Resource partitioning and functional diversity of worldwide freshwater fish communities

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Abstract. Despite significant progress in recent years, understanding the rules governing the assembly of natural communities is still challenging and knowledge of how the integration of nonnative species may disrupt community structure and function is needed. To address this challenge, we collated stable isotope data for 159 freshwater fish communities around the world with and without nonnative species and quantified spatial variation in both community isotopic functional diversity and intraspecific variation in species niches. Using a null model and partial least squares path analysis, we then evaluated how the interplay between abiotic (historical, energetic, climatic, habitat size) and biotic (niche segregation) factors shape community structure and functional diversity, and how these relationships have changed, and with what consequences, in the presence of nonnative species. We found that niche partitioning is a primary force underlying the structure and functional redundancy of native fish communities, which may be governed by a synergism between contemporary climate, productivity and habitat size. We also found evidence of a legacy of historical climate on functional diversity, independent from species richness. By contrast, path models of communities containing nonnative species demonstrated lower explanatory power and had no clear association with any of the abiotic or biotic factors. In conclusion, we demonstrated that strong spatial patterns in community structure and functional diversity of freshwater fish communities exist at the global scale, underlined by the complex interplay between external and internal filters, but that these patterns may be blurred by anthropogenic species introductions. Our results further highlighted the importance of accounting for realized species niches and species status (i.e., native and nonnative) when investigating questions related to the assembly and functional diversity of multitrophic communities.

Key words: biotic interactions; community structure; environmental filtering; functional redundancy; lakes; niche differentiation; processes of coexistence; realized niche; resource use plasticity; stable isotopes.

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INTRODUCTION

Environmental conditions, species interactions, and historical processes have been widely recognized to simultaneously influence the taxonomic and functional structure of communities, but their relative contribution in shaping the observed patterns of biodiversity is still largely unresolved (Cavender-Bares et al. 2009, Swenson 2013). This is particularly true for present-day communities in which continued introductions of nonnative species may be trumping natural
drivers of biodiversity patterns and overriding long-evolved networks of biotic interactions (Gotelli and Arnett 2000, Leprieur et al. 2008, Olden et al. 2008). Species introductions may reshuffle the number, abundance, and functional characteristics of species within local communities, by causing declines or extirpations of native populations and by adding new and/or redundant functional traits (Olden et al. 2004, Leprieur et al. 2009, Matsuzaki et al. 2013, Azzurro et al. 2014). In turn, interactions between coexisting species may cause rapid and drastic changes in community organization and functional diversity, even if the number of species remains unchanged (Gotelli and Arnett 2000, Sanders et al. 2003, Sagois et al. 2015). Additional research is therefore needed to more clearly elucidate the rules governing the assembly of natural communities and understand how the integration of nonnative species may disrupt community structure and functional biogeography (Hobbs et al. 2006, Sax et al. 2007).

The concept of environmental filtering posits that local abiotic conditions selects for species according to their environmental tolerances, thus limiting the number and functional attributes of species in a community (e.g., “physiological tolerance” hypothesis; Currie et al. 2004, “digestive constraint” hypothesis; González-Bergerzonzi et al. 2012). Similarly, evidence suggests that Quaternary climatic changes have induced taxonomic and functional legacies in regional species pool through differential processes of speciation, extinction, and dispersal (“historical climate stability” hypotheses; Araújo et al. 2008, Ordonez and Svenning 2015). By contrast, the principles of competitive exclusion and limiting similarity are expected to favor the coexistence of functionally dissimilar species by promoting the exploitation of different resources (“niche partitioning” hypothesis; Pianka 1974, Schoener 1974, Mason et al. 2008). However, previous investigations have demonstrated that the environmental context, such as microhabitat heterogeneity or resource availability, can greatly influence the partitioning of resources among species (Chesson 2000, Mouquet et al. 2002). Taken together, the functional diversity of communities is expected to result from a hierarchical process whereby external abiotic filters first sort species from a regional species pool and internal biotic filters (themselves influenced by abiotic factors) then regulate species coexistence within local communities through intraspecific niche differentiation (Farias and Jaksic 2009, Violle et al. 2012).

