



# Asymmetric foraging lowers the trophic level and omnivory in natural food webs

Junjie Zheng<sup>1</sup>  | Ulrich Brose<sup>2,3</sup>  | Dominique Gravel<sup>4</sup> | Benoit Gauzens<sup>2,3</sup>  |  
Mingyu Luo<sup>1</sup>  | Shaopeng Wang<sup>1</sup> 

<sup>1</sup>Institute of Ecology, College of Urban and Environmental Science, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, China

<sup>2</sup>EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

<sup>3</sup>Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany

<sup>4</sup>Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

## Correspondence

Shaopeng Wang

Email: shaopeng.wang@pku.edu.cn

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## Abstract

1. Food webs capture the trophic relationships and energy fluxes between species, which has fundamental impacts on ecosystem functioning and stability. Within a food web, the energy flux distribution between a predator and its prey species is shaped by food quantity–quality trade-offs and the contiguity of foraging. But the distribution of energy fluxes among prey species as well as its drivers and implications remain unclear.
2. Here we used 157 aquatic food webs, which contain explicit energy flux information, to examine whether a predator's foraging is asymmetric and biased towards lower or higher trophic levels, and how these patterns may change with trophic level. We also evaluate how traditional topology-based approaches may over- or under-estimate a predator's trophic level and omnivory by ignoring the asymmetric foraging patterns.
3. Our results demonstrated the prevalence of asymmetric foraging in natural aquatic food webs. Although predators prefer prey at higher trophic levels with potentially higher food quality, they obtain their energy mostly from lower trophic levels with a higher food quantity. Both tendencies, that is, stronger feeding preference for prey at higher trophic levels and stronger energetic reliance on prey at lower trophic levels are alleviated for predators at higher trophic levels.
4. The asymmetric foraging lowers trophic levels and omnivory at both species and food web levels, compared to estimates from traditional topology-based approaches. Such overestimations by topology-based approaches are most pronounced for predators at lower trophic levels and communities with higher number of trophic species.
5. Our study highlights the importance of energy flux information in understanding the foraging behaviour of predators as well as the structural complexity of natural food webs. The increasing availability of flux-based food web data will thus provide new opportunities to reconcile food web structure, functioning and stability.

## KEYWORDS

diet composition, feeding preference, flux-based food web, food quality, food quantity, predator, topology-based food web

## 1 | INTRODUCTION

Food webs characterize the complex trophic relationships and energy fluxes between species, which govern the functioning and stability of ecosystems (Barnes et al., 2018; Bascompte, 2010; Berlow et al., 2004; Gellner & McCann, 2012; Pimm & Lawton, 1978; Thompson et al., 2012). Within a food web, feeding links illustrate the direction of energy and elemental transfers from resources to consumers. For each species, the number of transfer steps from primary producers determines its trophic position in the ecosystem, referred to as the trophic level (Lindeman, 1942). The concept of trophic levels has served as a fundamental tool to understand the role of species in food webs and the functioning of ecosystems. That said, later studies demonstrated that predators often feed on prey from different trophic levels (i.e. omnivory), making it difficult to organize species into discrete layers, but instead into a trophic tangle (Pimm, 1982; Thompson et al., 2007). The prevalence of omnivory complicates the distribution of energy transfer and has raised debate on the validity of the trophic level concept (Cousins, 1987; Polis & Strong, 1996).

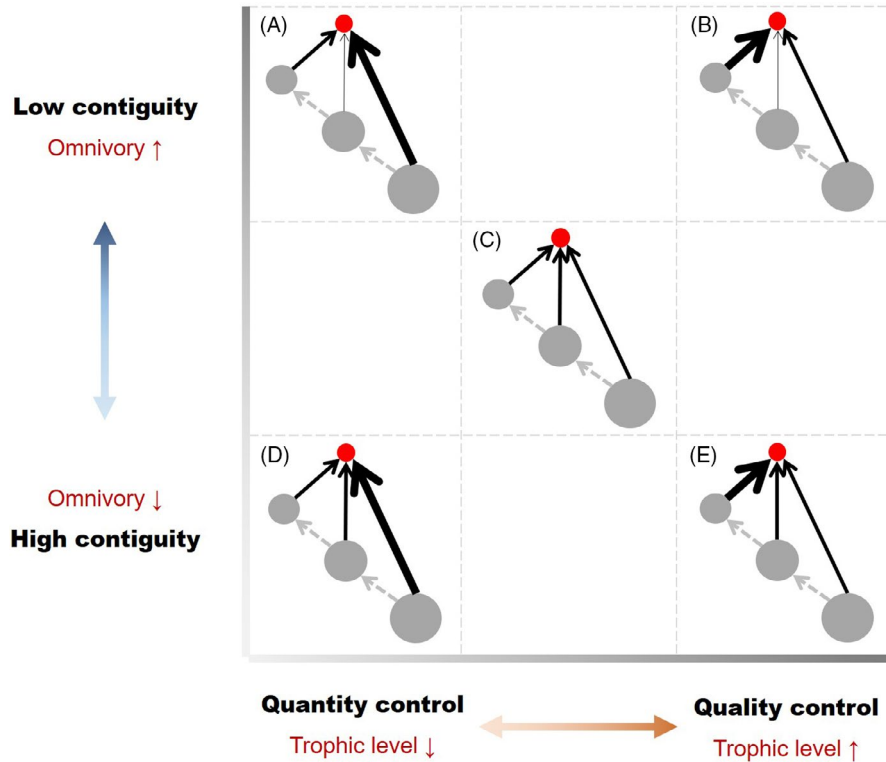
Existing evidence for omnivory is mostly derived from topology-based food webs, which contain only information on the presence and absence of feeding links between species. Such topology-based food webs are also referred to in the literature as binary food webs (e.g. Williams & Martinez, 2004) or connectance webs (e.g. Post, 2002). In quantifying omnivory, as well as other food web metrics, from such topology-based webs, it is implicitly assumed that energy fluxes between a predator and its multiple prey species are evenly distributed, thus ignoring the potential asymmetry in the energy flux distribution (Banašek-Richter et al., 2009). But accurate quantification of omnivory requires complete information about how a predator's feeding is split across its prey, which calls for food web data with explicit energy flux information. Here, we refer to such data as flux-based food webs, which were also referred to as quantitative food webs (e.g. Bersier et al., 2002; Gauzens et al., 2019) or energy webs (e.g. Post, 2002) in the literature. A few earlier studies have demonstrated the difference between omnivory indices calculated from topology- and flux-based webs (Banašek-Richter et al., 2009; Bersier et al., 2002; Williams & Martinez, 2004). By ignoring the foraging asymmetry among prey species, the topology-based approach was shown to overestimate the degree of omnivory in several natural food webs (Bersier et al., 2002; Williams & Martinez, 2004). That said, a systematic, quantitative evaluation on the prevalence of foraging asymmetry and its influence on food web structure is still lacking, despite the accumulating availability of high-resolution food web data (e.g. Brose et al., 2019; Colléter et al., 2012).

