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Article

Taxonomy-based differences in feeding guilds of fish

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Abstract

It has been taken for granted that feeding guilds and behavior in animals are linked to the taxonomic relatedness of species, but empirical evidence supporting such relationship is virtually missing. To examine the importance of taxonomy on trophic ecology, I here present the first well-resolved dietary taxonomy analysis based on feeding guilds (predation, herbivory, and filtering) among families and genera within the fish order Perciformes. Taxonomic relatedness in feeding did not vary with ecosystem dimension (marine vs. freshwater). Although predation dominates among Perciformes fishes, this study shows that in most cases taxonomic units (family or genus) are composed by species with several feeding guilds. Related species are more similar in feeding compared with species that are taxonomically more distant, demonstrating that there is a greater variation of feeding guilds within families than genera. Thus, there is no consistency in feeding guilds between family- and genus-level taxonomy. This study provides empirical support for the notion that genera are more informative than families, underlining that family-level taxonomy should be avoided to infer feeding habits of fish species at finer taxonomic resolution. Thus, the choice of taxonomic resolution (family or genus level) in ecological studies is key to avoid information loss and misleading results. I conclude that high-rank taxonomic units (i.e., above the generic level) are not appropriate to test research hypotheses about the feeding of fish.

Key words: aquatic systems, clades, FishBase, global datasets, taxonomic sufficiency, trophic ecology

Morphology is an important trait in the identification and classification (i.e., animal taxonomy) of fish (e.g., Nelson et al. 2016). Taxonomically related species share similar morphological traits and thus are likely to share similar feeding habits and ecological niches (e.g., German and Horn 2006; Lujan et al. 2012; Potapov et al. 2019). Theory predicts ("limiting similarity" hypothesis) that morphological similarity of taxonomically related species drives strong competition, which may favor trophic-niche divergence of species (MacArthur and Levins 1967; Abrams 1983; but also reviewed in Potapov et al. 2019). By contrast, the "taxonomic signal" hypothesis suggests that closely related taxa have more similar trophic niches than distantly related taxa (Potapov et al. 2019). Thus, recent evidence suggests that groups of closely related species are ecologically consistent (Potapov et al. 2019).

It is recognized that dietary habits can change across taxonomic relatedness of species and ecosystem type (e.g., German and Horn 2006; Davis et al. 2012; Sánchez-Hernández and Amundsen 2018; Pomeranz et al. 2019). For example, the proportion of herbivorous species is greater in freshwater than in marine ecosystems (Winemiller and Leslie 1992). In addition, omnivory is higher in marine than in freshwater ecosystems irrespective of feeding guild (Sánchez-Hernández and Amundsen 2018). From a taxonomic perspective, aspects of dietary habits may have significant associations with the taxonomic relatedness of species (e.g., German and Horn

2006; Romanuk et al. 2011; Davis et al. 2012). It is thought that feeding guilds (i.e., a group of species that exploit the same food resources) are predictable according to taxonomic level (e.g., Simberloff and Dayan 1991; Cummins 2016). The concept relies on the fact that closely related species often show the same feeding behavior (Simberloff and Dayan 1991; Potapov et al. 2016), but feeding can be rarely predictable above the generic level (Walter and Ikonen 1989). Thus, it is reasonable to posit that not all species in a given family have the same feeding guild. An exploration of whether feeding ecology is firmly organized according to taxonomic classifications can generate valuable information to understand differences in dietary habits among species and be instrumental in the theoretical development for understanding diversification and speciation in animal assemblages. In this regard, fish species serve as functional units (i.e., model animals) in studies focus on the link between taxonomic diversification and trophic ecology as they are widely diversified and occupy a broad range of environments (i.e., freshwater, brackish, and marine ecosystems) (e.g., Schaefer and Lauder 1986; Davis et al. 2012).