Trait-based approaches have been increasingly used to explore the potential mechanisms responsible for structuring functional diversity at both local and global scales (Mouillot et al. 2007, Swenson 2013, Violle et al. 2014). Empirical evidence points to both functional clustering (co-occurrence of functionally similar species) and overdispersion (co-occurrence of functionally dissimilar species), but the role of intraspecific niche variability in controlling the coexistence of species is still under-appreciated (Jung et al. 2010, Violle et al. 2012). This is partly because of the challenges associated with measuring the realized ecological niche of species in a community and the partitioning of niche space among species. Indeed, most studies measuring community functional space do so according to mean and fixed trait values of species to infer resource use and potential competition, thus disregarding inter- and intra-population niche variability. However, although an association between species traits similarity and resource overlap in animal communities is intuitively appealing, it does not capture the inherent, and often considerable, plasticity in animal resource exploitation (Albouy et al. 2011, Zhao et al. 2014). Stable isotope ratios, by integrating dietary history and providing an estimate of realized trophic interactions (Bearhop et al. 2004, Newsome et al. 2007), represent an appealing alternative to indirect measures of species niches based on ecomorphological traits (e.g., Villéger et al. 2008, Azzurro et al. 2014). Furthermore, stable isotope analyses provide insight into complementarity aspects of species realized niches (i.e., the origin of the carbon used by consumers and their trophic position within the food chain) and therefore relate isotopic niche space to the n-dimensional niche concept (Layman et al. 2012, Cucherousset and Villéger 2015, Rigolet et al. 2015). While patterns in resource use are likely captured by isotopic niches, isotopic overlap does not necessarily indicate the sole existence of direct interactions between organisms, as isotope values do not provide information regarding species feeding behavior and microhabitat use. Nonetheless, understanding the macro-ecological patterns...
in isotopic community structure may provide a promising way to bring new insights on how local species interactions contribute to community assembly and functional diversity.

Here, we quantify the relative importance of both external abiotic factors and internal biotic-mediated filters in structuring freshwater fish communities and patterns of isotopic functional diversity across the globe, and evaluate the role of nonnative species in altering these relationships. We collated data from a comprehensive review of stable isotope studies spanning a large gradient in species richness and environments to quantify both the isotopic functional diversity and the level of intraspecific variation in realized niches of freshwater fish communities with and without nonnative species. We first assessed patterns of functional redundancy across communities, and then evaluated how the interplay between abiotic (i.e., historical, energetic, climatic, habitat size) and biotic (i.e., niche segregation) factors shape community structure and functional diversity. Next, we explored how the putative mechanisms identified above may change in the presence of nonnative species.

**Methods**

**Data sources**

*Stable isotopes.*—A database quantifying the isotopic structure of freshwater fish communities using nitrogen ($\delta^{15}$N) and carbon ($\delta^{13}$C) stable isotopes was compiled from both peer-reviewed and gray literature. We focused exclusively on standing (lentic) water ecosystems to take advantage of the relative isolation of lacustrine ecosystems (i.e., lakes, reservoirs, and ponds) compared to flowing (lotic) water ecosystems. Studies were included only if the entire fish community was examined (species richness ranged from 4 to 40), excluding data from experimental manipulations. From this database, we extracted quantitative information on both mean stable isotope values (i.e., niche position) and their standard deviation (i.e., intraspecific niche variability) for each species in each community. Species were further classified as native or nonnative according to their known indigenous range on a country or state basis based on FishBase (Froese and Pauly 2015) and the USGS Nonindigenous Aquatic Species database (http://nas.er.usgs.gov) (see Sagouis et al. 2015 for details). The final database included 159 independent freshwater fish communities, among which half ($n = 80$) contained at least one nonnative species contributing between 6% and 100% of the total species richness (Fig. 1; Appendix S1: Table S1). Communities were located across six continents and a broad diversity of environmental conditions. The average human footprint index (1 km grid; LWP-2, 2005) calculated for each hydrographic basin did not differ significantly ($t$-test, $P = 0.63$) between communities with ($24.67 \pm 16.84$ SD) and without ($25.82 \pm 16.84$ SD) nonnative species.
Environmental descriptors.—We quantified a set of environmental variables expected to influence freshwater fish communities and patterns of isotopic functional diversity at the global scale. Based on previous research on macro-ecological patterns of freshwater fish taxonomic and functional diversity (Mason et al. 2008, Oberdorff et al. 2011, Schleuter et al. 2012), we tested three hypotheses related to: (1) climate history, (2) environmental filtering, and (3) niche partitioning (see Appendix S2: Table S1 for details about the hypotheses). To this end, we considered historical, energetic, climatic, and habitat size variables. Remotely sensed data were extracted from existing environmental layers in a Geographic Information System based on the geographical coordinates of each fish community, which were either reported in the original publications or determined using locality names. Historical factors were calculated as the climatic conditions during the last glacial maximum (CCSM3; Collins et al. 2006) minus the contemporary climatic conditions (Worldclim; Hijmans et al. 2005): quaternary anomalies in mean annual air temperature, maximum temperature of the warmest month and minimum temperature of the coldest month. Contemporary climate was characterized by the aforementioned temperature variables and also included temperature stability (Worldclim; Hijmans et al. 2005). Productivity estimates in lakes are not available at the macroecological scale but patterns of ecosystem productivity in terrestrial and aquatic ecosystems are likely to covary (Shurin et al. 2006). Consequently, energy availability was estimated using net terrestrial primary productivity (NPP; Imhoff et al. 2004) that was calculated using a buffer of 10 km around the sites to account for potentially diverse resource inputs from the drainage network. Habitat size was measured as lake surface area (km²; from original publications or other sources).