Given a predator, the distribution of energy uptake from its prey (i.e. foraging pattern) can be shaped by processes along two axes, forming four different functional motifs (Figure 1). The first axis captures the balance between food quality (stoichiometric match or nutrient content, i.e. what the predator

likes) and quantity (what is available; Burian et al., 2020; Jochum et al., 2017). That is, prey species with high quality (e.g. nutrient content) may be low in quantity (e.g. total number or biomass), and vice versa (Denno & Fagan, 2003; Sterner & Elser, 2002). For instance, in aquatic ecosystems, species at higher trophic levels tend to have a high nutrient concentration but low abundance, and species at low trophic levels have a low nutrient concentration but high abundance (Adams & Sterner, 2000; Chikaraishi et al., 2009, 2011; Cruz-Rivera & Hay, 2000; Mitra & Flynn, 2007; Pauly & Christensen, 1995; but see Lozano-Montes et al., 2011; Sergio et al., 2004). Thus, predator foraging may be biased towards either high or low trophic levels, depending on whether food quality or quantity is the major driver underlying the foraging process. Early observational studies suggested that omnivore predators gained their energy mostly from lower trophic levels (Hairston & Hairston, 1993; Hastings & Conrad, 1979). Such an asymmetric foraging towards lower trophic levels decreases the trophic level of predators (Figure 1A,D). However, the process of foraging comprises not only the ingestion of food but also digestion, which depends on the efficiency of assimilation. Assimilation efficiency generally increases with the quality of food, such as a higher nutrient concentration, better palatability or a higher stoichiometric match between resources and consumers, which leads to a higher energy transfer efficiency (Cebrian, 1999; Cebrian & Duarte, 1994; Jochum et al., 2017; Peace, 2015; Sterner & Elser, 2002). Thus, food quality may have significant effects on reproductive output and population growth, playing out via natural selection (Bukovinszky et al., 2012). Such a pursuit of food quality underpins foraging towards higher trophic levels, which increases the trophic level of predators (Figure 1B,E).

The second axis shaping the foraging pattern is the contiguity of diet, which captures the degree of concentration in a predator's diet distribution along with the axis of prey trophic level. Food web theory and data suggest that species can be organized along one or a few niche axes such that predators feed largely on species with lower niche values occurring within a certain range (Stouffer et al., 2006; Williams & Martinez, 2000). Similarly, among these realized feeding links, the predator may obtain energy mostly from a subset of species at neighbouring trophic levels, possibly because they have similar abundance (i.e. food quantity) or nutrient conditions (i.e. food quality). Such concentrated foraging along the axis of prey trophic level generates high contiguity, which decreases the omnivory degree of predators (Figure 1D,E; Figure S1). However, recent studies highlighted that the foraging process could be influenced by multi-dimensional niches (e.g. prey body mass, movement, colour, etc.), thus discontinuous foraging emerges if only one niche dimension is considered (Allesina et al., 2008; Brose et al., 2019). If predators exhibit low diet contiguity along with the axis of prey trophic level, the omnivory degree of predators will be high (Figure 1A,B; Figure S1).

In this study, we used a large dataset of aquatic flux-based food webs to investigate the distribution of energy fluxes among



