Ecosystem type shapes trophic position and omnivory in fishes

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Abstract

The identification of patterns in ecological characteristics of organisms is a central challenge in macroecology with a growing research interest. The goal of this study was to establish whether patterns in trophic ecology (trophic position and omnivory) of fishes can be extended to an ecosystem dimension (freshwater *versus* marine environments), based on the premise that differences in environmental and ecological conditions of aquatic ecosystems have a large influence on the feeding ecology of fishes. To elucidate any relationship between trophic ecology and ecosystem type, we compiled a database using a global dataset for fishes (http://www.fishbase.org). The database included 5726 species distributed in 53 orders based on three common feeding strategies (herbivory, filter-feeding and predatory). Trophic position and omnivory increased from freshwater to marine ecosystems in filter-feeding and predatory species. In herbivore species in contrast, omnivory decreased, whereas no statistically significant trends were found for trophic position, which may reflect a similar diet specialisation on primary producers regardless of ecosystem type. These findings suggest that ecosystem type has a marked effect on trophic position and omnivory in fishes, but the impact depends on the type of feeding strategy. Prey availability, inherent feeding traits linked to the phylogenetic relatedness of species, ontogenetic effects, spatial variability (habitat related factors) and body size are considered as responsible factors for the observed patterns. Our findings demonstrate consistent patterns in trophic characteristics of organisms linked to ecosystem type, and underline the usefulness of fishes as model organisms to test macroecology hypotheses.

Keywords: aquatic systems, FishBase, global datasets, macroecology, trophic ecology

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Introduction

The assessment of the trophic position of animals has been a keystone for the understanding of food web complexity and functioning (Hussey et al., 2014). Shifts in trophic position of animals have been associated with several abiotic and biotic factors such as prey availability, diet composition, body size, hydrologic stability, ecosystem area and environmental change (e.g., Stergiou & Karpouzi, 2002; Sabo, Finlay, Kennedy, & Post, 2010; Romanuk, Hayward, & Hutchings, 2011; Eloranta et al., 2015). A recent study focussed on an anadromous fish species Atlantic salmon (*Salmo salar*, Salmonidae) revealed a clear increasing gradient in trophic position from freshwater to marine ecosystems using stable isotopes (Dixon, Power, Dempson, Sheehan, & Chaput, 2012). The proposed mechanism driving this gradient is the distinct feeding shift from the freshwater to the marine environment, which leads to a marked change in the range of carbon and nitrogen sources utilised by the species with a concomitant increase in its trophic position (Dixon et al., 2012). The diet composition determines the trophic position of animals with primary and intermediate consumers being located at lower trophic levels than top predators (DeNiro & Epstein, 1978; McCutchan, Lewis, Kendall, & McGrath, 2003). Consequently, the trophic position of animals summarises their functional role in the trophic network of the ecological community and their specific contribution to the energy flow pathways of the ecosystem (Post, 2002; Hussey et al., 2014).

Past studies have connected trophic position of fishes with aspects of trophic ecology theory such as for example ontogenetic trajectories and dietary habits, highlighting that trophic position typically increases with body size (Romanuk et al., 2011; Sánchez-Hernández, Eloranta, Finstad, & Amundsen, 2017, but see Layman, Winemiller, Arrington, & Jespen, 2005), and increases from herbivorous to carnivorous species (Stergiou & Karpouzi, 2002). Additionally, species of the same order or family are expected to have similar dietary habits compared to species that are phylogenetically more distant (German & Horn, 2006). Thus, the exploration of patterns in trophic ecology across ecosystem type should include a framework that includes the interplay among dietary habits, body size and phylogeny. Yet, variations in trophic position of animals among different types of ecosystems are poorly explored, although some notable exceptions exist (Carscallen et al., 2012; Dixon et al., 2012). Understanding the ecological principles behind differences in feeding of animals among various types of ecosystems is a basis for understanding food web dynamics and ecosystem functioning, and thereby instrumental in the development of ecological theory (e.g., Shurin et al., 2002; Shurin, Gruner, & Hillebrand, 2006; Elser et al., 2007). Comparisons between aquatic and terrestrial ecosystems have demonstrated unambiguous differences in their food-web structure (see Shurin et al., 2006). Within aquatic systems, marine ecosystems have traditionally been considered more productive than freshwater ecosystems (Shurin et al., 2006), but freshwater and marine ecosystems are surprisingly similar in terms of N and P limitations (Elser et al., 2007 and references therein).

The commonness and importance of omnivory have drawn attention of many scientists, especially in relation to aspects of ecosystem stability (Long, Bruno, & Duffy, 2011; Kratina, LeCraw, Ingram, & Anholt, 2012; Wootton, 2017). Omnivores are polyphagous, consuming many types of prey from more than one trophic level, and thus having an important impact on energy flows, nutrient cycling and ecosystem functioning as promoters of stability (Fagan, 1997; Covich, Palmer, & Crowl, 1999; Kratina et al., 2012). However, contemporary studies have come to differing conclusions in respect to the commonness of omnivory among ecosystem types. Omnivory has traditionally been considered more common in marine systems compared to both terrestrial and freshwater ecosystems (Chase, 2000; Shurin et al., 2006; Thompson, Hemberg, Starzomski, & Shurin, 2007). On the other hand, González-Bergonzoni et al. (2012) concluded that the prevalence of omnivorous fish species is higher in freshwater than in marine ecosystems, but with a consistent decreasing trend with latitude regardless of type of ecosystem. Likewise, other researchers noted that omnivory within the family Terapontidae is less frequent (in terms of number of species) in marine and euryhaline environments than in freshwater systems (Davis, Unmack, Pusey, Johnson, & Pearson, 2012). Besides, omnivory in some freshwater systems, such as alpine lakes, can be very high (above 80% of omnivore species), and even higher or similar to marine food webs (Sánchez-Hernández, Cobo, & Amundsen, 2015 and references therein). However, differences in omnivory among ecosystems are still under scientific debate and the factors responsible of such differences in omnivory are currently unexplored, representing a topical subject for ecological research.