The importance of phylogenetic–taxonomic relationships has drawn the attention of many scientists to face comparative studies exploring dietary habits of organisms (e.g., Linde et al. 2004; German and Horn 2006; Betancur et al. 2017; Sánchez-Hernández and Amundsen 2018). Species of the same order or family are generally expected to have more similar dietary habits compared with species that are phylogenetically more distant (German and Horn 2006). However, we currently lack empirical evidence about whether taxonomy can be used to predict feeding guilds in fish species as it has been shown for invertebrates (Cummins 2016; Potapov et al. 2016), and thereby whether high taxonomic resolution (e.g., family) is useful to infer feeding habits of species at lower taxonomic levels (genus level). The exploration of dissimilarity in feeding guilds across taxonomic levels will provide new insights about how feeding guilds vary among taxonomic units, but also a better foundation for decision-making of taxonomic resolution (family or genus level) to be adopted in studies testing trophic hypotheses. Thus, the exploration of the relationship between taxonomic and feeding dissimilarity can provide evidence whether finer taxonomic resolution provides more information on feeding habits compared with family-level taxonomy. This article explores possible taxonomy-based differences in 3 common feeding guilds (herbivory, filter-feeding, and predation) of the order Perciformes, aiming to establish whether taxonomic-level resolution and ecosystem type (freshwater vs. marine) matter on fish feeding guilds. Therefore, I test the hypothesis that 1) related species are more similar in feeding (feeding guilds) compared with species that are taxonomically more distant, expecting that variability of feeding guilds within high-rank taxa (family) is retained at genus-level taxonomy and 2) taxonomic relatedness in feeding does not vary with ecosystem dimension.

Materials and Methods

Compiled dataset (Perciformes)

Data were retrieved from FishBase, a global database including more than 33,000 fish species inhabiting freshwater, brackish, and marine ecosystems (Froese and Pauly 2017), using the "species_list" and "ecology" functions in the R package "rFishBase" version 3.4.3 (Boettiger et al. 2012). This study focused on the order Perciformes, which is highly diverse and the largest vertebrate order (Nelson et al. 2016). Fish species were classified according to: 1) ecosystem type (marine and freshwater), 2) feeding guilds (herbivory, filter-feeding, and predation), and 3) taxonomy (families and genera) based on the categorical typologies supplied in FishBase. In FishBase, each fish species is classified as a single feeding guild according to quantitative reports of diet composition data (percentage of volume or weight) (see The DIET Table in FishBase; Palomares and Sa-A 2000). In addition, the main food type that dominated in the diet of each fish species was used to confirm feeding guild assignation. That said, 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.

The dataset included information about ecosystem type, feeding guild, main food, and taxonomic rank of 3,032 species of the order Perciformes distributed in 139 families and 922 genera. However, many families had a low number of species ($n < 30$), which prevented their use in the present analysis. Therefore, I performed a comparative study of 20 families based on the selection criteria of a minimum number of 30 species. Thus, the selection criteria of families were based on number of species, regardless of number of genera. Next, I performed a comparative study at the genus level only from the 20 selected families to test whether variability of feeding guilds within high-rank taxa (family) is retained at genus-level taxonomy. Because most genera in the dataset included low numbers of species, I restricted this analysis to genera with more than 10 species ($n > 10$), which included the 5 largest families within the dataset in terms of number of species (i.e., $n_{\mathrm{Cichlidae}} = 461$, $n_{\mathrm{Serranidae}} = 206$, $n_{\mathrm{Pomacentridae}} = 202$, $n_{\mathrm{Labridae}} = 199$, $n_{\mathrm{Blenniidae}} = 171$) (Table 1).

Statistics

For each taxon, the prevalence (i.e., the proportion of species with specific feeding strategy) of the feeding guilds was estimated. Each taxon (family or genus) was assigned as obligatory and facultative feeder regarding to feeding guilds. For example, obligatory herbivory included only herbivorous species within taxa (family or genus), whereas facultative herbivory was assigned to families and genera when there were species with feeding guilds other than herbivory, but herbivory was the most common feeding guild (>50%). The similarity in feeding guilds associated with the taxonomic relatedness of species was examined through a hierarchical cluster analysis (i.e., dendrogram) with heatmaps using the R package "gplots" (Warnes et al. 2016). The optimal number of clusters was determined using the R package "factoextra" (Kassambara and Mundt 2017) based on the K-means method with 999 bootstrap replicates (Monte Carlo resampling simulation). Clustering was performed using the Manhattan dissimilarity measure and Ward's clustering algorithm (Strauss and von Maltitz 2017). I ran 2 clustering approaches based on 1) family-level taxonomy and 2) genus-level taxonomy to account for dissimilarity in feeding guilds across taxonomic levels. The combination (dendrogram with heatmaps) provides a color-scaled representation of the dataset arranging groups (here taxonomy and feeding guilds) in a hierarchy based on the dissimilarity among them. Using previously described methods (Potapov et al. 2019), taxonomic and trophic (feeding guilds) dissimilarity matrices (calculated using "daisy" function in R package "cluster," Maechler et al. 2017), were correlated using Mantel test with 999 permutations in R package "ade4" (Dray and Dufour 2007) to test the null hypothesis that these 2 matrices are unrelated. Finally, the low numbers of freshwater species of Apogonidae