**FIGURE 1** Illustration of different functional motifs for a four-species food web. Red node represents the predator and grey ones represent its three prey with varying trophic levels (indicated by their heights). Arrows indicate feeding links. The size of nodes and the thickness of arrows indicate the biomass quantity and the magnitude of energy fluxes. Given such a four-species food web (C), four different types of energy flux distributions can occur (A, B, D, E), which we refer to as 'functional motif'. A quality-dominated foraging process will result in feeding towards prey at higher trophic levels and thus a higher trophic level of the predator (B, E), whereas a quantity-dominated foraging process will result in feeding towards lower trophic levels and thus a lower trophic level of the predator (A, D). A higher diet contiguity represents more concentrated foraging along the axis of prey trophic level and thus a lower omnivory (D, E), and a lower diet contiguity represents more scattering foraging and thus a higher omnivory (A, B). Note that this figure illustrates the different functional motifs for a predator species with three prey, but in our data a predator can have 1–71 prey species (Figure S7)

prey species (Figure 1) in natural food webs and how it affects the empirical estimation of omnivory and trophic levels. We ask three questions. (a) Is predator foraging asymmetric and biased towards lower or higher trophic levels? (b) Do topology-based approaches over- or under-estimate a predator's trophic level and degree of omnivory, compared to flux-based approaches? (c) Are deviations between topology- and flux-based approaches related to species (e.g. predator trophic level) and community (e.g. ecosystem types, number of trophic species) properties? We hypothesize that predators will generally exhibit asymmetric foraging because of asymmetries in both food quality and quantity among prey species. Although predators may prefer prey at higher trophic levels, their overall foraging can be biased towards lower trophic levels due to the highly asymmetric distribution of biomass, which concentrates at lower trophic levels (Trebilco et al., 2013). Such asymmetric foraging towards lower trophic levels will not only reduce the trophic level but also the degree of omnivory due to increased diet contiguity (i.e. concentrated foraging at lower trophic levels). Consequently, we expect that topology-based approaches should generally overestimate a predator's trophic levels and omnivory, compared to flux-based approaches.

## 2 | MATERIALS AND METHODS

### 2.1 | Data

We gathered 157 Ecopath models that cover diverse ecosystem types including open ocean, coral reef, coastal lagoon, bar/fjord, upwelling, estuary, continental shelf and channel/strait (<http://ecoba.se.ecopath.org/>). Based on the mass-balance assumption, Ecopath models provide quantitative information on energy flows between species. Specifically, for any species, an equilibrium is achieved when energy intake equals energy export plus a predator's consumption:

$$B_j \times \left(\frac{P}{B}\right)_j \times EE_j = \sum_{i=1}^n B_i \times \left(\frac{Q}{B}\right)_i \times DC_{ij} + EX_j, \quad (1)$$

where  $B_j$  (t/km<sup>2</sup>) and  $(P/B)_j$  are biomass and production/biomass ratio of prey  $j$ , and  $EE_j$  corresponds to the 'ecotrophic efficiency', measured as the fraction of prey production utilized in the system.  $(Q/B)_i$  is the consumption/biomass ratio of predator  $i$ .  $DC_{ij}$  captures the diet composition of predator  $i$ , that is, the proportion of prey  $j$  in the diet of predator  $i$ , which can be estimated from stomach or gut content analysis,

isotope analysis, etc. (Coll  ter et al., 2012; Lassalle et al., 2012; Wolff et al., 2000).  $EX_j$  represents the total export production, including fishery catch rate, net migration rate and biomass accumulation rate. Note that in Ecopath models, species that have similar physiological characteristics and share the same prey and predators are aggregated as a trophic species (Christensen et al., 2005).

## 2.2 | Feeding preference, trophic level and omnivory

Using these flux-based food webs, we defined several metrics to characterize the foraging patterns and trophic structure. For predator  $i$ , the diet composition ( $DC_{ij}$ ) captures the proportion of energy that it obtained from prey  $j$ . The total amount of energy that predator  $i$  obtained from prey  $j$  (i.e.  $B_i \times \left(\frac{Q}{B}\right)_i \times DC_{ij}$ ) is jointly determined by the biomass of prey  $j$  ( $B_j$ ) and the feeding preference ( $FP_{ij}$ ) on prey  $j$ . Here, following de Ruiter et al., (1998), we defined the feeding preference by the rate for a unit biomass of prey  $j$  being eaten by its predator  $i$ :

$$FP_{ij} = \frac{B_i \times \left(\frac{Q}{B}\right)_i \times DC_{ij}}{B_j}.$$

Such a definition is an equivalent of interaction coefficients in Lotka–Volterra models, which serves as a first linear approximation of energy fluxes around the equilibrium (de Ruiter et al., 1998). We then defined the trophic level and omnivory of a species based on the flux information. The species  $i$ 's trophic level ( $TL_i$ ) was defined as one plus the average of prey trophic levels, weighted by the diet proportion of the respective prey species (Levine, 1980; Williams & Martinez, 2004):

$$TL_i^{(F)} = \sum_{j \in \{\text{prey of } i\}} TL_j \times DC_{ij} + 1, \quad (2)$$

where the superscript '(F)' indicates that metrics are calculated based on flux information. The degree of omnivory for a predator species was then defined as the weighted variance of its prey's trophic level around their weighted average (Levine, 1980):

$$O_i^{(F)} = \sum_{j \in \{\text{prey of } i\}} \left( TL_j^{(F)} - \left( TL_i^{(F)} - 1 \right) \right)^2 \times DC_{ij} \quad (3)$$

Note that since the squared deviation between prey's trophic level and their average was also weighted by the diet proportion,  $O_i^{(F)}$  emphasized the contribution of the dominant prey (see Figure S1). Based on species-level metrics of trophic level, we derived the community-wide average trophic level ( $TL_{ave}^{(F)}$ ) as the simple average of trophic level across all species within the food web. We also calculated the community-wide average omnivory ( $O_{ave}^{(F)}$ ) as the simple average of omnivory across all predators (with plants and herbivores excluded). Lastly, we defined the maximum trophic level of the food web ( $TL_{max}^{(F)}$ ) by the highest trophic level across all predators (Wang & Brose, 2018).

