once (Dolédec and Chessel, 1987). Then, the way environmental variables influence the structure of freshwater fish and crustacean communities was investigated using gradient forest analyses (GF, Ellis et al., 2012) for each island separately. GF is a multivariate analysis that comprises two main steps. The first one consists in modeling how the abundance of each taxon vary in response to environmental variables using random forest models (RF, Breiman, 2001). During a second step, the RF models obtained for each taxon are aggregated in order to calculate the overall importance of each environmental variable. The importance of environmental variables and the performance of RF for each species are thus ranked based on their aggregated goodness of fit values (pseudo-R^2). As GF analyses are based on RF models, GF inherits the main advantages of RF which are: to not depend on the normality or homoscedasticity of the data, to not require transformation of the data, and to integrate nonlinear responses (Pitcher et al., 2012). This latter advantage appeared particularly relevant in the context of our study as data preview revealed non-linear relationships between taxa abundances and several environmental variables. To limit the bias caused by rare species, GF analyses were performed on species occurring in more than 3.5% of the surveys only (Roubeix et al., 2017).

Finally, the changes in abundances of primary consumers, omnivores and predators along environmental gradients were modeled to describe how trophic groups shape fish and crustacean communities' structures in the two islands. In this purpose, RF models were adjusted with primary consumers, omnivores or predators' abundances as response variables, whereas the same environmental gradients as in GF analyses were used as explanatory variables. The importance of each variable was assessed based on the node purity index (Banerjee et al., 2019). For each variable, the significance of the node purity index was estimated by comparing the predicted values to a null distribution obtained with 1000 random permutations of the values. A significant decrease of the node purity index is interpreted as an information gain associated with the variable compared to the null distribution (Archer, 2016).

Statistical analyses were performed with the open source R v.3.3.1 software (R Development Core Team, 2016) implemented with the packages *ade4* (Dray and Dufour, 2007) for PCA analyses, *gradientForest* (Ellis et al., 2012) for GF analyses, *randomForest* (Liaw and Wiener, 2002) and *rfPermute* (Archer, 2016) for RF analyses.

3. RESULTS

1. Environmental dissimilarities between islands

Due to missing data, the between-sites PCA was performed on 12 environmental variables and 153 surveys in Mayotte and 262 in Reunion (Figure 2). Globally, the sites of Mayotte and Reunion were well discriminated along the first PCA axis, and only slightly along the second and the third axis, which represented 34%, 18% and 12% of the total inertia, respectively. The first axis of the PCA was mainly associated with the conductivity, the percentage of shoals and the main river length (Figure 2a-b). The second axis of the PCA was mainly related to the slope of the sites and their elevation (Figure 2a), whereas the third axis was chiefly related to the cumulative height of migration barriers located downstream to the site (Figure 2b).

In Mayotte, the sites were characterized by higher proportions of shoals (i.e. lentic and shallow hydromorphic units), higher conductivity, and lower dissolved oxygen compared to Reunionese sites (Table 1). Within each watershed, the sites sampled in Mayotte were generally located at a lower elevation with a lower cumulative height of the downstream barriers compared to Reunionese sites. Finally, in Mayotte the main river lengths were shorter.

2. Fish and crustacean communities

A total of 39 indigenous fish and crustacean taxa were captured in Mayotte (Figure 3a), among them 26 (67% of the total) were diadromous and 13 (33%) were marine and estuarine (Table S1). Thirteen taxa were observed in less than 3.5% of the surveys (Figure 3a) and were thus excluded from the following analyses. In Reunion, all the 21 taxa captured (100%) were diadromous (Figure 3b, Table S1). All these taxa were present in more than 3.5% of the surveys (Figure 3b). The most abundant fish and crustacean species in Mayotte were *Anguilla marmorata* and *Eleotris klunzingerii*, *Caridina longirostris* and *C. typus*, respectively (Figure 3c) while in Reunion they were *Sicyopterus lagocephalus* and *Cotylopus acutipinnis*, *Atyoida serrata* and *Macrobrachium australe*, respectively (Figure 3d).

3. Importance of environmental variables

The response of the taxa abundances to 12 environmental variables was modelled using two separate GF: one for 26 taxa in Mayotte, and one for 21 taxa in Reunion. A total of 153 surveys in Mayotte, and 262 in Reunion, were included in these analyses due to missing data. The average R^2 was 0.19 in Mayotte and 0.28 in Reunion which means that the variance in species abundances was moderately explained by environmental variables in both islands (Roubeix et al., 2017). The four taxa for which the total deviance was best explained by GF were *Ophieleotris* cf. *aporos*, *A. marmorata*, *Glossogobius* spp. and *Eleotris mauritiana* in Mayotte (Figure 4a), *E. klunzingerii*, *A. marmorata*, *M. australe* and *C. acutipinnis* in Reunion (Figure 4b). In both islands, freshwater fish and crustacean communities were mostly structured along the elevation and slope gradients (Figure 5a-b), which represent the watershed scale. However, in Mayotte the relative importance of slope for structuring freshwater fish and crustacean communities was much lower than the relative importance of the elevation (Figure 5a).