Table 1. Prevalence (%) of fish species according to feeding strategies (fil = filter-feeding, her = herbivory, pre = predation) for all the taxa (family and genus) included in this study

	Freshwater			Marine			Total		
	Fil	Her	Pred	Fil	Her	Pred	Fil	Her	Pred
Acanthuridae ($n = 31$)	–	–	–	29.0	67.7	3.2	29.0	67.7	3.2
Apogonidae ($n = 65$)	0	0	100	15.6	0	84.4	15.4	0	84.6
Blenniidae ($n = 171$)	0	0	100	2.5	95.0	2.5	2.5	94.4	3.1
Cirripectes ($n = 21$)	–	–	–	0	100	0	0	100	0
Ecsenius ($n = 51$)	–	–	–	2.0	98.0	0	2	98	0
Entomacrodus ($n = 24$)	–	–	–	0	100	0	0	100	0
Istiblennius ($n = 14$)	–	–	–	0	100	0	0	100	0
Salarias ($n = 13$)	–	–	–	0	100	0	0	100	0
Carangidae ($n = 100$)	–	–	–	9	0	91	9	0	91
Chaetodontidae ($n = 82$)	–	–	–	7.3	2.4	90.2	7.3	2.4	90.2
Cichlidae ($n = 461$)	13	17.8	69.2	–	–	–	13	17.8	69.2
Aulonocara ($n =15$)	0	0	100	–	–	–	0	0	100
Haplochromis ($n =119$)	7.6	12.6	79.8	–	–	–	7.6	12.6	79.8
Lethrinops ($n =14$)	21.4	0	78.6	–	–	–	21.4	0	78.6
Neolamprologus ($n = 14$)	14.3	0	85.7	–	–	–	14.3	0	85.7
Oreochromis ($n =18$)	44.4	55.6	0	–	–	–	44.4	55.6	0
Gobiidae ($n = 82$)	10	10	80	11.3	14.5	74.2	11.0	13.4	75.6
Haemulidae ($n = 62$)	–	–	–	4.9	0	95.1	4.9	0	95.1
Labridae ($n = 199$)	–	–	–	15.4	0.5	84.1	15.4	0.5	84.1
Bodianus ($n = 19$)	–	–	–	0	5.3	94.7	0	5.3	94.7
Cirrhilabrus ($n = 14$)	–	–	–	100	0	0	100	0	0
Coris ($n = 12$)	–	–	–	0	0	100	0	0	100
Halichoeres ($n = 21$)	–	–	–	0	0	100	0	0	100
Thalassoma ($n = 15$)	–	–	–	20	0	80	20	0	80
Lethrinidae ($n = 34$)	–	–	–	0	0	100	0	0	100
Lutjanidae ($n = 81$)	–	–	–	3.7	0	96.3	3.7	0	96.3
Mullidae ($n = 40$)	–	–	–	0	0	100	0	0	100
Nemipteridae ($n = 42$)	–	–	–	0	0	100	0	0	100
Pomacanthidae ($n = 50$)	–	–	–	16	32	52	16	32	52
Pomacentridae ($n = 202$)	–	–	–	48.5	44.1	7.4	48.8	43.8	7.4
Amphiprion ($n = 18$)	–	–	–	0	94.4	5.6	0	94.4	5.6
Chromis ($n = 52$)	–	–	–	94.2	0	5.8	94.2	0	5.8
Chrysiptera ($n = 17$)	–	–	–	64.7	35.3	0	64.7	35.3	0
Pomacentrus ($n = 30$)	–	–	–	26.7	70	3.3	26.7	70	3.3
Stegastes ($n = 17$)	–	–	–	0	100	0	0	100	0
Scaridae ($n = 45$)	–	–	–	0	100	0	0	100	0
Sciaenidae ($n = 125$)	0	0	100	5.1	0.8	94.1	4.8	0.8	94.4
Scombridae ($n = 45$)	–	–	–	6.7	0	93.3	6.7	0	93.3
Serranidae ($n = 206$)	–	–	–	20	0	80	20	0	80
Cephalopholis ($n = 15$)	–	–	–	0	0	100	0	0	100
Epinephelus ($n = 54$)	–	–	–	0	0	100	0	0	100
Pseudanthias ($n = 21$)	–	–	–	95.2	0	4.8	95.2	0	4.8
Sparidae ($n = 78$)	–	–	–	2.6	3.8	93.6	2.6	3.8	93.6

n = the number of species within each family/genus.