Trophic level and omnivory could also be computed with binary information, by ignoring the flux information, that is,

$$TL_i^{(T)} = \frac{1}{K_i} \sum_{j \in \{\text{prey of } i\}} TL_j + 1, \quad (4)$$

$$O_i^{(T)} = \frac{1}{K_i} \sum_{j \in \{\text{prey of } i\}} \left( TL_j^{(T)} - \left( TL_i^{(T)} - 1 \right) \right)^2, \quad (5)$$

where  $K_i$  denotes the total number of prey species for predator  $i$  and the superscript '(T)' indicates that metrics were calculated based solely on topology information. Note that the topology-based metrics can be regarded as a special case of flux-based ones when the feeding proportions ( $DC_{ij}$ ) are equal among all prey species. Community-wide average trophic level ( $TL_{ave}^{(T)}$ ), omnivory ( $O_{ave}^{(T)}$ ) and maximum trophic level ( $TL_{max}^{(T)}$ ) were derived similarly for each food web.

We quantified the differences between flux- and topology-based metrics of species and community-averaged trophic level and omnivory as the relative deviation normalized by flux-based metrics:

$$\Delta TL = \frac{TL^{(T)} - TL^{(F)}}{TL^{(F)}}, \quad (6)$$

$$\Delta O = \frac{O^{(T)} - O^{(F)}}{O^{(F)}}, \quad (7)$$

$$\Delta TL_{max} = \frac{TL_{max}^{(T)} - TL_{max}^{(F)}}{TL_{max}^{(F)}}. \quad (8)$$

Positive or negative deviations quantify the degree at which the topology-based approach overestimates or underestimates the trophic levels and omnivory, compared to the flux-based approach. We calculated the species-level deviation in trophic level for all 4,135 predator species that had at least three prey species; to avoid zeros in the denominator, we calculated the deviation in omnivory only for predators with  $O^{(F)} > 0.01$ , resulting in 4,037 out of 4,135 predators.

## 2.3 | Statistical analysis

We first examined how a predator's diet composition (DC) and feeding preference (FP) were related to the prey trophic level. We used mixed-effects models to test their overall relationships across all food webs, where DC or FP is the dependent variable, prey trophic level is the fixed effect, and the food web and the predator species nested within food web are random effects. We also tested these relationships at individual food web or predator levels. Specifically, for each food web, we used a mixed-effect model to explain DC or FP with prey trophic level as the fixed effect and the predator species as the random effect; for each of the 4,135 predators with at least three prey species, we performed simple regression models between DC or FP and prey trophic level.

We then tested whether these relationships changed with predator trophic levels. We used mixed-effects models with DC or FP as the dependent variable, prey trophic level and the interaction between prey and predator trophic levels as fixed effects, and the food web as the random effect. If the coefficient of the interaction term has the same sign as that of the prey trophic level, it suggests that the relationships between DC or FP and prey trophic levels are stronger for predators at higher trophic levels. In contrast, if they have opposite signs, the relationships between DC or FP and prey trophic levels are weaker for predators at higher trophic levels.

Based on metrics of trophic level and omnivory estimated from topology- and flux-based approaches, we explored how the deviation between these two approaches ( $\Delta TL$ ,  $\Delta O$  and  $\Delta TL_{\max}$ ) might depend on species- and community-level properties. For species-level metrics, we explored how the deviation changed with the predator trophic level using a mixed-effect model, with the relative deviation of specific metrics as the dependent variable, predator trophic level as the fixed effect and the food web as the random effect. For community-level metrics, we first tested whether the deviation differed among ecosystem types using the Tukey test; we then tested whether it was related to species diversity using a mixed-effects model with the ecosystem type as the random effect.

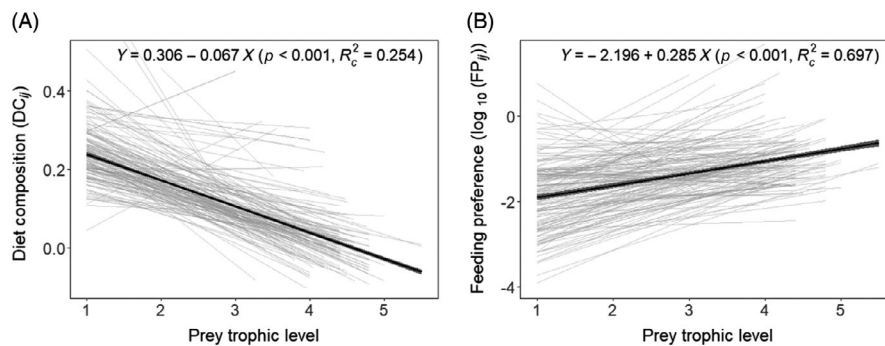
### 3 | RESULTS

Our mixed-effects models showed that given a predator, energy sources tend to come from the lowest trophic levels despite a preference for higher trophic levels (Figure 2). These overall trends were

highly consistent at the individual food web or predator species level. Among all 157 food webs, 151 (96%) exhibited negative relationships between diet composition (DC) and prey trophic level, and 137 (87%) exhibited positive relationships between feeding preference (FP) and prey trophic level (Figure 2). At the predator species level, 71% of the 4,135 predators that had at least three prey species exhibited a negative relationship between its DC and prey trophic level (12% with  $p < 0.05$ ), whereas 71% exhibited a positive relationship between FP and prey trophic level (21% with  $p < 0.05$ ).