4. Response of primary consumers, omnivores and predators

The RF describing the response of primary consumers and omnivores to environmental gradients explained only 6% and 1% of the variance of primary consumers and omnivores abundance in Mayotte versus 42%

and 43 % in Reunion, respectively. The RF describing the response of predators to environmental gradients were well adjusted for both islands with 51% of the variance of predators' abundance explained in Mayotte and 64% in Reunion. In Mayotte, the abundances of primary consumers and omnivores were not significantly associated with all the explanatory variables (Table S2, Figure 6a-c-e-g, $P \geq 0.05$). By contrast, the abundances of primary consumer and omnivores were significantly explained by the elevation, the slope, the cumulative migration barriers height and the main river length in the watershed in Reunion (Table S2, $P \leq 0.02$). More precisely, the abundance of primary consumers decreased when elevation and slope increased (Figure 6b-d). The peak observed for a slope of approx. 3% is probably an artefact related to the high abundances recorded in one single site with a 3% slope but sampled during 11 different years. The elevated abundance of primary consumers at this site can be explained by the presence of an intermittent river section immediately upstream. Consequently, when the section becomes dry, migrating juveniles are blocked and their abundance at the sampling site increases. The abundance of omnivores globally decreases when elevation and slope increased (Figure 6f-h). The abundance of predators was significantly related to the elevation of the site, its slope, the cumulative migration barriers height downstream to the site and the length of the main river of the watershed in Mayotte and Reunion (Table S2, $P \leq 0.01$). In both islands, predators' abundance decreased when elevation and slope increased (Figure 6i-j-k-l).

4. DISCUSSION

1. Taxa richness in Mayotte and Reunion

At a regional scale, species richness is generally structured by dispersal-based process limiting the connectivity between habitat patches (Henriques et al., 2017). The effects of dispersal-based processes are expected to be more important in the context of small oceanic islands where freshwater habitats consist in discrete patches, distant from each other. However, although dispersal-based processes are supposed to be dominant, our findings suggest that the difference of fish and crustacean taxonomic richness between Mayotte (39 taxa) and Reunion (21 taxa) likely results from a combination of both dispersal- and niche-based processes. Indeed, the difference in diadromous fish and crustacean richness between the two islands appeared primarily explained by dispersal limitation, whereas changes in marine and estuarine taxa are probably more related to niche-based process.

Diadromous taxa correspond to 67% of the total in Mayotte, and 100% in Reunion, indicating they play a crucial role for structuring the fish and crustacean communities of these islands. The higher taxonomic richness of diadromous taxa recorded in Mayotte can be explained by the proximity to Madagascar and the African continent (300 km compared to 700 km for Reunion). Indeed, due to the general oceanic circulation and distances between sites, the pelagic stage of fish larvae should connect more easily between Mayotte and Madagascar, or east Africa, than between the later localities and Reunion (Crochelet et al., 2016). This hypothesis is supported by the presence of several diadromous species observed in Mayotte during our study such as *Redigobius bikolakus*, *Hypseleotris cyprinoides* and *Ophiocara porocephala* which are also present in Madagascar (Fricke et al., 2018) or *R. bikolakus* present in South Africa (Whitfield, 1994). All these species are not present in Reunion.

In contrast, dispersal-based processes at the regional scale appeared less important for explaining that 13 marine and estuarine taxa were observed in Mayotte but not in Reunion. This difference in the number of marine and estuarine taxa can be explained by the higher proportion of sites with low elevation (i.e. between 0 and 5 meters a.s.l), and the higher amplitude of tides, in Mayotte compared to Reunion. High tide amplitude probably allows marine and estuarine taxa to progress inland more easily and to reach the downstream sites surveyed in this study. Indeed, numerous marine and estuarine taxa recorded in Mayotte downstream sites, such as *Megalops cyprinoides*, *Kuhlia caudavittata*, *Lutjanus argentimaculatus* and *Ambassis* spp., are also frequently observed in coastal waters of Reunion (Fricke et al., 2009). These species do occur at proximity to the Reunionese rivers but their absence in downstream riverine habitats is probably related to the lack of suitable local environmental conditions, particularly the low proportion of lentic areas. The absence of marine and estuarine taxa in downstream Reunionese sites is thus better explained by niche-based processes. However, these comparisons of taxonomic richness between the two islands should be considered carefully. Indeed, the taxonomic status of many of these species are still discussed and may be reevaluated in the future. For example, using molecular analyses of COI gene, Mennesson and Keith (2017) demonstrated that *Eleotris fusca* was not a unique species distributed in the Indo-Pacific area, but a complex of two species: one, *E. fusca*, being restricted to the Pacific Ocean, the other one, *E. klunzingerii*, observed in the Indian Ocean only.