This paper explores possible differences in trophic position and omnivory of fish among two main types of aquatic ecosystems (freshwater and marine environments), aiming to disentangle the magnitude and direction of any ecosystem-level dissimilarities in trophic ecology. Fish species represent suitable model organisms to face comparative ecological studies as they are widely distributed among contrasting ecosystem configurations (i.e., freshwater, brackish and marine ecosystems). Utilising data from FishBase, we here present the first comprehensive study comparing trophic position and omnivory of fishes among ecosystem types including a broad dataset (5726 fish species) based on three common feeding strategies (herbivory, filter-feeding and predatory), main food types (plants, zooplankton, zoobenthos and nekton), spatial variability (habitat and geographic range) and phylogeny (orders and families). The aim of the present study was to establish whether patterns in trophic ecology (trophic position and omnivory) can be extended to an ecosystem dimension. We expected an increasing trend in trophic position and omnivory from freshwater to marine ecosystems related to differences in their prey communities (Emery, 1978; Shurin et al., 2006; Grosberg, Vermeij, & Wainwright, 2012), testing the hypothesis that fish species having the same dietary habits or phylogeny vary their trophic position and omnivory with ecosystem dimension. As the marine environment could be dominated by larger-bodied fish species compared to freshwater systems, we further explored whether patterns in trophic ecology of fishes can be related to ecosystem-specific differences in body size. We finally tested the hypothesis that changes in trophic position and omnivory across ecosystems remain the same regardless of habitat and geographic range.

Methods

Data were retrieved from FishBase, a global database including more than 33000 fish species inhabiting freshwater, brackish and marine ecosystems (Froese & Pauly, 2017), using “rFishBase” package (Boettiger, Lang, & Wainwright, 2012). Our study addresses relevant information about trophic position, omnivory, feeding habits and type of ecosystem to provide comprehensive coverage of the relevant trophic and ecological aspects of our analyses. Fish species were classified according to: (i) ecosystem type, (ii) feeding strategies, (iii) main food type, (iv) habitat type, (v) geographic range, and (vi) phylogeny (orders and families) based on the categorical typologies supplied in FishBase.

Ecosystem type

Concerning ecosystem types, the dataset retrieved from FishBase included fish species strictly limited to freshwater, brackish and marine ecosystems. Species strictly limited to brackish waters were only represented by 21 species of which just four had available the complete information needed for the analyses (trophic position, omnivory and feeding strategy). Hence, the low numbers of brackish water species prevented their further use in this study. Species inhabiting freshwater or marine ecosystems in combination to brackish ecosystems were assigned as freshwater or marine, respectively. However, species inhabiting all three ecosystem types (n = 298) were not included in the further analyses to avoid possible bias related to the nature of the data uploaded to FishBase, and eliminate the risk of including biased information from only one ecosystem type instead of information including all three environments.

Feeding strategies

FishBase includes three categories (herbivory, filter-feeding and predatory) to give a general idea of the feeding strategy in fishes. Herbivorous species include different species predominantly grazing on aquatic (i.e., benthic algae, macrophytes or periphyton) and terrestrial plants (i.e., riparian fruits and leaves), whereas filter feeders and predators typically feed on animal material. Predators hunt macrofauna (insects, crustaceans, worms, cephalopods, fish, etc), whereas filter feeders forage on plankton at different depths of the water column. Because diet composition of animals shapes their trophic position (DeNiro & Epstein, 1978; McCutchan et al., 2003), the three selected feeding strategies may cover functional roles of fish species in the ecosystem at three different food web levels: lower, intermediate and top. Herbivorous species exploiting benthic sources such as algae (i.e., lower trophic taxa) reflect the lower levels of the food webs. Filter feeders are adapted to exploit particles, especially zooplankton, suspended in the water column and they may reflect the intermediate levels of food webs through the pelagic production pathways. Predators, which actively hunt, catch and ingest animals, are typically at the top of the food web and they are commonly used as sentinel species of ecosystems.

Main food type

Predators species were partitioned into two groups (zoobenthivore and nekton feeders) according to which main food type (zoobenthos and nekton, respectively) that was dominant (>50% contribution) in the diet of each species. Zoobenthos comprises a wide variety of prey categories including many taxa of insects, crustaceans, molluscs, sponges, ascidians and polychaetes. Nekton includes organisms of relatively large size capable of swimming against currents (mainly fish and cephalopods). This allowed us to compare two broad foraging modes (zoobenthivore and nekton feeders) between ecosystem types to reveal more accurate differences in trophic ecology between ecosystem configurations. In contrast, the lack of categorical breakdown of herbivory (with plants as main food) and filter-feeding (with zooplankton as main food) restricted the further exploration of underlying dietary patterns between ecosystem types to predatory species only.

Habitat

Because both freshwater and marine systems encompass several habitats with contrasting food availabilities and variable conditions, species were grouped in eight habitat typologies: (i) bathydemersal (living and feeding on the bottom below 200 m), (ii) bathypelagic (living or feeding in open waters at depths between 1,000 and 4,000 m), (iii) benthopelagic (living and feeding near the bottom as well as in midwaters or near the surface), (iv) demersal (living on or near the bottom and feeding on benthic organisms), (v) pelagic (living and feeding in the open waters), (vi) pelagic-neritic (living and feeding in nearshore areas of open waters), (vii) pelagic-oceanic (living and feeding in open waters beyond the continental shelf) and (viii) reef-associated (living and feeding on or near coral reefs). While marine species included all habitat types except the demersal, freshwater species were restricted to five of these habitat types (see Appendix 1).

Geographic range

To guarantee that both the freshwater and marine fishes analysed are evenly distributed across environments of similar temperature and environmental conditions, geographic range was taken into account. All fish species were sorted into four broad geographic zones or climatic domains according to its distribution, including (i) tropical, (ii) subtropical (broadly located between 23.5° and 35.0° north or south latitude), (iii) temperate (middle latitudes, spanning between the tropics and the polar regions), and (iv) polar (including north of the Arctic and south of the Antarctic Circles) species. Many bathydemersal and bathypelagic species show a wide geographic range including several geographic zones and were assigned as cosmopolitan species (see Appendix 1). When geographic range was not provided in FishBase, the geographic range was assigned based upon assessments of location information or maps provided in FishBase.

Phylogenetic-taxonomic classification

As indicated in the Introduction, key components of this study such as aspects of dietary habits and covariates such as body size and habitat type may all have significant associations with the phylogenetic relatedness of species (e.g., German & Horn, 2006; Romanuk et al., 2011; Davis et al., 2012). Thus, we assigned phylogeny (order and family) to each species to be more accurate in our analyses. However, many of the orders belonged to only one type of ecosystem, and in other cases the low numbers ($n <$ 10) of species belonging to the same order prevented its use (see Appendix 2). In this regard, we performed a comparative study of five orders (Clupeiformes, Osmeriformes, Perciformes, Scorpaeniformes and Siluriformes) based on the selection criteria of a minimum number of ten species (i.e., $n \geq 10$). Additionally, a good representation in terms of species numbers of some families in both ecosystem types, allowed us also to perform analyses at the family level for Clupeidae (Clupeiformes), Gobiidae (Perciformes) and Ariidae (Siluriformes).