We further tested whether the relationships between DC or FP and prey trophic level depended on predator trophic level, using mixed-effects models with both prey trophic level and the interaction between prey and predator trophic levels as fixed effects (Table 1). For DC, the interaction between prey and predator trophic levels is marginally positive (coefficient = 0.0008,  $t = 1.70$ ,  $p = 0.089$ ). This contrasts with the negative main effect of prey trophic level, suggesting that predators at higher trophic levels have a relatively weaker tendency for food quantity. For FP, in contrast to the positive effect of the prey trophic level, the interaction between prey and predator trophic levels is negative (coefficient =  $-0.23$ ,  $t = -53.7$ ,  $p < 0.001$ ), suggesting that predators at higher trophic levels have a relatively weaker preference for food quality.

We then calculated the trophic level and omnivory for all 4,037 predator species (that feeds on at least three prey species and  $O^{(F)} > 0.01$ ) and compared their values between flux- and topology-based calculations. We found that across all predator species, 74% exhibited a lower flux-based trophic level ( $TL^{(F)}$ ) than their topology-based counterpart ( $TL^{(T)}$ ) by at least 5%, and 89%



**FIGURE 2** Relationship between diet composition (A) or feeding preference (B) with prey trophic level. The black line shows the overall relationship across all 157 food webs, obtained from a mixed-effects model with nested random effects (i.e. the predator species nested within the food web). The grey lines represent the fitted relationship for each food web based on mixed-effects models with the predator as the random effect (see Figure S8). Note that the feeding preference in (B) is on a logarithm scale

	DC			FP		
	Estimate	t	p	Estimate	t	p
Intercept	0.28	64.9	<0.001	-1.92	-43.4	<0.001
Prey TL	-0.059	-24.7	<0.001	0.99	48.1	<0.001
Prey TL × predator TL	0.00084	1.7	0.089	-0.23	-53.7	<0.001

**TABLE 1** Relationship of DC and FP with prey trophic level (prey TL) and the interaction between prey and predator trophic levels (predator TL), using mixed-effects models with the food web as the random effect

exhibited a lower flux-based omnivory ( $O^{(F)}$ ) than their topology-based counterpart ( $O^{(T)}$ ) (Table 2). Only 5% of predators exhibited a higher flux-based trophic level ( $TL^{(F)}$ ) than their topology-based counterpart ( $TL^{(T)}$ ), and only 8% of predators exhibited a higher

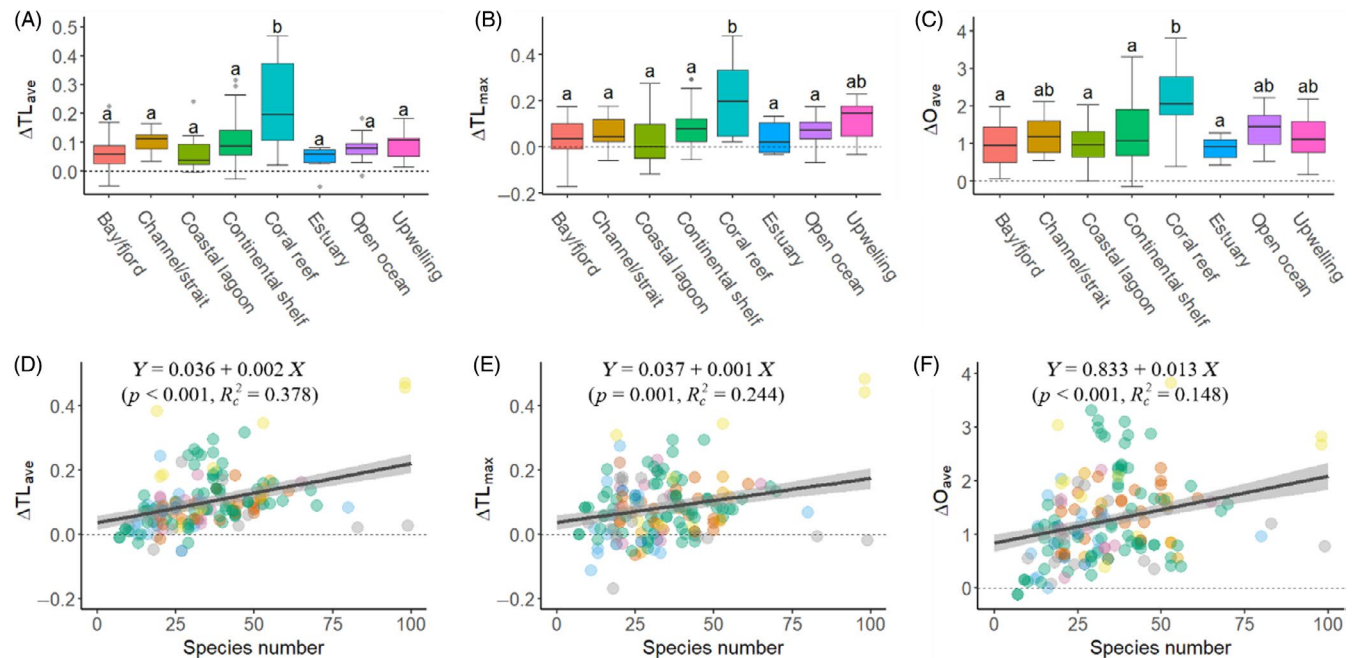
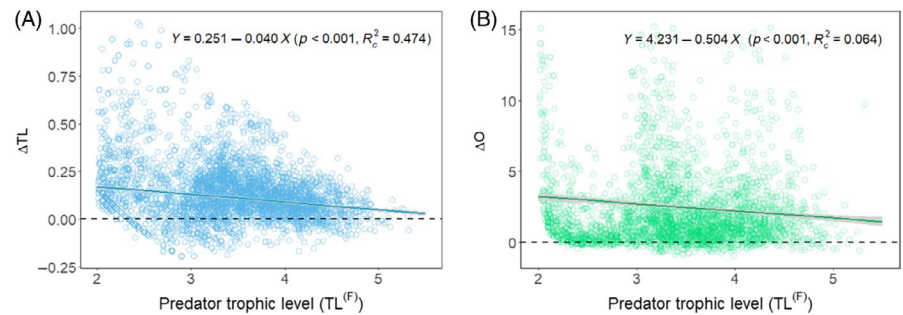
flux-based omnivory ( $O^{(F)}$ ) than their topology-based counterpart ( $O^{(T)}$ ) (Table 2). Combined, 68% of all predator species exhibited lower  $TL^{(F)}$  and  $O^{(F)}$  compared to their topology-based counterparts (Table 2). In comparison, 4% of predators exhibited a lower  $TL^{(F)}$  and a higher  $O^{(F)}$ , 4% exhibited a higher  $TL^{(F)}$  and a lower  $O^{(F)}$ , and 1% exhibited a higher  $TL^{(F)}$  and  $O^{(F)}$ , compared to their topology-based counterparts. For only 1% of predators, their trophic level and omnivory are similar between flux- and topology-based metrics, that is, with relative differences <5%. Therefore, the foraging pattern captured by Figure 1D was proved most prevalent, suggesting that predators forage towards lower trophic levels and exhibit high diet contiguity in natural aquatic food webs. This result was robust when a higher threshold was used to define a significant difference (e.g. 10% or 20%, see Table S1).