2. Process structuring freshwater communities from island to site scales

From the island to the site scales, the distance separating distinct habitat patches is usually not greater than a few kilometers. In such a situation, the relative importance of dispersal-based process is expected to be reduced in favor to niche-based process (Henriques et al., 2017). However, this hypothesis was not fully supported for freshwater fish and crustacean communities in Mayotte and Reunion. Indeed, our results suggested that freshwater communities are primarily influenced by factors associated with dispersal-based process at the watershed scale. Despite obvious differences in environmental conditions between the two islands, the communities are mainly structured by the same abiotic variables, i.e. the elevation and the slope of the site. This pattern was similar in both islands although rivers in Mayotte are shorter with more lentic habitats compared to those in Reunion. The elevation of a site and, to a lesser extent its slope, are two variables reflecting its position within a watershed. These abiotic variables are thus closely related to dispersal constraints that may limit accessibility to upper river sites for the juveniles of most species. Accordingly, individuals, and thus species, with lesser locomotor abilities are not able to cross the river sites presenting strong water velocities, and/or the most downstream migration barriers. The sites featured by high water velocities are associated with steep hydromorphic units (i.e. rapid, cascade) which occur more frequently when the slope of the river increases (Malavoi and Souchon, 2002). Therefore, the more upstream is a site, the more likely individuals observed there have been obliged to cross physical barriers when migrating from the river mouth.

3. Functional groups contribution to communities' structure

Taxa intrinsic characteristics, such as their trophic position or maximal body size, are known to influence communities as they relate to their dispersal capacities and/or habitat preferences (Soininen, 2010). This hypothesis was supported by our results as the effects of elevation and slope on the variation of predatory species abundances were highly significant and RF models explained more than 50% of the deviance in both islands. By contrast, primary consumers and omnivores abundances responded moderately to these gradients in Reunion (approx. 40% of the deviance explained by RF model) and did not respond significantly to the same gradients in Mayotte (less than 6% of the deviance explained by RF model). Such differences can be explained by the limited locomotor, and thus dispersal, capacities of predators compared to primary consumers and omnivores (Cooney and Kwak, 2013). For example, the eleotrids, which are among the most abundant predatory species in the studied rivers, present poor swimming performances. Fitzsimons et al. (1997) demonstrated experimentally that the Hawaiian *Eleotris sandwicensis* could not resist to flows greater than 20 $cm.s^{-1}$. By contrast, sympatric species of the primary consumer Sicydiinae gobies can resist to velocities as elevated as 100 $cm.s^{-1}$ (Fitzsimons et al., 1997) using their pelvic sucker to attach the substrate (Maie et al., 2012). The strong locomotor capacities of Sicydiinae allows them to pass migration barriers tens of meters high, or areas of very high water velocities (Schoenfuss et al., 2013). Similar observations were made by Fièvet (1999) in Guadeloupe concerning two Atyidae species, *Xiphocaris elongata* and *Atya innocus* and one Palaemonidae, *Macrobrachium faustinum*, and by Schoenfuss and Blob (2003) in Hawaii concerning *Awaous guamensis.* The strong locomotor capacities of Sicydiinae, Atyidae, Palaemonidae and *Awaous* spp., which are the more abundant species of primary consumers and omnivores in Mayotte and Reunion, can probably explain the lower variation of abundance of these trophic groups along environmental gradients.

To definitely conclude on the relative importance of dispersal- and niche-based processes for shaping freshwater communities of small tropical islands, accurate descriptions of habitat preferences of each fish and crustacean species are required. Even if dispersal-based processes appeared preponderant in structuring predators along environmental gradients, it could also be possible that some individuals reach upstream sites but cannot settle there because suitable habitats are lacking. Indeed, micro-habitat preferences of predatory species are still largely unknown in small tropical islands. For primary consumers and omnivores, previous studies demonstrated that micro-habitat conditions (e.g. water depth or flow velocity) have a limited importance for explaining the repartition of Sicydiinae, Atyidae and Palaemonidae (Girard et al., 2014; Teichert et al., 2014). Our results are consistent with these findings as primary consumer and omnivores communities did not appear significantly structured by site environmental variables (i.e. temperature, conductivity, percentage of hydromorphic units…). However, a stronger variation of abundance of these two trophic groups along elevation and slope gradients would have been expected if dispersal-based process shapes their distribution. Indeed, inter-individual difference in locomotor performances can limit species abundances in upstream sites with only the most performant individuals being able to reach these sites (Lagarde et al. 2018, 2020). In this context, other environmental factors such as the availability of food resources (Julius et al., 2005), prey/predators or competitive interactions (Monti and Legendre, 2009), can be more essential for shaping primary consumers and omnivores communities. If this hypothesis is true, the structure of these communities could differ between the two islands. Further studies are required to disentangle the effect of food availability, prey/predator and competitive interactions on primary consumers and omnivores abundances, and definitely conclude on the relative importance of dispersal- and niche-based processes in structuring these functional groups.