Trophic position and omnivory index

In FishBase, trophic position (*Troph*) is estimated according to Pauly & Christensen (1995) by adding 1 to the mean trophic position of each prey species in the diet (*DIET Table* in FishBase; Palomares & Sa-a, 2000) utilised by a species:

$$Troph = 1 + \sum_{j=1}^{G} DC_{ij} \times Troph_j$$

where $Troph_j$ is the fractional trophic level of prey j, DC_{ij} represents the fraction of j in the diet of the fish species i and G is the total number of prey species. *Troph* usually vary around 2 and 5 in herbivorous and carnivorous organisms, respectively (Pauly, Trites, Capuli, & Christensen, 1998; Froese & Pauly, 2017). For example, if the fish species i shows a diet composed by, in terms of relative abundance, 50% phytoplankton

(*Troph* = 1) and 50% zooplankton (*Troph* = 2); the fish species *i* would have *Troph* of 2.5. In this regard, there has been a continuous debate over the use of gut content analysis *versus* stable isotopes methods for estimates of trophic position of animals (e.g., Post, 2002; Rybczynski, Walters, Fritz, & Johnson, 2008; Carscallen et al., 2012). Often, gut content analyses have been criticised as being less powerful and accurate than stable-isotope-based estimates of trophic position (Post, 2002). However, several studies have demonstrated that estimates of trophic position based on dietary observations are straightforward and highly correlated to isotope-based methods (Kline & Pauly, 1998; Carscallen et al., 2012). FishBase contains two trophic position metrics (*FoodTroph* and *DietTroph*); here we relied on *FoodTroph* because of its higher abundance of records compared to *DietTroph*.

The omnivory index (*OI*) is calculated from the variance of the *Troph* of the consumed food resources:

$$OI = \sum_{j=1}^{n} \Big(TL_j - (TL_i - 1)\Big)^2 \times DC_{ij}$$

where n is the number of prey categories, TL_j is the *Troph* of prey j, TL_i is the trophic level of predator i, and DC_{ij} is the fraction of prey j in the diet of predator i. The index values vary from zero (when all feeding occurs at the same trophic level) to increasing values with an increasing variety of *Troph* of the utilised prey categories.

Body size

Since fish size is an important factor, particularly in respect to trophic position (Romanuk et al., 2011), we retrieved body size information (here maximum length) from FishBase. This allowed us to test whether any differences observed between ecosystem types in trophic position and omnivory can be related to ecosystem-specific differences in body size.

Compiled dataset

The final dataset consisted of data for trophic position, omnivory index, body size, dietary habits (feeding strategies and main food type), habitat type, geographic range and ecosystem type in 5426 species distributed in 53 orders and 387 families (Appendix 2). Additionally, the nature of the compiled dataset comprising several categorical covariates, allowed us to run two comparative approaches, including coarse and finer scaled dietary habits. The coarse-scaled approach was covered by using a broad fish classification into the above-described feeding strategies. On the other hand, the categorical breakdown of predatory species into two dietary groups (i.e., zoobenthivore and nekton feeders) together with the phylogenetic considerations and spatial variability (habitat and geographic range) enabled a finer treatment of the dataset. The low sampling size ($n < 5$; Appendix 1) in freshwater species inhabiting bathydemersal and pelagic-neritic habitats prevented its use for the comparative approach. All data used in this study are available from FishBase (see *Data accessibility*).

Statistics

Statistical analyses and graphical outputs were performed using R 3.4.2 (R Core Team, 2017). Shapiro–Wilk tests indicated non-normality in the data. To identify the possible differences in trophic ecology (trophic position and omnivory) and body size of fishes between ecosystem types, we used the nonparametric Mann-Whitney-Wilcoxon test for two independent groups of samples. This comparative approach was repeated for coarse (feeding strategies) and finer (main food type, phylogeny, habitat and geographic range) scale dietary habits. Significance levels were adjusted by applying the Bonferroni method using the ‘‘dunn.test’’ package (Dinno, 2017).

Because the FishBase data relies on the original data uploaded and may be biased towards frequently studied or economically important species, there is a need to control possible data biases. Statistical procedures carried out in this study were aimed to control these limitations by using finer scale dietary habits and mixed modelling with random effects. If the outcomes remain similar across finer scale dietary habits and spatial covariates, the robustness of our findings regardless of possible biases is supported. In addition, random effects control for heterogeneity and variation attributable to different studies being conducted by different researchers, and can reduce publication bias (Zuur, Ieno, Walker, Saveliev, & Smith, 2009; Stanley, Doucouliagos, & Ioannidis, 2017; Gurevitch, Koricheva, Nakagawa, & Stewart, 2018). Because our data did not meet normality and hence the assumptions for linear regression models (Zuur et al., 2009), we used generalised additive mixed models (GAMMs) to test whether ecosystem type affects the trophic ecology of fishes using the “mgcv” package (Wood, 2017). We modelled each dependent variable separately (i.e., one model for trophic position and another for omnivory) with ecosystem type as smoothed term, and adjusted for phylogenetic effects by adding order as a random intercept in the GAMMs. Thus, by introducing order as a random factor, we model between-order variation in diet composition resulting from variables not possible to consider in the current study such as e.g. morphological constrains (gape size, gill raker length and interraker spacing) and variation and potential biases attributable to a plausible non-random selection of species uploaded to FishBase (e.g., frequently studied or economically important species are more likely to be represented). Additionally, to account for dietary habits and spatial effects in our models, feeding strategies, main food type, habitat type and geographic range were also included as smoothed terms. Thus, the full model consisted of one predictor variable and five smooth terms [~ body size + s(ecosystem) + s(feeding strategies) + s(main food type) + s(habitat)+ s(geographic range)] with order as random factor. The smooth terms represent categorical variables with data hierarchically structured (i.e., data structure organised in several categories). GAMMs and model selection was done by model comparison using the “MuMIn” package (Bartoń, 2017). Using a model selection method (Burnham & Anderson, 2002), we ranked the candidate models according to the Akaike information criterion (AIC, the best model being the one with the lowest AIC values). Residuals of the final selected models were visually inspected for deviations from normality and heteroscedasticity without finding evidence for any violation of model assumptions (see Appendix 3). Analyses were considered statistically significant at $p<0.05$.