Quantification of community structure and functional diversity

For each community, we characterized: (1) species richness, representing the number of locally interacting species, (2) isotopic functional diversity, representing the amount of functional niche space occupied by all co-occurring species, and (3) the degree of niche segregation, representing within-community intraspecific niche variability. Isotopic functional diversity and the degree of niche segregation were calculated within the bi-dimensional δ¹³C and δ¹⁵N isotopic space characterizing the range of resources used and the number of trophic levels within a community respectively (Layman et al. 2012). Isotopic functional diversity therefore encompasses information on the structure of communities, the realized interactions among species and the transfers of energy within communities, whereas the degree of niche segregation is integrative of the extent of overlap in realized niche and resource partitioning across species. To account for potential spatial or temporal variability in the isotopic composition of baselines across food web, all species isotopic values were standardized according to their community centroid following Schmidt et al. (2011).

At the community level, isotopic functional diversity was then calculated using the standard ellipse area (SEAc) based on population mean isotopic values that unlike the convex hull methods, is less sensitive to outliers (Jackson et al. 2011). At the species level, intraspecific niche variability was first quantified for each species within each community from the SEAc using intraspecific population variability along the two isotopic axes. This represents a powerful approach as it relies on measures of standard deviation from the species centroid in two-dimensional isotopic space, a formulation that is faithful to the concept of ecological niches (Bearhop et al. 2004, Newsome et al. 2007). As stable isotope values of individual fish sampled in the community were rarely reported, we used the sample variance as an unbiased estimate of the population variance along the two isotope axes. Population isotopic niches were drawn using a Monte Carlo simulation comprising 1000 random draws for each species of a given community according to two normal distributions based on the sample mean and standard deviation of δ¹³C and δ¹⁵N, and propagating an error of 10⁻³. As the realized functional niche of a species is inherently community-dependent as it can include only the range of resources available in a given community, the degree of niche segregation was calculated as the ratio between each population SEAc and the total community SEAc and averaged across species (i.e., mean value per community). Hence, this ratio quantifies the strength
of ecological interactions and local processes on species coexistence, such as micro-environmental heterogeneity or competition, with values of zero indicating complete niche segregation with non-overlapping niches (Pianka 1974, Violle et al. 2012).

Statistical analyses

Testing for redundancy.—In each community, potential redundancy was estimated using a null model approach that simulates randomly assembled communities (Mouchet et al. 2010). In each case, null distributions were generated by randomly sampling 1000 times the same number of species from a global species pool defined by all species without distinction between native and nonnative species and recalculating the metrics each time. Standardized effect sizes (SES) were then calculated for each community by subtracting the mean of the null distribution from the observed value and dividing by the standard deviation of the null distribution. SESs thus quantified community functional redundancy relative to the global species pool independently from any sampling effect due to species richness. Positive isotopic functional diversity SES values were considered overdispersed, exhibiting higher diversity than expected by random assembly as a consequence of limiting similarity, and negative SES values were considered underdispersed, exhibiting lower diversity than expected under random assembly as a consequence of environmental filtering (Mouillot et al. 2007). Similarly, negative niche segregation SES values indicated that species niches were more complementary than expected by chance, while positive SES values indicated that species niches were more aggregated and thus more redundant with one another than expected by chance.