The topology-based metrics overestimated the predator trophic level by on average 14% (-20% to 103%) and the omnivory by 262% (-97% to 14,180%). Moreover, for both trophic level and omnivory, the relative deviation between flux- and topology-based food webs decreased with predator trophic level (Figure 3). At the community

**TABLE 2** Comparison of flux- and topology-based metrics of trophic levels and omnivory.  $TL^{(F)}$  and  $TL^{(T)}$  represent the predator's trophic level estimated from flux- and topology-based approaches, respectively, and similarly for the omnivory index,  $O^{(F)}$  and  $O^{(T)}$ . Each value represents the proportion of predators that fall into different categories characterizing the relationships between  $TL^{(F)}$  and  $TL^{(T)}$  and between  $O^{(F)}$  and  $O^{(T)}$ , where a significant difference (either higher or lower) is defined if the relative deviation is <5%. Bold values correspond to the four corners in Figure 1. Results derived from difference of 10% and 20% are shown in Table S1

	$TL^{(F)} < TL^{(T)}$	$TL^{(F)} \approx TL^{(T)}$	$TL^{(F)} > TL^{(T)}$
$O^{(F)} > O^{(T)}$	4%	3%	1%
$O^{(F)} \approx O^{(T)}$	2%	1%	0%
$O^{(F)} < O^{(T)}$	<b>68%</b>	17%	4%

**FIGURE 3** Deviation between topology- and flux-based metrics of trophic level (A) and omnivory (B), as a function of predator trophic level. Each point corresponds to a predator, and the solid lines represent results from linear mixed-effect regressions across 4,037 predators (i.e. predators with at least three prey species and  $O^{(F)} > 0.01$ ). The dashed lines indicate zero deviation



**FIGURE 4** Deviation between flux- and topology-based estimates of average trophic level (A, D), maximum trophic level (B, E) and omnivory (C, F), as a function of ecosystem types (A-C) or species number (D-F). The relative deviations exhibit significant differences among the eight types of ecosystems ( $p < 0.05$  for all) (A-C), and they increase with species number of the food web ( $p < 0.001$  for all) (D-F). Eight ecosystem types are colour-coded

level, the topology-based average trophic level, maximum trophic level and omnivory were significantly higher than their flux-based counterparts (Figure S2), with an overestimation of 9.8% (–5% to 47%), 8.3% (–17% to 48%) and 126.9% (–14% to 382%), respectively. The magnitude of overestimation depended on the ecosystem type and species diversity. Food webs from coral reef ecosystems exhibited the largest deviations between flux- and topology-based metrics, and those from estuary exhibited the smallest deviations (Figure 4A–C). Moreover, ecosystems with higher number of trophic species exhibited larger deviations (Figure 4D–F).

## 4 | DISCUSSION

Our study reveals the prevalence of asymmetric foraging in natural aquatic food webs. Although predators prefer prey at higher trophic levels with potentially higher food quality, they obtain their energy mostly from lower trophic levels with a higher food quantity. Such tendencies, that is, stronger feeding preference for prey at higher trophic levels and stronger energetic reliance on prey at lower trophic levels, are alleviated for predators at high trophic levels. By ignoring such asymmetric foraging patterns, the traditional topology-based approaches overestimate the trophic level and omnivory at both species and community levels. Such overestimations are most pronounced for predators at lower trophic levels and communities with higher species diversity.