Results

Overall, *Troph* tended to increase from freshwater to marine ecosystems (Figure 1), but statistically significant differences were only found in eleven out of nineteen cases (see Table 1). Specifically, ecosystem type shaped *Troph* in filter-feeding (W = 27039, p = 0.001), predatory (W = 1017400, p < 0.001) and zoobenthivore (W = 465690, p < 0.001) species, with higher values in marine than in freshwater ecosystems. Trophic position was also significantly higher in marine species of Osmeriformes (W = 98, p = 0.022) and Scorpaeniformes (W = 523, p = 0.025), but higher in freshwater species of

Gobiidae (W = 718.5, $p = 0.006$). Except for polar species (W = 155, $p = 0.671$), the higher *Troph* values observed in marine species compared to freshwater species were remained across habitat types and geographic range (Figure 2 and Table 1). All statistically significant tests remained significant after Bonferroni correction.

Also omnivory increased from freshwater to marine ecosystems in filter-feeding (W = 28416, $p = 0.012$), predatory (W = 1183600, $p < 0.001$), zoobenthivore (W = 574290, $p < 0.001$), benthopelagic (W = 61054, $p < 0.001$), demersal (W = 241040, $p = 0.001$), subtropical (W = 27927, $p < 0.001$) and temperate (W = 44672, $p < 0.001$) species (Figures 1 and 2), whereas the direction of increase was the inverse (i.e., from marine to freshwater ecosystems) in herbivorous species (W = 39480, $p = 0.036$), nekton-feeders (W = 128920, $p < 0.001$) and Perciformes (W = 717230, $p < 0.001$). All statistically significant tests remained significant after Bonferroni correction (Table 1).

The best model configurations for *Troph* and omnivory highlighted the importance of ecosystem type and dietary habits (i.e., feeding strategies and main food type) to understand the observed patterns in ecological characteristics of fish species (Table 2). Habitat type and body size (here maximum size) were influential variables of the most satisfactory model for omnivory, whereas geographic range and body size had a substantial influence on trophic position (see Appendix 4 for summary table of the 10 best model simulations). Thus, body size may be a contributing factor for the observed patterns across the ecosystem dimension, but again this impact largely depended on the dietary habits of species as *Troph* and omnivory seemed to be strongly linked to body size only in predatory, zoobenthivore, benthopelagic, demersal, subtropical and temperate species as well as in Scorpaneiformes (see Table 1). Moreover, despite the higher *Troph* revealed in marine compared to freshwater species of Osmeriformes, the species within this order tended to be larger in freshwater ecosystems (W = 61.5, $p < 0.001$). The model configurations showed the ubiquitous importance of ecosystem differences in dietary habits (i.e., feeding strategy and main food type) to understand differences in trophic characteristics of organisms across ecosystems (Table 2 and Appendix 4).

Discussion

Ecosystem type had a marked effect on trophic position and omnivory in fishes, but the impact depended on the type of feeding strategy and inherent food preferences linked to the phylogenetic relatedness of species. More specifically, trophic position and omnivory revealed an increasing trend from freshwater to marine ecosystems in both filter-feeding and predatory species, as well as within some specific taxonomic groups (Osmeriformes and Scorpaeniformes), whereas a decreasing trend was found for herbivory species and Gobiidae. These trends seemed partly to be related to ecosystem-specific differences in body size. However, the impact largely depended on the type of feeding strategy as body size was an important factor for ecosystem differences in the trophic ecology of predatory species (especially those with zoobenthos as main food) and Scorpaneiformes, whereas less effects of body size was seen in filter-feeding and herbivory species and also within most orders as indicated in Table 1. The increasing trend from freshwater to marine ecosystems in trophic position and omnivory remained the same regardless of spatial variability (habitat and geographic range). In line with macroecological theory, the revealed patterns in trophic position and omnivory of aquatic animals between ecosystem type may in part also result from a greater production and biodiversity in marine compared to freshwater ecosystems (Shurin et al., 2006; Grosberg et al., 2012).

Our hypothesis that the trophic position of fishes would be associated with ecosystem type was partially supported. Trophic position increased from freshwater to marine ecosystems in filter-feeding, predatory (only statistically significant in those species feeding mainly on zoobenthos), benthopelagic, demersal, tropical, subtropical and temperate species, and in Osmeriformes and Scorpaneiformes, but not in herbivory species and most other taxonomic classifications (i.e., six out of eight). This suggests that species grazing on benthic resources, most typically algae, may have similar trophic levels regardless of ecosystem type (France, 1996). We posit that the similarity in trophic level of herbivore species between ecosystem types may be a result of these species being highly specialised on consuming primary producers and thus having a lower ability to utilise prey at other (i.e., higher) trophic levels. This is strongly supported by their low degree of omnivory, which thus locates them at the lowest consumer position in all ecosystem types.

Because energy transfer efficiencies can vary among ecosystems (see Pauly & Christensen, 1992), the response to changes in prey availability among ecosystems and geographic territories within the same ecosystem is central in many theories of aquatic ecosystem functioning and dynamics (Ives, Cardinale, & Snyder, 2005; Dixon et al., 2012; Schmitz, Miller, Trainor, & Abrahms, 2017). Our findings corroborate this view as a clear increasing gradient in trophic position was found between freshwater and marine ecosystems in filter-feeding and predatory species. Our analyses also provide solid evidence that the increasing gradient in trophic position between freshwater and marine species is maintained at a more localised range (here habitat and geographic range). It is reasonable to posit that this shift from low to high trophic positions between aquatic ecosystems is a response to changes in prey availability, which is usually more diverse, productive and abundant in the marine systems (Shurin et al., 2006; Grosberg et al., 2012). Trophic position of fish species is very variable among species and commonly range from 2.0 to 5.29 (Vander Zanden & Rasmussen, 1996; Vander Zanden, Cabana, & Rasmussen, 1997; Stergiou & Karpouzi, 2002; Romanuk et al., 2011), being positively related to maximum body size of the species (Romanuk et al., 2011). Our results provide important advances on these previous studies by contributing new evidence of the importance of ecosystem type and type of feeding strategy to understand the variation in trophic position of fish species. Noteworthy, ecosystem-specific differences in body size, most likely associated with morphological constraints (i.e., gape limitation), appear to play a key role in determining trends in trophic position across ecosystems in predatory species, but not in filter-feeding and herbivory species. An important mechanism driving this trend might be piscivorous behaviour. Piscivory leads to increases in trophic position and typically a specialisation in resource use (Sánchez-Hernández et al., 2017 and references therein). Additionally, it seems like the proportion of piscivorous species is greater in marine than in freshwater systems (Winemiller & Leslie, 1992). Opposite, cannibalism has been assumed to be more common in freshwater than in marine systems (Pereira, Keppeler, Agostinho, & Winemiller, 2017a), but a recent review suggests that the degree of cannibalism is similar between marine and freshwater fishes (Pereira, Agostinho, & Winemiller, 2017b). Thus, our findings and those of other authors (e.g., Winemiller & Leslie, 1992), indicate that the capacity to forage on fish and other nekton resources seems to be more common in marine than in freshwater predators as indicated here by their higher trophic position. That said, we postulate that the positive trend in trophic position from freshwater to marine ecosystems by predatory species, apparently shaped by body size, is highly linked to piscivorous behaviour since piscivory drives an increase in trophic position and increases over the ontogeny (e.g., Mittelbach & Persson, 1998; Sánchez-Hernández et al., 2017). Additionally, we posit that the unexpectedly higher trophic position of Gobiidae in the freshwater environment is related to phylogenetic-related differences in dietary habits across ecosystem, with nekton feeders in this taxon being more prevalent in freshwater environments (15% and 1.6% in freshwater and marine, respectively), and consequently responsible of its overall higher trophic position. This underpins that differences in inherent dietary habits linked to the phylogenetic relatedness of species across type of ecosystems may be a keystone for understanding patterns in trophic position of fishes. Additional work will be needed to explore whether or not similar patterns can be generalised to other aquatic consumers.