TABLES

Table 1: Median and range of values for the environmental variables recorded in Mayotte and Reunion islands at the scale of sampling sites, watersheds and islands. With N: number of sampling sites and surveys (in bracket) for which the information was available. The geographic scale at which environmental variables were compared is specified in the last column.

Environmental variable	Abbreviation	Mayotte			Reunion			Study scale
		N	Median	Range	N	Median	Range	
Percentage of cascades	% cascade	86 (155)	0	0-44.5	61 (365)	7.3	0-84.0	Site
Percentage of rapids	% rapid	86 (155)	0	0-54.5	61 (365)	10.2	0-75.4	
Percentage of riffles	% riffle	86 (155)	33.1	0-100	61 (365)	22.5	0-100	
Percentage of runs	% run	86 (155)	0	0-100	61 (365)	23.3	0-83.5	
Percentage of shoals	% shoal	86 (155)	50.7	0-100	61 (365)	9.7	0-94.7	
Percentage of pools	% pool	86 (155)	0	0-68.8	61 (365)	7.7	0-85.0	
Temperature (°C)	-	86 (161)	24.3	20-30.7	61 (328)	19.0	13.6-29.5	
pH	-	79 (153)	7.7	5.9-9.6	61 (261)	7.9	6.0-10.0	
Conductivity ($\mu S.cm^{-1}$)	conductivity	85 (160)	231.0	85.0-1199	60 (355)	113.1	25.0-696	
O_2 ($mg.l^{-1}$)	O_2	86 (161)	7.3	1.0-12.6	59 (267)	9.0	3-12	
Elevation (m)	elevation	86 (161)	47.1	2-220	61 (366)	225.0	5-890	Watershed
Distance from river mouth (km)	-	86 (161)	2.2	0.1-13.9	61 (366)	9.4	0.1-30,5	
Slope (%)	slope	86 (161)	3.1	0.4-16	61 (366)	2.7	0.2-13.1	
Number of migration barriers	-	86 (161)	1.0	0-9	61 (366)	2.0	0-11	
Migration barriers maximum height (m)	-	86 (161)	0.8	0-27	61 (366)	5.0	0-200	
Migration barriers cumulative height (m)	barrier H	86 (161)	1.5	0-29	61 (366)	6.3	0-332	
Main river length (km)	river L	86 (161)	6.7	2.4-19.7	61 (366)	31.0	14.0-35.0	Island