($n = 1$) and Blenniidae ($n = 1$) prevented their use in this study for comparisons between ecosystems (freshwater vs. marine). Therefore, only Gobiidae and Sciaenidae, which had higher numbers of freshwater species (20 and 7, respectively) enabled the identification of possible differences in feeding of fish (i.e., proportion of species with a feeding guild) between ecosystem types (freshwater and marine) at the family level.

Results

Overall, predators dominated in both ecosystems (Table 1). The cases with species represented in both ecosystem types (Gobiidae and Sciaenidae) provided evidence that the main feeding guilds are retained between marine and freshwater ecosystems (Table 1). Most families included species with several feeding guilds. Only 3 families (15%) contained species which were all predators (Lethrinidae, Mullidae, and Nemipteridae) and 1 family (5%) contained species which were all herbivore species (Scaridae) (Table 1). I identified 3 clusters with similar feeding at the family level with most families showing a high reliance on predation (80%, Figure 1). However, a few families (20%) had a higher dependency on herbivory (Blenniidae, Scaridae, and Acanthuridae) or filtering (Pomacentridae) habits (Figure 1).

I identified 5 clusters at the genus level, showing a clear dependence on predation (2 clusters including 43.5% of genera), herbivory (1 cluster including 30.4% of genera), or filtering (1 cluster

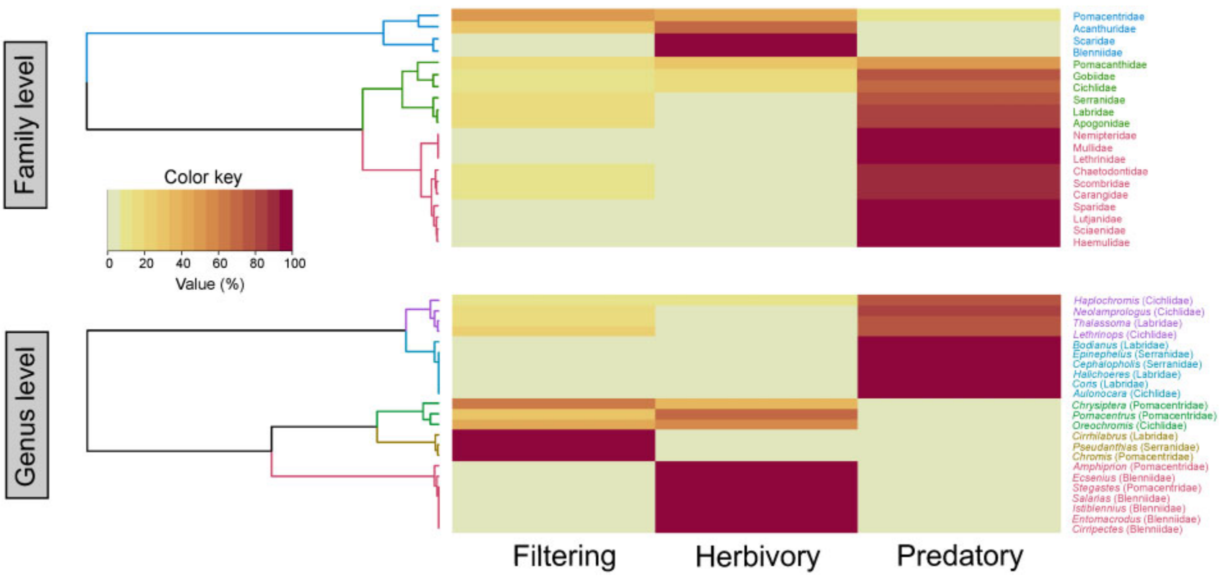

Figure 1. Hierarchical cluster analysis with heatmaps showing taxonomy-based differences in feeding of Perciformes fish at the family (upper panel) and genus (lower panel) levels. See Table 1 for raw data.