To assess the potential influence of nonnative species on community functional redundancy, we related the SESs for the degree of niche segregation and isotopic functional diversity to species richness using a linear model including a pairwise interaction with nonnative species presence.

Determinants of community structure and functional diversity.—We used partial least squares path modeling, a robust form of structural equation modeling, to examine the relative importance of external and internal factors to predict the structure and functional diversity of freshwater fish communities (Esposito-Vinzi et al. 2010). Path analysis seeks to elucidate the causal processes underlying the observed relationships and estimates the relative importance of alternative paths of influence. Specifically, we tested the (1) direct effects of abiotic factors on niche segregation, (2) direct effects of abiotic factors on species richness and isotopic functional diversity, (3) direct effects between niche segregation, species richness and isotopic functional diversity.

To limit model complexity while simultaneously gaining a better understanding of the underlying drivers of functional diversity, we grouped correlated abiotic variables into latent variables (historical factors, contemporary climate, energy availability, and habitat size) according to the hypothesized causal mechanisms (see Appendix S2 for details on model construction). Through an iterative procedure, the algorithm calculates the path coefficients (i.e., standardized beta coefficients between variables in the structural model) and their significance via bootstrapping. Non-significant paths were then dropped until the goodness of fit decreased (GOF) to obtain the most parsimonious model (see Appendix S2: Tables S2–S5 for details on model evaluation). Lastly, to test whether the inferred causal mechanisms were affected by species introduction, potential differences in the strength and direction of the path coefficients between communities with and without nonnative species were assessed using bootstrap t-tests (Chin 2003).

All statistical analyses were performed with R (R Development Core Team 2015) using the siar (Jackson et al. 2011) and plspm (Sanchez 2013) packages.

Results

There was evidence for both overdispersion and clustering on the degree of niche segregation and isotopic functional diversity (Fig. 2a). We found a negative relationship between species richness and the degree of niche similarity of the co-existing species in native communities but not in communities containing nonnative species ($F = 8.23, P < 0.01$; Fig. 2b; Appendix S3: Table S1). Similarly, while the isotopic functional diversity increased with increasing species richness in communities with only native species,
indicating that communities were more functionally complementary than expected at random in species-rich communities, communities with nonnative species displayed higher level of functional redundancy ($F = 9.99, P < 0.01$; Fig. 2c; Appendix S3: Table S2).

We also found evidence that the structural mechanisms underlying community structure and functional diversity differed between communities with and without nonnative species (bootstrap t-tests; $P < 0.05$; Appendix S2: Table S4). In communities containing only native species, the path model indicated that the degree of niche segregation was significantly related to net primary productivity (path coefficient = 0.41) and contemporary climate ($-0.27$) and marginally related to habitat size ($-0.17, 95\% \text{ CL: } -0.35 \text{ to } 0.06$) (Fig. 3a). Species niches were therefore more segregated in larger and less productive habitats and under warmer and more stable climates.

Species richness was positively associated with contemporary climatic factors ($0.33$) and habitat size ($0.34$), indicating that warm and climatically stable areas, as well as larger habitats, harbor the highest number of species. The negative association between species richness and the degree of niche segregation ($-0.25$) further supports the role of niche specialization and niche complementarity in promoting species coexistence in communities. Similarly, the degree of niche segregation appeared to promote isotopic functional diversity ($-0.63$). Isotopic functional diversity was also negatively correlated with historical factors ($-0.15$), independently from the effect of niche segregation. As a result, we found that global patterns in fish taxonomic and functional diversity along environment gradients were the product of both external abiotic factors and internal biotic-mediated filters (Fig. 4a, b).