FIGURES

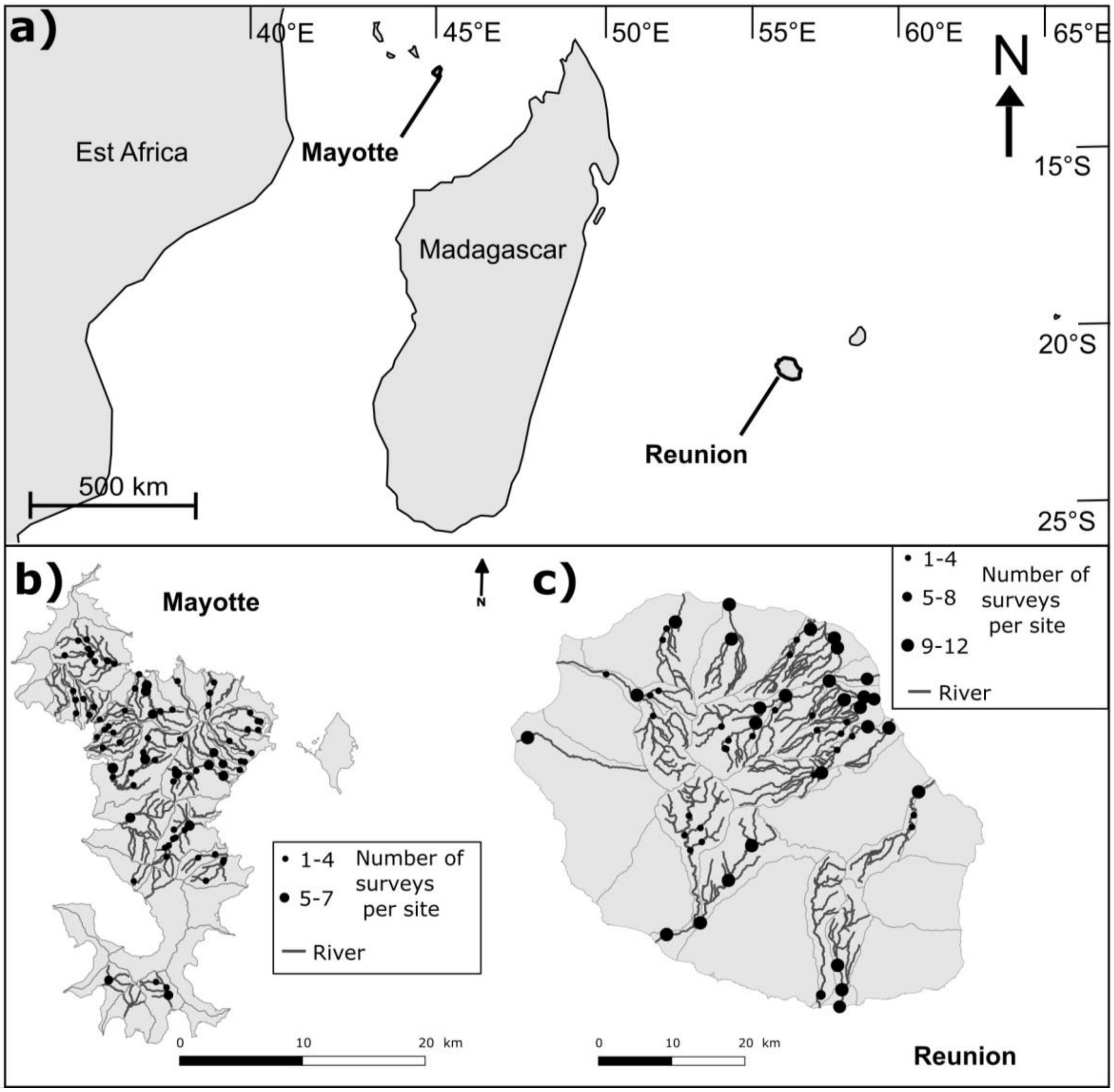

Figure 1: Localization of Mayotte and Reunion islands in the southwestern Indian Ocean (**a**), and of the sampling sites within the watersheds in Mayotte (**b**) and Reunion islands (**c**). The number of surveys is indicated for each site.

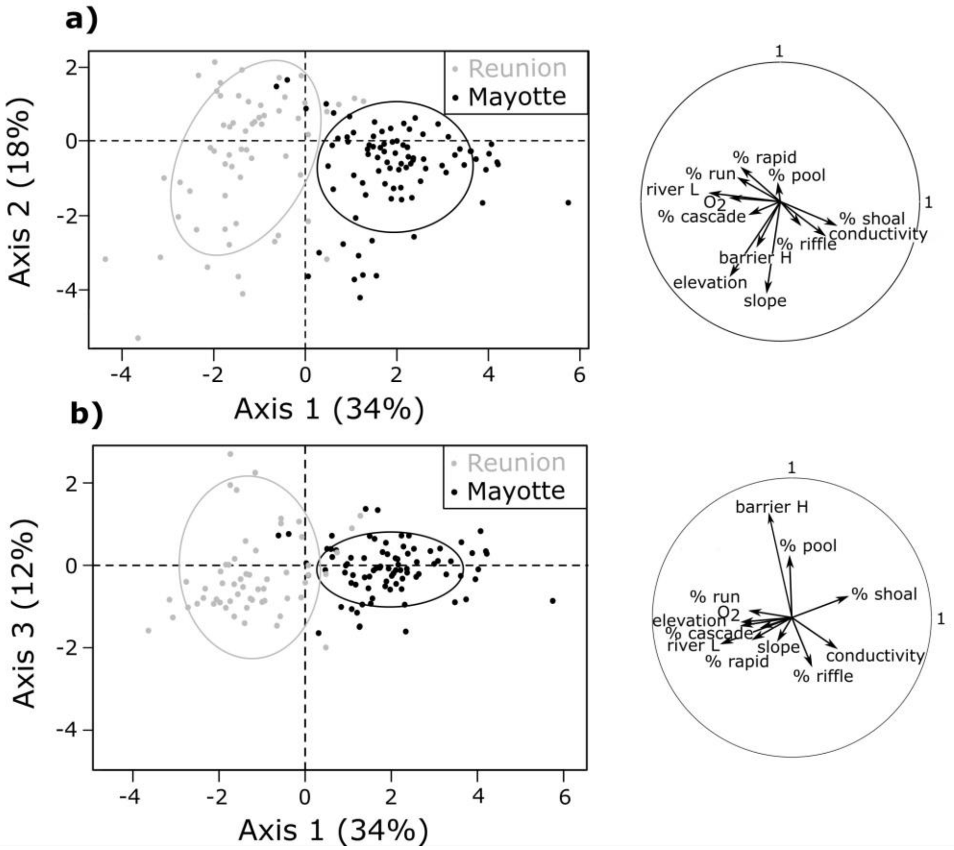

Figure 2: First two factorial plans (**a, b**) of a between sites PCA describing environmental factors recorded at each site in Mayotte (black) and Reunion (grey) islands with 90% confidence ellipses. The contribution of environmental factors is presented by the correlations circles. See table 1 for the complete name of the abbreviated environmental factors.