Previous studies have reached contrasting conclusions in respect to the prevalence of omnivory in different aquatic ecosystems, but the present study confirms that the importance of omnivory can be extended to an ecosystem dimension (i.e., higher in marine environments) and our findings also provide novel insight to the causes that lead to differences in omnivory levels across ecosystems. Hence, the revealed patterns in omnivory of fishes corroborate the hypothesis that ecosystem dimension shape the prevalence of omnivory in aquatic consumers. With a few exceptions (nekton-feeders, herbivory species, tropical species, polar species and Perciformes), omnivory increased from freshwater to marine ecosystem. Thus, our study largely supports previous findings on the notion that omnivory is more prevalent in marine compared to both terrestrial and freshwater ecosystems (Chase, 2000; Shurin et al., 2006; Thompson et al., 2007). However, recent studies have shown that the prevalence of omnivorous species seems to be higher in freshwater than in marine ecosystems (González-Bergonzoni et al., 2012; Sánchez-Hernández et al., 2015). These are seemingly contradictory standpoints. The first consideration encapsulates that the variety of trophic positions of prey categories consumed by fishes (henceforth “degree of omnivory”) is higher in marine than in freshwater ecosystems, and the second that the relative proportion of species that can exploit resources at multiple trophic levels is actually greater in freshwater ecosystems. We suggest that these apparent contradictions can be resolved if the nature of omnivory by fish species, the prey availability and the ontogenetic dietary shifts of species are taken into account. That is, although the number or prevalence of omnivore species can be higher in freshwater, the degree of omnivory is higher in marine species, most likely because of a higher plasticity of marine species to exploit available resources at a higher number of trophic levels compared to freshwater species. This can clearly be illustrated through the example of filter-feeding fish species. Although these species may select food particles suspended in the water (seston) by size based on morphological constrains (gape size, gill raker length and interraker spacing), they do usually not select by prey type (Gerking, 1994). It should be kept in mind that in contrast to marine systems, freshwater systems contain comparatively simple communities of organisms suspended in the water. More precisely, food resources available for filter feeders are limited to zooplankton in freshwater systems, whereas available resources are much wider in the marine systems, including also taxa other than common zooplankton (i.e., copepods and cladocerans), such as krill, worms, mollusks and fish larvae (Garrido et al., 2008; Costalago, Garrido, & Palomera, 2015). It is possible that this broader variety of food resources available in the marine environment is connected to the observed positive trends in omnivory and trophic position from freshwater to marine ecosystems by fishes.

On the other hand, the differences in ontogenetic dietary shifts between ecosystems can be vital to understand the magnitude and direction of any ecosystem-level dissimilarities in omnivory. Taking as example the nekton feeders, we accept the view that the nature of the ontogenetic dietary shifts is responsible for their higher omnivory in freshwater ecosystems. We posit that the occurrence of several distinct ontogenetic dietary shifts might be less plausible in marine predator species because they usually switch to piscivory very early in the ontogeny or undergo smooth dietary shifts, such as many species of e.g. Squaliformes, tunas (*Thunnus* spp., Scombridae) or anglerfish (*Lophius* spp., Lophiidae) (e.g., Preciado, Velasco, Olaso, & Landa, 2006; Reglero, Urtizberea, Torres, Alemany, & Fiksen, 2011). In contrast, freshwater nekton feeders may appear to undergo several steps before they become piscivorous, thereby consuming prey types from more trophic levels than marine species. From the FishBase data, this is the case for many freshwater predators such as pikeperch (*Sander lucioperca*, Percidae) and some salmonids, who initially prey upon zooplankton and zoobenthos, but later switch to fish. Similar as for trophic position, it is reasonable to posit that ecosystem type impacts omnivory in fishes in response to changes in prey availability across ecosystems. Factors other than prey availability, such as inherent food preferences and ontogenetic dietary shifts may also have a major influence on omnivory in fishes, and thus the differences that occur between ecosystems.

As already pointed out, a caveat should be exercised regarding conclusions from analyses of dietary data uploaded to FishBase. These may suffer limitations from heterogeneity and other data issues due to possible biases towards (i) frequently studied or economically important species and (ii) uneven sampling effort across the different dietary habits and spatial variability (e.g., habitat and geographic related factors), which may hinder our ability to identify gradients across ecosystems. Here, these potential biases were addressed by implementing analytical approaches using random effects (Zuur et al., 2009; Stanley et al., 2016; Gurevitch et al., 2018; see the *Statistics* section). In addition, the key conclusions of this study (i.e., trophic position and omnivory increase from freshwater to marine species) broadly remained the same across habitat, geographic range and finer scaled dietary habits (main food type and phylogeny), suggesting a strong robustness of our findings regardless of any possible biases in the data archive. Still, there are some limitations and considerations that need to be acknowledged when using the available FishBase dataset as in the present study. In fact, one of the main disadvantages of this approach could be the lack of a comprehensive database covering ontogenetic and seasonal effects on dietary habits of fish species as was thoroughly highlighted by Stergiou & Karpouzi (2002). It seems that in FishBase, ontogenetic dietary shifts are well covered for some species, whereas information about ontogenetic trajectories is limited for other species. A good representation of these dietary shift in FishBase can e.g. be found in European perch (*Perca fluviatilis*, Percidae), which is known for showing characteristic ontogenetic dietary shifts with juveniles primarily feeding upon zooplankton before switching to benthic invertebrates and later to small and subsequently to large fish prey (e.g., Amundsen et al., 2003). In contrast, many omnivorous and herbivorous species undergo ontogenetic dietary shifts from utilising animal resources to the comprehensive use of vegetal resources (plants and detritus) (e.g., Drewe, Horn, Dickson, & Gawlicka, 2004; Reckendorfer et al., 2011; Sánchez-Hernández & Cobo, 2012), which, in turn, might not be well covered in