Fig. 2. (a) Functional structure of the communities described by the isotopic functional diversity (FiD) and the degree of niche segregation among coexisting species (Niche). FiD and Niche were expressed as standardized effect sizes (SES) relative to a null model of random community assembly. Positive FiDSES values indicate higher diversity (overdispersion) and negative values indicate lower diversity (clustering) than random expectations. Positive NicheSES values indicate niche aggregation and negative values indicate niche segregation. (b, c) Relationships between niche segregation and isotopic functional diversity with species richness fitted using linear models with an interaction term accounting for the presence of nonnative species. Blue indicates communities with nonnative species and orange communities without nonnative species.
In contrast with native-only communities, those containing nonnative species appeared less structured, as indicated by the decrease in the GOF of the path model and the limited and weaker significant associations with both abiotic and biotic factors (Figs. 3b, 4c, d). In particular, we found little evidence of strong associations between abiotic factors, the degree of niche segregation and the isotopic functional diversity, or between the degree of niche segregation and species richness. We also observed a decrease in the strength of the relationships between contemporary climate and species richness (0.24), and between the degree of niche segregation and the isotopic functional diversity (−0.32). These results suggest that the presence of nonnative species modify community structure by reshuffling both the number and functional identity of species within communities, in addition to disrupting the internal organization of biotic interactions.

**Discussion**

Our study highlights the importance of niche segregation in determining the structure of freshwater fish communities (Tedesco et al. 2007, Mason et al. 2008, Matsuzaki et al. 2013) and supports that habitat and environmental filters interact with niche specialization through multiple pathways to mediate the strength of interspecific competition (Chesson 2000, Adler et al. 2013). We found evidence that broad-scale variations in species richness and niche segregation were directly associated with contemporary climate. Although the causal mechanisms underlying these patterns elude correlative studies such as ours (and others), these results are consistent with the hypothesis that warm areas with stable climate are within the physiological range of more species, and that increase specialization may amplify this underlying gradient (Currie et al. 2004). In turn, this may...
allow more functional strategies to coexist within local communities, thus enhancing functional diversity. Our study provides the first support for this finding at the global scale.

Our results indicate that the positive association between fish species richness and habitat size may be the result of increased niche availability, as well as the addition of functionally differentiated species (Evans et al. 2005). Moreover, the negative relationship between productivity and the degree of niche segregation suggests that elevated resource opportunities (e.g., availability and/or diversity of resources) may promote coexistence of functionally similar species, and therefore may promote greater functional redundancy at the community level. High overlap in resource use might be well-accommodated by separation along other dimensions of the niche (Schoener 1974) or through individual specialization (Araújo and Costa-Pereira 2013). This might
be especially true for isotopic niches as species with highly overlapping niches may also display microhabitat or temporal niche partitioning (e.g., Codron et al. 2015). Coupling stable isotope data with behavioral and habitat use information should allow to gain a better understanding of the mechanisms underlying the observed variation in species’ isotopic niches. Nonetheless, our results still suggest that the role of ecological interactions in shaping the assembly and functional diversity of multitrophic communities should not be dismissed in macro-ecological studies, as their role may be discernable even at broad spatial scales.

We provide evidence supporting the hypothesis that historical processes have played a non-negligible role in determining the functional diversity of natural communities at macroecological scales (Ordonez and Svenning 2015). Whereas freshwater fish communities that have been subjected to higher Quaternary climatic anomalies showed signs of functional clustering, communities in historical stable climatic areas displayed more functionally dissimilar species. This suggests that such effects are likely to occur directly via filtering of unsuitable trophic strategies and/or differential postglacial colonization lags, rather than through historical legacies on species richness (e.g., via a sampling effect). This is surprising as historical factors, especially Quaternary temperature anomalies, have been previously proposed as important predictors of species richness (Tedesco et al. 2005, Araújo et al. 2008). Nevertheless, at a global scale, paleoclimate variations are likely to co-vary with other spatial gradients, which highlights the inherent difficulty in distinguishing between historical and environmental filters in shaping present-day distribution patterns of diversity. In addition, other historical factors that were not included in the present study, such as historical connectivity and distance to climate refuges, are potentially involved in the spatial variation in freshwater species richness (Dias et al. 2014). Despite the convincing patterns observed, further investigations are thus required to confirm our conclusions regarding the relative importance of these underlying mechanisms and their consequences on community functional diversity.