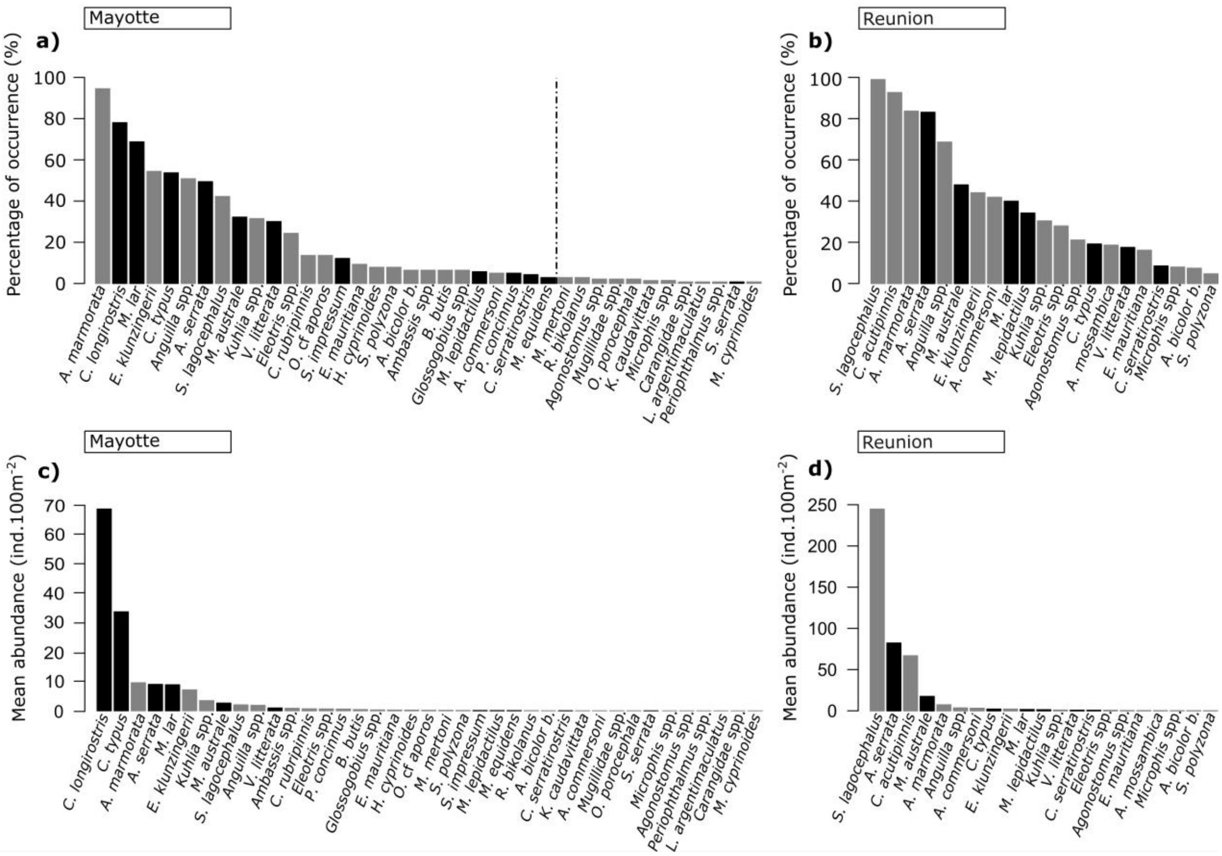

Figure 3: Percentage of occurrence (**a**, **b**) and mean abundance (**c**, **d**) of freshwater indigenous fish (grey bars) and crustacean (black bars) taxa captured in all sites in Mayotte (**a**, **c**) and Reunion (**b**, **d**) islands. The dash line delimits species for which the percentage of presence is lower than 3.5%. See table S1 for the complete name of the taxa and their systematic position.