FishBase. For example, the Common nase (*Chondrostoma nasus*, Cyprinidae), is in FishBase considered as a strict herbivore species, but studies have shown that this species rather should be considered as a facultative herbivory species with ontogenetic dietary shifts that also include animal resources in the diet early in the ontogeny (Reckendorfer et al., 2011). Thus, while trophic position and omnivory seem to be accurately estimated in FishBase for many species undergoing ontogenetic dietary shifts, the generic lists of all dietary items included in FishBase may for many other uncommon and unstudied species not fully cover the ontogenetic dietary effects. Another limiting factor for the FishBase estimation of trophic ecology (trophic position and omnivory) could be related to the indices used for the expression of diet composition data (e.g., numeric, volumetric, gravimetric, frequency of occurrence, etc). As previously highlighted by Stergiou & Karpouzi (2002), frequency of occurrence and numerical data are not good indicators of diet because they provide little information about the relative amount of each prey category present in the stomach or the information may be biased according to the size of the prey items, respectively. Although FishBase aims only to use quantitative reports of diet composition data (percentage of volume or weight) (see *The DIET Table* in FishBase; Palomares & Sa-a, 2000), more effort needs to be paid to make such diet data of poorly studied species available in order to provide more accurate measures of their trophic position and degree of omnivory. Because the data used in this study depends on the original dietary data uploaded to FishBase, the revealed patterns might potentially be biased from the inclusion of estimates of trophic position and omnivory that are not covering seasonal and ontogenetic effects for some fish species. Additionally, the dataset used in this study was not equally represented across habitats and phylogeny, which may impose a limitation to explore ecosystem changes in trophic position and omnivory. Yet, the increasing trend from freshwater to marine ecosystems in trophic position and omnivory was homogeneous regardless of habitat, geographic range and phylogeny, underlining the replicability of our key findings and thus supporting their robustness regardless of any possible biases that may occur in the used dataset. Hence, despite these potential problems, the promising results of this study encourage the extension of this approach by using data from different sources and combining stomach and isotope based methods in order to improve the robustness and reliability of the used dataset and thereby enhance the exploration of macroecological questions in trophic ecology.

In conclusion, ecosystem type evidently shapes trophic position and omnivory in fishes, but the magnitudes of their effects are often quite variable depending on the type of feeding strategy (here herbivory, filter-feeding and predatory) and the resource preferences linked to the phylogenetic relatedness of species. Changes with ecosystem type were less pronounced in herbivore species as they are specialised on primary producers and thus to a small extent omnivorous, which, in turn, results in the same basal trophic position among ecosystems. The study provides novel insight to macroecological theory by demonstrating patterns in trophic characteristics of organisms across ecosystems and identifying the most influential drivers for trophic position and omnivory of fishes.

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Table legends

Table 1. Mean values (± SE) of trophic position, omnivory and body size (maximum length) with pairwise comparisons between systems according to feeding strategy, main food type, habitat, geographic range and phylogeny. *Main food type is only shown for predatory species and **habitat type is only shown for benthopelagic and demersal species (see *Methods*). Significant values are marked in bold.