including 13.0% of genera), whereas the last cluster revealed similar prevalence for herbivory and filtering habits (Figure 1). Taxonomic and trophic dissimilarity matrices were correlated (Mantel test $R = 0.34$, simulated $p = 0.001$), indicating that matrices are positively associated. The prevalence of genera with a clear dependency on herbivory or filtering habits was 56.5% and thus higher than at the family level. Taxonomic relatedness in feeding guilds of species is not always retained at the genus level as 52.2% of the genera included species with different feeding habits (Table 1). For example, within the family Pomacentridae some genera included obligatory herbivory (*Stegastes*), facultative herbivory (*Amphiprion* and *Pomacentrus*), and facultative filtering (*Chromis* and *Chrysiptera*) species. That said, although some species belonging to the same genus showed a remarkable consistency in feeding and could be classified as herbivory (e.g., *Entomacrodus*, *Istiblennius*, *Salarias*, and *Cirripectes*), filtering (*Cirrhilabrus*), or predatory (*Cephalopholis*, *Epinephelus*, *Mullidae*, and *Nemipteridae*) taxa, I also in some cases observed high plasticity in feeding within the same genus (Figure 1; *Pomacentrus*, *Chrysiptera*, *Oreochromis*, and *Haplochromis*).

Discussion

The findings of this study underline the importance of a cause-and-effect relationship between taxonomy and feeding in fish species. In general, the order Perciformes showed a high dependence on predatory feeding, but still not all the species within the same family or genus had similar feeding guilds. In fact, in some cases, I observed high feeding plasticity within the same genus (*Pomacentrus*, *Chrysiptera*, *Oreochromis*, and *Haplochromis*), whereas other genera exhibited a remarkable feeding stability (*Entomacrodus*, *Istiblennius*, *Salarias*, *Cirripectes*, *Cirrhilabrus*, *Cephalopholis*, *Epinephelus*, *Mullidae*, and *Nemipteridae*). This identifies promising future research directions to explore why some genera are stable in feeding whereas others are different, including morphological, phylogenetic, and evolutionary considerations.

The first hypothesis (related species are more similar in feeding compared with species that are taxonomically more distant) was supported. I identified that family-level taxonomy covers higher prevalence of species with different feeding guilds than genus-level taxonomy (80% and 52.2%, respectively). Indeed, taxonomic and trophic dissimilarity matrices were positively associated, which supports recent conclusions that closely related taxa have more similar trophic niches than distantly related taxa as predicted by the "taxonomic signal" hypothesis (Potapov et al. 2019). This supports the general view that related species are more similar in feeding compared with species that are taxonomically and phylogenetically more distant (German and Horn 2006; Potapov et al. 2019). Thus, this study provides solid arguments that genera are more informative than families, underlining that low-rank taxonomic units provide a higher precision and thus a lower chance of information loss (Potapov et al. 2019). On the contrary, the results from the cluster analyses revealed an increasing dependency on herbivory or filtering habits from the family (20%) to the genus (56.5%) level. This underscores that the identification of taxonomy-based differences in feeding may be masked by the commonness of the feeding guilds of animals (here predation), and thereby taxonomy-based differences in uncommon feeding guilds (here herbivory or filtering) can be less evident at high taxonomic ranks (e.g., order or family) compared with lower taxonomic levels (genus). In taxa which are generally not predaceous, feeding consistency can be higher at family-level taxonomy such as many herbivorous fish families. For example, this study demonstrates that the family Blenniidae (mostly composed by herbivorous species) showed higher feeding consistency than predominantly herbivorous families (e.g., Acanthuridae and Pomacentridae) as indicated in Table 1. Thus, this article accepts the view that feeding often overlap with taxonomy (Simberloff and Dayan 1991; Potapov et al. 2016, 2019), but feeding can be rarely predictably above the generic level (Walter and Ikonen 1989). That said, future studies in trophic ecology require researchers to be cognizant of the limitations posed by taxonomic grouping (family or genus level) of data to avoid producing misleading results. In this regard, this study supports the view of Mueller et al. (2013) that fishes should be identified to genus and species level in ecological studies. Outcomes from this study can be used as true/false positive rate to account for what a given assumption would mean in other studies. For example, if it is assumed that all Cichlidae are predators, it would be correct ~70% of the time, but wrong ~30%. In addition, it is possible that in some cases genera may not be fully reliable as I observed high feeding plasticity within the same genus (*Pomacentrus*, *Chrysiptera*, *Oreochromis*, and *Haplochromis*). For example, *Oreochromis* comprised of filtering (44.4%) and herbivores (55.6%), being needed to go on species level. So, this study underscores the need to adequate taxonomic level to meet particular research objectives as coarser levels of taxonomic resolution may violate the assumptions (e.g., all species within a specific taxon have the same feeding guild) in the analyses. The use of coarse levels of taxonomic resolution can make difficult to achieve research objectives of studies assessing, for example, functional guilds, food–web interactions, and ecological similarity in aquatic communities. Therefore, the functional units (family, genus, or species) may depend on the research question, but this study underlines the precision and usefulness of genus as the functional unit in ecological studies using fish as model organisms. It should be kept in mind that with the current growing sophistication of analytical approaches available and meta-analytical opportunities (e.g., Zuur et al. 2009; Gurevitch et al. 2018), researchers need to be cognizant of the limitations posed by lumping of data to overcome heterogeneity, publication bias and inherent traits linked to the taxonomic and phylogenetic relatedness of species (e.g., German and Horn 2006; Logez et al. 2013; Sánchez-Hernández and Amundsen 2018; Potapov et al. 2019).