### 4.1 | The prevalence of asymmetric foraging

The foraging behaviour of predators is determined by both food quality and quantity, which often exhibit trade-offs (Burian et al., 2020). Our results demonstrate that predators prefer prey at higher trophic levels (Figure 2B), which usually have a higher nutrient concentration in their body tissues (Jochum et al., 2017; Lang et al., 2017; Sterner & Elser, 2002). Our results also show that species at higher trophic levels have low biomass (Figure S3a), consistent with the classic paradigm of biomass pyramid (Trebilco et al., 2016). Whereas the low biomass of high-quality food may still satisfy the nutrient requirements of predators, high-quantity food (even though low-quality) is necessary to balance their carbon requirements. To cope with the excess carbon of low-quality food, one solution is compensatory feeding, where the excess carbon is excreted (Jochum et al., 2017). Our results reveal that food quantity outperforms food quality. Thus, a predator's foraging is biased towards more abundant prey at lower trophic levels. In other words, although predators prefer prey at higher trophic levels, they have to rely on low-quality but more abundant food to balance their total energy and nutrient requirement (Mitra & Flynn, 2007; Figure 2A; Figure S3b).

We found that the tendency of feeding on lower trophic levels, or the degree of foraging asymmetry, decreased with predator trophic level. This result contrasts with our expectation that the largest

discrepancy in food quality at the plant–animal interface should increase the relative importance of food quality at lower trophic levels, thus weakening the foraging asymmetry of predators at lower trophic levels. One possible explanation for the alleviated foraging asymmetry at higher trophic levels is that the asymmetry in prey biomass is also much more pronounced between two lower trophic levels than that between two higher ones. This can be understood from the fact that the biomass pyramid is usually presented on a logarithmic scale; thus, the absolute difference in biomass is much larger between two lower trophic levels than that between two higher ones (Figure S3a). Therefore, for a predator feeding at lower trophic levels, the dramatic decay of prey biomass with trophic levels far outweighs the effect of prey's ascending quality, leading to a stronger quantity control over the foraging process. For predators at higher trophic levels, prey biomass is less asymmetric and thus the quantity control is relatively alleviated (Figure S4).

Our results revealed a consistently lower flux-based omnivory compared to its topology-based counterpart, suggesting that predators obtained their energy mostly from a narrow range along the axis of prey trophic levels (Figure 1; Figure S1). Previous studies have shown that trophic interactions within a food web exhibit some degree of intervality, that is, among all potential prey species, predators feed only on those occurring in an interval along some niche axis (i.e. realized predation; Stouffer et al., 2006). Here, our results further demonstrated a high degree of diet contiguity in the foraging process, that is, among all realized prey species, predators obtain their energy mostly from a subset of prey that occurs within a narrow range along the trophic level axis. We note that such concentrated foraging may be partially explained by the quantity control, that is, predators forage asymmetrically towards prey species at lower trophic levels. An interesting direction for future studies is to test the generality of the diet contiguity along other niche axes, for example, whether predators obtain energy mostly from prey within a narrow range of body size or phosphorus concentration (Schneider et al., 2016; Zhou & Declerck, 2019).

### 4.2 | Topology-based approaches overestimate the trophic level and degree of omnivory

The asymmetric foraging of predators resulted in deviations between topology- and flux-based measures of trophic level and omnivory. By ignoring the foraging asymmetry towards lower trophic levels, the topology-based approach significantly overestimates the trophic level of predators across 157 food webs from eight types of ecosystems, at both species (Figure S5) and community levels (Figure S2, by on average 9.8% for the average trophic level and 8.3% for the maximum trophic level). Moreover, by ignoring the contiguity of energy flux across the axis of prey trophic level, the topology-based approach substantially overestimates the degree of omnivory by 126.9%, thus supporting the functional motif *d* depicted in Figure 1.

The lower omnivory revealed by the flux-based approach is consistent with early results from Bersier et al., (2002) and Williams and

Martinez (2004), although these studies used different definitions of omnivory. While we have used the amount of flux as weights in the calculation of omnivory (similar in Williams & Martinez, 2004), Bersier et al., (2002) derived their omnivory index using weights by prey species' biomasses. Using a large dataset, our study extends these early results and concludes a consistent overestimation of omnivory by topology-based approaches (Thompson et al., 2007). Thus, although omnivory occurs commonly in nature, its strength and impact might be much weaker than previously thought from the traditional topology-based perspective. The lower omnivory revealed here may contribute to some extent to relaxing the debate on the trophic level concept, where the relevance of (integer) trophic levels were questioned by the prevalence of feeding across trophic levels in natural food webs (e.g. Polis & Strong, 1996; Thompson et al., 2007). In particular, it explains the apparent conflict noted by Polis and Strong (1996) that omnivory may predominate but that strong food chain interactions such as trophic cascades also appear to be common.

The deviations between topology- and flux-based measures decreased with the predator trophic level (Figure 3), which is also explained by the alleviated quantity control and the relatively more even distribution of energy flux at higher trophic levels (Table 1, Figures S3a and S4). Deviations in the community-level metrics (i.e. average and maximum trophic level and the average degree of omnivory) exhibited large variations across ecosystems and increased with the number of trophic species. The larger deviations in more diverse ecosystems may be understood from the association between species number and network properties. Specifically, the number of trophic species has been shown to be positively related to the average generality (i.e. the number of prey species given the predator) and diet continuity (Cirtwill et al., 2015; Riede et al., 2010). A larger generality can increase the probability of including prey species from lower trophic levels, leading to a larger overestimation of topology-based approaches. Also, as explained above, higher diet contiguity (or concentrated foraging) can increase the deviation between flux- and topology-based approaches. Among ecosystems, the coral reef ecosystems exhibited the largest deviations in all metrics of trophic level and omnivory (Figure 4). To understand this, we examined the patterns of species number and biomass distributions across ecosystems. Although coral reefs usually host a higher biodiversity (Paulay, 1997), the number of trophic species does not differ between coral reef and other types of ecosystems in our data (Figure S6a), possibly due to the aggregation of functionally similar species in Ecopath models (see Section 4.3). On the other hand, we find that the coral reef ecosystems exhibit a relatively faster decay of biomass across trophic levels than other ecosystem types (though statistically insignificant; Figure S6b). Such a faster biomass decay implies a stronger quantity control and a higher foraging asymmetry among prey, which may explain the larger deviations in coral reef ecosystems. Taken together, the dependency of overestimation on ecosystem types and biodiversity suggests that testing hypotheses on inter-ecosystem differences that have been explored based on analyses of topological webs should be reassessed.