		Mean ± SE			Pairwise comparisons					
					Trophic position		Omnivory		L_{max}	
		Trophic position	Omnivory	Body size (cm)	Mann-Whitney-Wilcoxon	Bonferroni	Mann-Whitney-Wilcoxon	Bonferroni	Mann-Whitney-Wilcoxon	Bonferroni
Feeding strategies										
Herbivory ($n = 612$)	Freshwater	2.27 ± 0.026	0.12 ± 0.011	28.45 ± 2.02	$W = 38666$, $p = 0.116$	$p = 0.116$	$W = 39480$, **$p = 0.036$**	**$p = 0.036$**	$W = 48688$, **$p < 0.001$**	**$p < 0.001$**
	Marine	2.24 ± 0.018	0.09 ± 0.007	21.20 ± 0.92						
Filter-feeding ($n = 703$)	Freshwater	3.05 ± 0.045	0.33 ± 0.015	22.21 ± 2.51	$W = 27039$, **$p = 0.001$**	**$p = 0.001$**	$W = 28416$, **$p = 0.012$**	**$p = 0.012$**	$W = 32845$, $p = 0.491$	$p = 0.491$
	Marine	3.23 ± 0.013	0.37 ± 0.005	27.82 ± 3.97						
Predators ($n = 4111$)	Freshwater	3.55 ± 0.014	0.51 ± 0.005	38.74 ± 1.55	$W = 1017400$, **$p < 0.001$**	**$p < 0.001$**	$W = 1183600$, **$p < 0.001$**	**$p < 0.001$**	$W = 1077100$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.73 ± 0.008	0.54 ± 0.003	61.02 ± 1.24						
Main food type*										
Zoobenthos ($n = 28969$)	Freshwater	3.37 ± 0.011	0.45 ± 0.004	31.59 ± 1.41	$W = 465690$, **$p < 0.001$**	**$p < 0.001$**	$W = 574290$, **$p < 0.001$**	**$p < 0.001$**	$W = 571980$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.53 ± 0.007	0.48 ± 0.003	42.49 ± 0.83						
Nekton ($n = 1226$)	Freshwater	4.10 ± 0.019	0.70 ± 0.006	60.31 ± 4.29	$W = 104470$, $p = 0.099$	$p = 0.099$	$W = 128920$, **$p < 0.001$**	**$p < 0.001$**	$W = 76337$, **$p < 0.001$**	**$p < 0.001$**
	Marine	4.16 ± 0.009	0.67 ± 0.004	101.20 ± 3.12						
Habitat**										
Benthopelagic ($n = 1011$)	Freshwater	3.26 ± 0.024	0.42 ± 0.008	30.61 ± 1.51	$W = 53473$, **$p < 0.001$**	**$p < 0.001$**	$W = 61054$, **$p < 0.001$**	**$p < 0.001$**	$W = 41416$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.69 ± 0.031	0.52 ± 0.011	76.04 ± 5.24						
Demersal ($n = 1740$)	Freshwater	3.37 ± 0.027	0.45 ± 0.009	43.98 ± 2.32	$W = 211160$, **$p < 0.001$**	**$p < 0.001$**	$W = 241040$, **$p = 0.001$**	**$p < 0.001$**	$W = 266300$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.55 ± 0.014	0.49 ± 0.005	50.08 ± 1.35						
Geographic range										
Tropical ($n = 3171$)	Freshwater	3.31 ± 0.021	0.44 ± 0.007	32.74 ± 1.33	$W = 880700$, **$p < 0.001$**	**$p < 0.001$**	$W = 972120$, $p = 0.804$	$p = 0.805$	$W = 934390$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.39 ± 0.015	0.44 ± 0.005	40.68 ± 1.02						
Subtropical ($n = 1061$)	Freshwater	3.24 ± 0.053	0.41 ± 0.018	44.22 ± 5.25	$W = 23750$, **$p < 0.001$**	**$p < 0.001$**	$W = 27927$, **$p < 0.001$**	**$p < 0.001$**	$W = 35454$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.66 ± 0.018	0.52 ± 0.006	75.17 ± 3.44						
Temperate ($n = 853$)	Freshwater	3.40 ± 0.031	0.46 ± 0.011	45.59 ± 3.61	$W = 41498$, **$p < 0.001$**	**$p < 0.001$**	$W = 44672$, **$p < 0.001$**	**$p < 0.001$**	$W = 57051$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.61 ± 0.019	0.51 ± 0.007	59.58 ± 2.93						
Polar ($n = 100$)	Freshwater	3.51 ± 0.232	0.50 ± 0.028	26.25 ± 6.58	$W = 155$, $p = 0.671$	$p = 0.664$	$W = 171$, $p = 0.440$	$p = 0.433$	$W = 255$, $p = 0.164$	$p = 0.162$
	Marine	3.43 ± 0.032	0.47 ± 0.016	39.40 ± 3.09						
Phylogeny										
Clupeiformes ($n = 121$)	Freshwater	3.31 ± 0.077	0.42 ± 0.028	21.66 ± 3.39	$W = 1685.5$, $p = 0.251$	$p = 0.250$	$W = 1712.5$, $p = 0.191$	$p = 0.190$	$W = 1120.5$, **$p = 0.028$**	**$p = 0.028$**
	Marine	3.18 ± 0.055	0.37 ± 0.018	25.63 ± 1.97						
Clupeidae ($n = 80$)	Freshwater	3.19 ± 0.084	0.39 ± 0.027	16.30 ± 2.73	$W = 708.5$, $p = 0.725$	$p = 0.721$	$W = 739$, $p = 0.497$	$p = 0.494$	$W = 369.5$, **$p = 0.001$**	**$p = 0.001$**
	Marine	3.10 ± 0.060	0.35 ± 0.020	25.25 ± 1.58						
Osmeriformes ($n = 38$)	Freshwater	3.31 ± 0.084	0.42 ± 0.037	40.11 ± 27.36	$W = 98$, **$p = 0.022$**	**$p = 0.021$**	$W = 165.5$, $p = 0.767$	$p = 0.755$	$W = 59$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.41 ± 0.047	0.41 ± 0.026	35.87 ± 6.46						
Perciformes ($n = 3033$)	Freshwater	3.41 ± 0.028	0.46 ± 0.009	24.31 ± 1.02	$W = 686800$, $p = 0.056$	$p = 0.055$	$W = 717230$, **$p < 0.001$**	**$p < 0.001$**	$W = 551050$, **$p < 0.001$**	**$p < 0.001$**
	Marine	3.35 ± 0.014	0.43 ± 0.004	42.52 ± 0.99						
Gobiidae ($n = 81$)	Freshwater	3.50 ± 0.072	0.46 ± 0.028	16.25 ± 4.04	$W = 718.5$, **$p = 0.006$**	**$p = 0.006$**	$W = 609.5$, $p = 0.176$	$p = 0.174$	$W = 650$, $p = 0.665$	$p = 0.661$
	Marine	3.25 ± 0.045	0.38 ± 0.022	11.77 ± 1.28						
Scorpaeniformes ($n = 257$)	Freshwater	3.42 ± 0.096	0.49 ± 0.023	17.63 ± 0.98	$W = 523$, **$p = 0.025$**	**$p = 0.025$**	$W = 607.5$, $p = 0.075$	$p = 0.075$	$W = 1029.5$, **$p = 0.001$**	**$p < 0.001$**
	Marine	3.67 ± 0.023	0.55 ± 0.009	35.97 ± 1.59						
Siluriformes ($n = 257$)	Freshwater	3.42 ± 0.039	0.49 ± 0.013	55.27 ± 4.34	$W = 1810$, $p = 0.081$	$p = 0.081$	$W = 2307.5$, $p = 0.887$	$p = 0.886$	$W = 1988$, $p = 0.410$	$p = 0.410$
	Marine	3.59 ± 0.095	0.51 ± 0.031	55.07 ± 7.51						
Ariidae ($n = 34$)	Freshwater	3.50 ± 0.149	0.53 ± 0.039	58.43 ± 8.23	$W = 99.5$, $p = 0.365$	$p = 0.355$	$W = 115$, $p = 0.758$	$p = 0.744$	$W = 162$, $p = 0.451$	$p = 0.440$
	Marine	3.68 ± 0.082	0.53 ± 0.032	53.53 ± 8.10						

Table 2. Summary table of the best model simulations for trophic position (*Troph*) and omnivory index (*OI*) according to AIC values (summary table for the 10 best model simulations is shown in Appendix 4). The parametric coefficients with significance values are given for each variable. ***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$.

Variable	Intercept	Predictor variables	Smooth terms					Model statistics
		Body size	Ecosystem	Feeding strategies	Main food type	Geographic range	Habitat	R^2
Troph	3.361***	—	5.340***	1.999***	1.997***	1.000	—	0.76
OI	0.458***	0.001**	5.292***	1.997***	1.992***	—	1.544*	0.65

Figure legends:

Figure 1. Trophic position (*Troph*) and omnivory (omnivory index) of fishes according to feeding strategies (Fil = filter-feeding, Her = herbivory, Pre = predatory), main food type (Nek = nekton, Zoo = zoobenthos), phylogeny (Clu = Clupeiformes, Osm = Osmeriformes, Per = Perciformes, Sco = Scorpaeniformes, Sil = Siluriformes), and ecosystem type (F = freshwater, M = marine). Omnivory = 0 (all feeding occurs at the same *troph*).

Figure 2. Trophic position (*Troph*) and omnivory (omnivory index) of fishes according to habitat type (BD = bathydemersal, BP = bathypelagic, BeP = benthopelagic, D = demersal, P = pelagic, PN = pelagic-neritic, PO = pelagic-oceanic, and R = reef-associated), geographic range (Tro = tropical, Sub = subtropical, Tem = temperate, Pol = polar, and Cos = cosmopolitan), and ecosystem type (F = freshwater, M = marine). Omnivory = 0 (all feeding occurs at the same *troph*).