Because competition is considered an important factor in speciation (Winkelmann et al. 2014), it is reasonable to posit that competition forces closely related species to diverge and specialize in feeding as predicted by the "limiting similarity" hypothesis (MacArthur and Levins 1967; Abrams 1983; but also see Potapov et al. 2019). In addition, jaw morphology and other feeding apparatus characteristics likely play a crucial role in the identified taxonomy-based differences in dietary habits of fish (Linde et al. 2004; Takahashi et al. 2007; Lujan et al. 2012), but further feeding studies with a broader scope covering most bony fishes (Betancur et al. 2017) should be instigated to corroborate the implication of morphological species traits (e.g., mouth position and pectoral fins size) in the processes of promoting feeding diversification within the same taxa.

The second hypothesis (taxonomic relatedness in feeding does not vary with ecosystem dimension) was supported as taxonomic relatedness in feeding did not vary with ecosystem dimension. The cases with species represented in both ecosystem types (Gobiidae and Sciaenidae) provided evidence that the main feeding guilds are retained between marine and freshwater ecosystems. By contrast, Winemiller and Leslie (1992) observed that the proportion of herbivorous species is greater in freshwater than in marine ecosystems. These same authors demonstrated that the proportion of piscivorous species is greater in marine than in freshwater environments, but the prevalence (i.e., the percentage of occurrence in a species) can be higher in coastal lagoons (Winemiller and Leslie 1992). In contrast, Sánchez-Hernández and Amundsen (2018) underlined that nekton feeders in Blenniidae are more prevalent in freshwater environments. Thus, previous studies have reported evidence of differences in feeding guilds across ecosystem types (Winemiller and Leslie 1992; Sánchez-Hernández and Amundsen 2018). However, this study supports the view that differences in taxonomic relatedness in feeding does not vary with ecosystem dimension. As a caveat, caution should be exercised regarding this conclusion because the low numbers of freshwater species prevented an adequate comparison. It is possible that ecosystem type may have a key role in understanding processes promoting dietary specialization, but much attention needs to be paid to identify taxonomy-based differences in feeding guilds of fish across ecosystem types. Future research needs to be contextualized under evolutionary branching in feeding as it is thought that many families of the order Perciformes presumably originated from a carnivorous ancestor (e.g., Davis et al. 2012 and references therein). Thus, it is recommended that feeding guilds in the animal kingdom are examined across environments, so that novel ecological theories can be formulated and tested.

In conclusion, this study supports the view that taxonomic relatedness of species may not always imply similar feeding guilds, which underpins the importance of incorporating taxonomy information when contrasting the trophic ecology of different taxa (Romanuk et al. 2011; Potapov et al. 2016; Pomeranz et al. 2019). The study provides novel insights to trophic ecology theory by demonstrating that genera are more accurate than families in predicting feeding guilds of species, underlining the potential dangers of assuming feeding guilds at broader taxonomic scales.

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