### 4.3 | Limitations

Our analyses required explicit information of biomass stock and energy fluxes, for which the Ecopath models provided a valuable source of information on food webs across aquatic ecosystem types. That said, several limitations associated with the Ecopath data need to be acknowledged. First, parameters in Ecopath models (i.e.  $B_j$ ,  $(P/B)_j$ ,  $(Q/B)_j$ ,  $EE_j$ ) are not all derived from observations but instead involve missing parameters that are estimated based on the mass-balance principle. Such estimation processes induce uncertainty in model parameters and calculations of our flux-based metrics, which may potentially influence our results. Moreover, in Ecopath models, species generally represent aggregated groups that integrate different ontogenetic life stages. However, from juvenile to adult, the trophic level can either increase (e.g. from herbivore to carnivore; Neill & Peacock, 1980) or decrease (e.g. from carnivore to herbivore; Stoner, 1980; Stoner & Livingston, 1984). Aggregation across ontogenetic stages may thus obscure the foraging patterns and cause biased estimation of trophic levels and omnivory. Besides, species with similar functions (e.g. prey and predators) are often aggregated in Ecopath models, particularly for taxa at lower trophic levels. Such aggregation may cause an overestimation of quantity control, because the energy uptakes from different prey at lower trophic levels are summed and regarded as from one prey. But such aggregation should have a weak effect on the quality control, which was defined as the ratio of (summed) energy uptake and (summed) prey biomass.

Some of these problems could be solved by new datasets comprising food webs of high resolution, but in their current version they do not contain population biomasses or energy fluxes (Brose et al., 2019). Until such high-quality data are available to resolve the above limitations, our study fills an important gap in our understanding of quantitative food web structures. While the limited resolution of parameters and trophic species in Ecopath models can potentially bias the quantification of trophic level and omnivory, our exploratory tests of robustness suggest that the patterns that we revealed using a larger number of Ecopath models may transcend the above limitations and biases of individual Ecopath model (Appendix S2). That said, we advocate the calling for food web data with highly resolved parameters and ontogenetic stages to advance our understanding of foraging patterns, as well as to assess the impact of data quality on food web inference (Mougi, 2017; de Roos, 2018; Rudolf & Lafferty, 2011).

## 5 | CONCLUSIONS

Our study demonstrates the prevalence of asymmetric foraging in natural aquatic food webs, which causes a systematic overestimation of trophic level and omnivory by traditional topology-based approaches. Our results highlight the importance of flux-based approaches in understanding the structure of food webs and their relationship with ecosystem functioning and stability. On the one hand, the prevalence of omnivory in natural food webs has raised debate on the validity of the



trophic level concept (Cousins, 1987; Polis & Strong, 1996; Thompson et al., 2007). The significantly lower omnivory after incorporating flux information may contribute to relaxing the debate on the trophic level concept to some extent (Polis & Strong, 1996; Williams & Martinez, 2004). On the other hand, flux-based quantification of food web structure may allow a better understanding of ecosystem functioning and stability (Berlow et al., 2004; Rooney et al., 2006). For instance, omnivory has been shown to either increase or decrease the stability of food webs (Long et al., 2011; McCann & Hastings, 1997; Pimm & Lawton, 1978; Wang et al., 2019). The energy flux perspective provides a key to reconcile these contrasting results by clarifying that weak omnivorous interactions stabilize population dynamics, whereas strong interactions destabilize them (Gellner & McCann, 2012). Moreover, recent theory predicted that the primary productivity of the ecosystem increased exponentially with the maximum trophic level (Wang & Brose, 2018); thus, an overestimate of the maximum trophic level will lead to a substantially overestimated primary productivity. Taken together, we conclude that the flux-based approach provides new opportunities to reconcile food web structure, functioning and stability, which should be better adopted in future studies. Such approaches will benefit from the advance of both empirical and theoretical tools, which contributes to high-resolution food web data and new techniques to derive the energy flux information (Brose et al., 2019; Gauzens et al., 2019).

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#### AUTHORS' CONTRIBUTIONS

S.W. conceived the idea; S.W., U.B. and J.Z. designed the methodology; J.Z. collected and analysed the data; J.Z. and S.W. wrote the first draft of the manuscript; all authors contributed substantially to the revision and interpretation of the results.

#### DATA AVAILABILITY STATEMENT

Data are available from EcoBase: <http://ecobase.ecopath.org/>

#### ORCID

Junjie Zheng  <https://orcid.org/0000-0002-6794-3586>

Ulrich Brose  <https://orcid.org/0000-0001-9156-583X>

Benoit Gauzens  <https://orcid.org/0000-0001-7748-0362>

Mingyu Luo  <https://orcid.org/0000-0002-2975-5218>

Shaopeng Wang  <https://orcid.org/0000-0002-9430-8879>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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