Retrospective analyses of species invasions can provide new insight into the processes underlying community assembly (Sax et al. 2007). Here, we found that the taxonomic and functional diversity of communities with non-native species were poorly predicted by both abiotic and biotic factors; this contrasts with communities containing only native species where these relationships were considerably stronger. Our results thus support previous studies reporting that distribution patterns of nonnative species are more likely to reflect the context-dependence and idiosyncratic nature of the introduction (and subsequent establishment), rather than natural processes (Blackburn et al. 2008, Olden et al. 2008). For instance, the weaker association between species richness and contemporary climate implied that at the global scale, fish introductions may not co-vary with the biogeography of native species (Leprieur et al. 2008). Similarly, the lack of relationship between Quaternary climatic oscillations and functional diversity may indicate that human-mediated dispersal have overcome historical legacies in shaping large-scale distribution patterns of freshwater fish (Leprieur et al. 2009, Wilson et al. 2009).

We showed that species introductions may not only alter the number and functional identity of species, but could also disrupt the structure of biotic interactions among co-existing species. In the presence of nonnative species, the degree of niche segregation was unrelated to environmental and species richness gradients, and communities displayed higher levels of functional redundancy. This may indicate that changes in functional structure were associated with the nonrandom selection of particular feeding strategies. For instance, Sagouis et al. (2015) suggested that in lakes, humans tend to introduce omnivorous freshwater fish species, which may increase overlap in species functional roles. An alternative hypothesis might be that increased competition with nonnative species may lead to increased diet variation in order for species to maintain energy requirements (Svanbäck and Bolnick 2007). It is also likely that in such recently assembled communities, nonnative species have not evolved in their environment for a sufficient long period for co-evolutionary adjustments to occur. Therefore, it may still be expected that niche partitioning play an important role in structuring fish communities in the presence of nonnative species. Most communities have been the recipient of
several nonnative species with different introduction histories and a further step would be to investigate whether time since introduction affects the dynamic of species’ niches and to quantify the effects of assembly history on community structure.

An important consideration of our study is that our conclusions regarding the consequences of species introductions on community functional diversity does not benefit from comparable community structure data before and after species introductions. Using the history of fish species invasions in Japanese fresh waters, Matsuzaki et al. (2013) found that nonnative species increased the overall functional space of historical communities, seemingly through the selection of larger bodied-size, piscivorous species with wider niche breadth. Similarly, Azzurro et al. (2014) showed that successful marine fish invaders tended to be morphologically differentiated from native species. We therefore cannot eliminate the possibility that the presence of nonnative species was the consequence of other forms of ecosystem changes, rather than being the drivers of the observed change themselves (Didham et al. 2005). It is important to note, however, that in this study we documented changes at the local, rather than regional (e.g., watershed) scale, and using species realized niches instead of fixed traits-values across communities. This suggests that nonnative species might induce a greater functional overlap even if they show differences in their mean ecomorphological traits (see also Walsworth et al. 2013).

There has been a greater application of trait-based approaches to tackle questions related to community assembly and diversity (Mouchet et al. 2010, Adler et al. 2013, Violle et al. 2014). Although such approaches are well-suited to this challenge, by often describing the potential niche of species based on a priori functional attributes and by disregarding intraspecific variability, trait-based methods may confound the interpretation of the eco-evolutionary dynamics of communities and associated ecosystem functions (Farias and Jaksic 2009, Jung et al. 2010, Violle et al. 2012). By integrating information about the realized niche of interacting species at a local scale, we were able to document changes in several aspects of community structure along resource, species richness, and species introduction gradients. However, potential variations in basal resources across communities may render the interpretation of changes in isotopic space sometimes difficult and this is because differences in species’ isotopic niches may be driven by baseline variations that could be linked to environmental conditions (Hoeinghaus and Zeug 2008). Although some challenges remain, the development of new analytical procedures (e.g., Cucherousset and Villéger 2015, Rigolet et al. 2015) coupled with mathematical null models may offer a promising avenue to reveal species coexistence processes and assembly rules driven by classical niche-based coexistence theory, and to improve our understanding of the functional consequences of non native species introductions.

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LITERATURE CITED


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