Data accessibility

Data used in this study are available from FishBase (http://www.fishbase.org). Data from the manuscript will be archived in the Figshare Digital Repository (https://figshare.com/) on acceptance of the manuscript for publication.

Supporting information

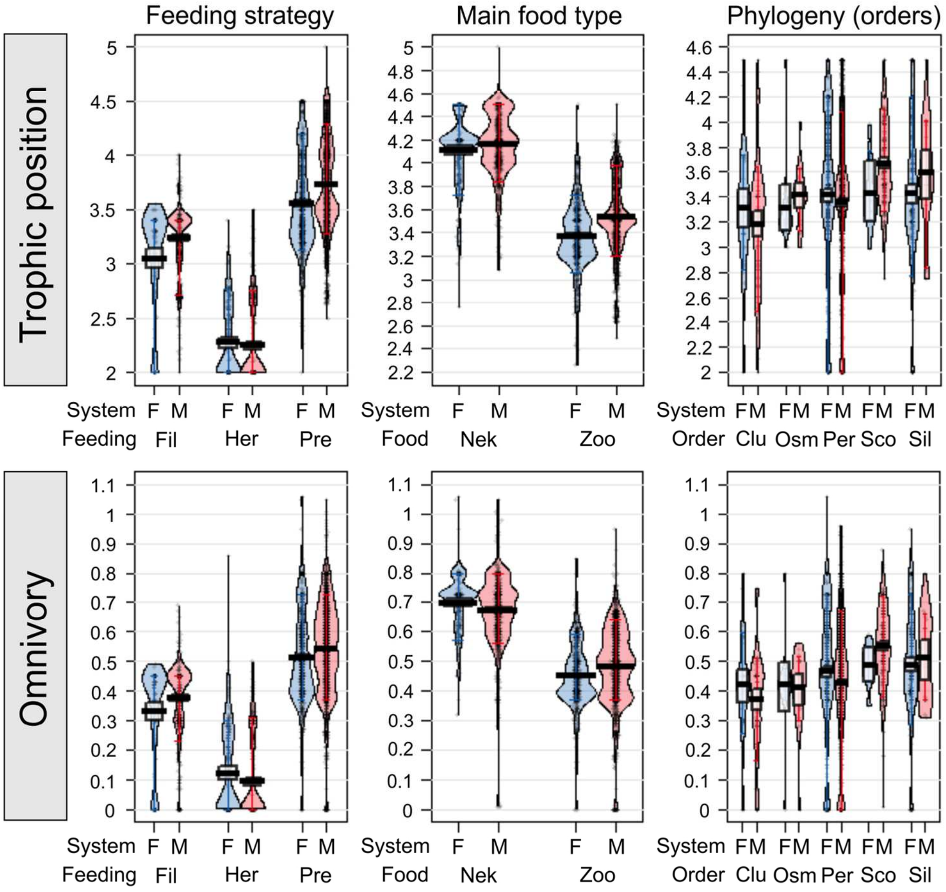
List of items in the supporting information:

-Appendix 1. Information regarding how sample size varied between main food type, habitat and geographic range.

-Appendix 2. List of orders and families incorporated into the study. Families are grouped by type of ecosystem. The number of species per order or family is shown in brackets.

-Appendix 3. Residual structure (GAMMs) of the best model simulations.

-Appendix 4. Summary table for the 10 best model simulations explaining the variation of trophic position and omnivory in fishes.



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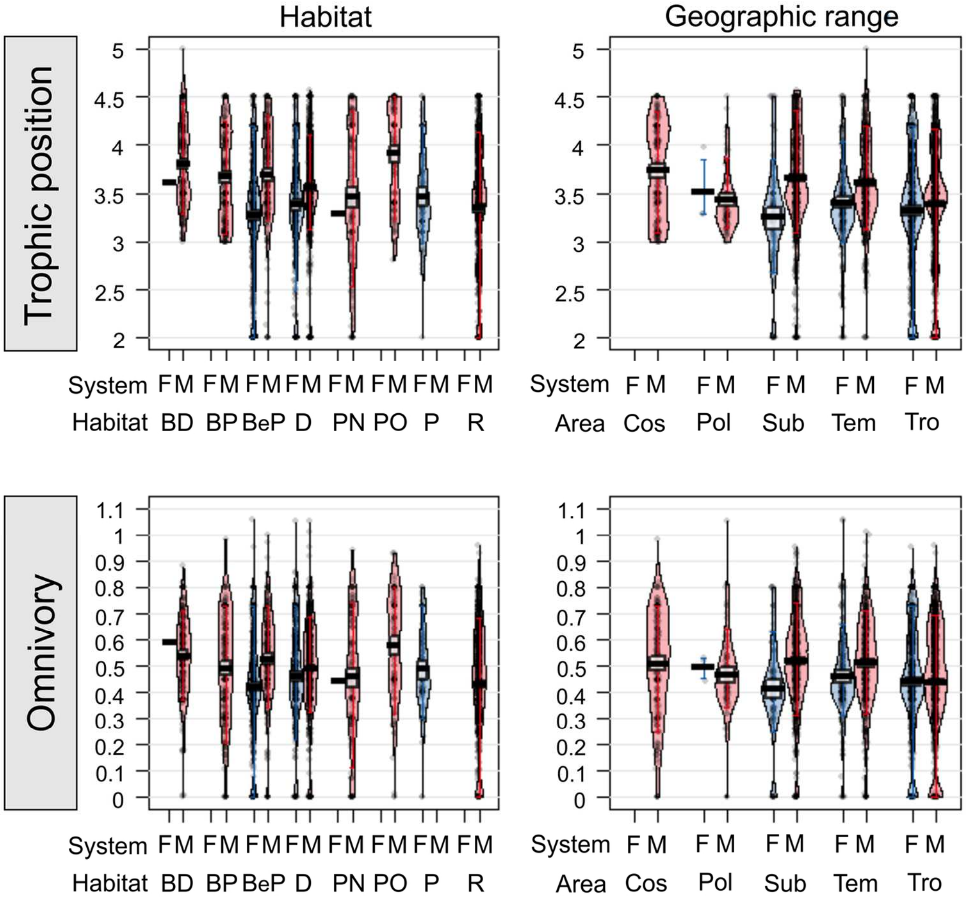
145x138mm (300 x 300 DPI)



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128x124mm (300 x 300 DPI)