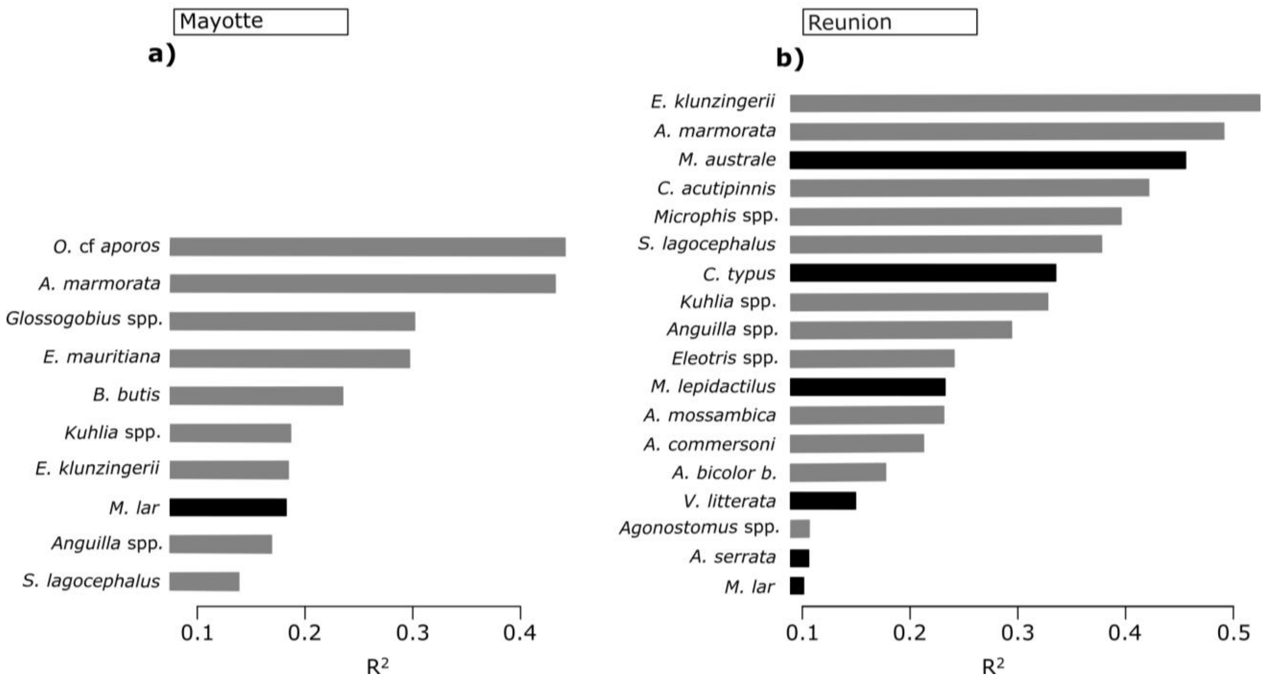

Figure 4: Ranking of fish and crustacean taxa structuring communities based of the pseudo R^2 values for Mayotte (**a**) and Reunion (**b**) islands. Only taxa for which the R^2 value was superior to 0.1 are represented. The grey bars represent fish taxa when the black bars represent crustacean taxa. For the complete name of the taxa refer to table S1.

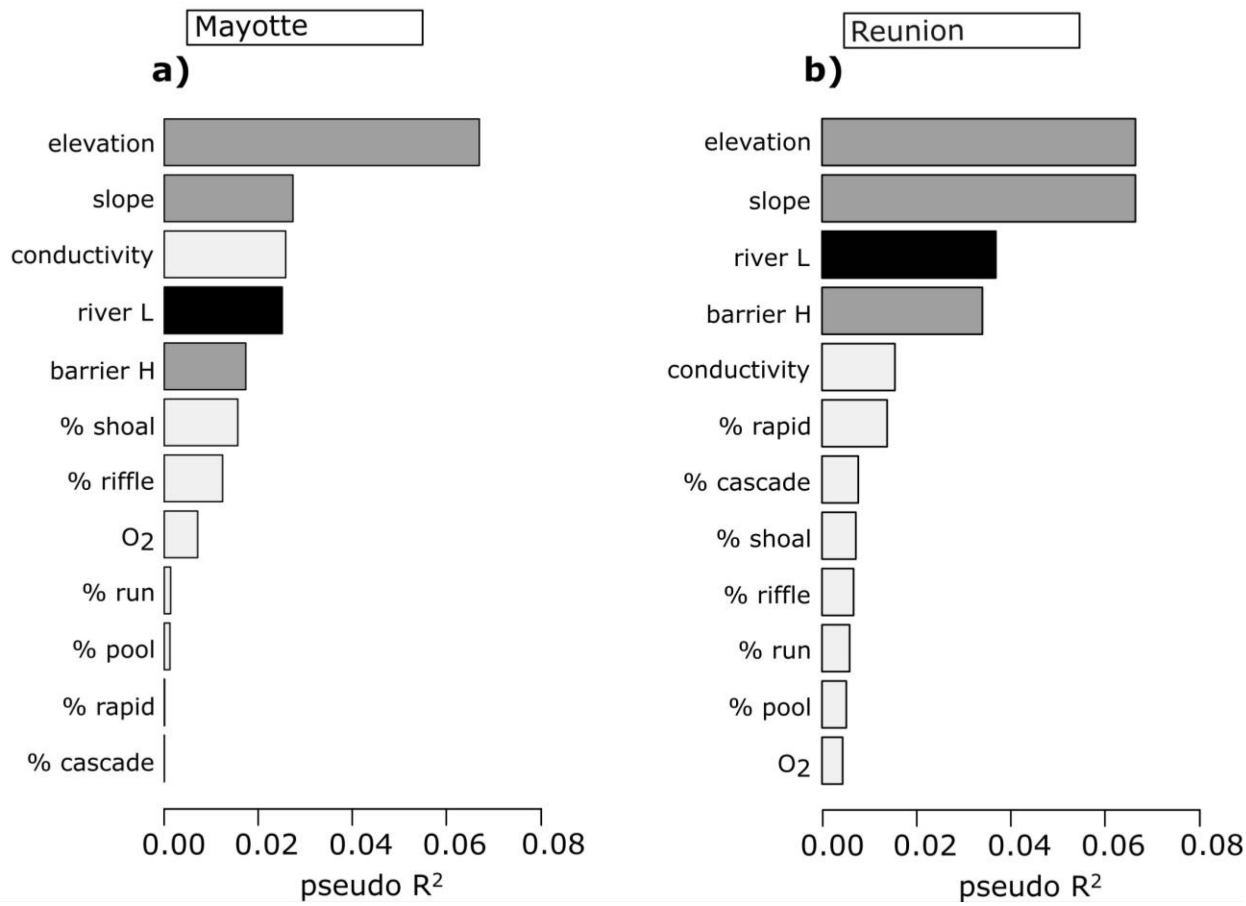

Figure 5: Ranking of environmental variables structuring fish and crustacean communities based of the pseudo R^2 values of gradient forest analyses performed separately for Mayotte (**a**) and Reunion (**b**) islands. The light grey bars correspond to variables considered at the site scale, grey bars to variables considered at the watershed scale, and black bars to variables considered at the island scale. See table 1 for the complete name of the abbreviated environmental factors.

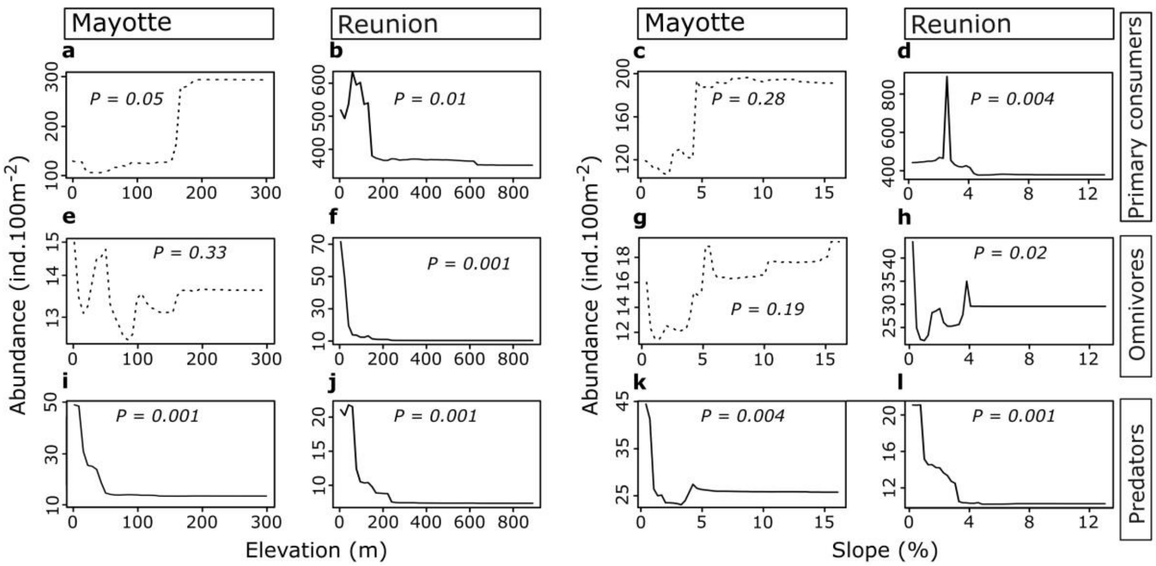

Figure 6: Partial response plots of primary consumers (**a** to **d**) omnivores (**e** to **h**) and predators (**i** to **l**) taxa abundances along elevation (**a-b-e-f-i-j**) and slope (**c-d-g-h-k-l**) gradients in Mayotte and Reunion islands based on random forest analyses. The p-value associated with each response was evaluated with the node purity index. Full lines represent significant responses (P<0.05) when dashed lines represent non-significant responses ($P \geq 0.05$).

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Data availability statement

Survey data cannot be made public for legal reasons but they are available upon request from the authors and data producers

Authors contribution statement

RL, NT, PV and DP conceived and designed the study. PV, RL and NT performed the field work. RL, NT and DP analyzed the data. RL wrote the manuscript; other authors provided editorial advice

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical guidelines

All applicable regional and/or national guidelines for the care and use of animals were followed

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