

## TROPHIC LEVELS AND TROPHIC TANGLES: THE PREVALENCE OF OMNIVORY IN REAL FOOD WEBS

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**Abstract.** The concept of trophic levels is one of the oldest in ecology and informs our understanding of energy flow and top-down control within food webs, but it has been criticized for ignoring omnivory. We tested whether trophic levels were apparent in 58 real food webs in four habitat types by examining patterns of trophic position. A large proportion of taxa (64.4%) occupied integer trophic positions, suggesting that discrete trophic levels do exist. Importantly however, the majority of those trophic positions were aggregated around integer values of 0 and 1, representing plants and herbivores. For the majority of the real food webs considered here, secondary consumers were no more likely to occupy an integer trophic position than in randomized food webs. This means that, above the herbivore trophic level, food webs are better characterized as a tangled web of omnivores. Omnivory was most common in marine systems, rarest in streams, and intermediate in lakes and terrestrial food webs. Trophic-level-based concepts such as trophic cascades may apply to systems with short food chains, but they become less valid as food chains lengthen.

**Key words:** *food webs; meta-analysis; null models; omnivory; trophic levels; trophic position.*

### INTRODUCTION

The importance of trophic omnivory for the structure and dynamics of food webs is a long-standing controversy in ecology (Cousins 1987, Burns 1989, Polis 1991). Trophic position represents the number of feeding links separating an organism from the base of production. Primary producers occupy trophic position 0, herbivores have a trophic position of 1, and higher consumers have a trophic position reflecting the mix of resources which they feed upon. Traditionally, ecology has viewed food webs as a collection of linear chains, with grazers feeding on plants, predators feeding on grazers, and clear distinctions between trophic levels. Under this scenario, organisms' trophic positions tend to fall at integer values defining discrete trophic levels such as grazers or predators. Trophic omnivory occurs when taxa feed at more than one trophic level, resulting in non-integer trophic positions.

The prevalence of omnivory has fundamental importance for our understanding of food web dynamics (Holt and Polis 1997, Vandermeer 2006), and for that reason has been the subject of vigorous debate (Polis and Strong 1996, Hairston and Hairston 1997). Theoretical models suggest that omnivory may stabilize complex food webs (McCann and Hastings 1997, Borrvall et al. 2000, Krivan 2000, Emmerson and Yearsley 2004; but

see Vandermeer 2006), and there is some evidence that very large food webs do support high levels of omnivory (e.g., Goldwasser and Roughgarden 1993, Fagan 1997, Woodward and Hildrew 2002). The most recent of these studies has suggested that omnivory diffuses top-down influences through food webs and reduces the probability of trophic cascades (Bascompte et al. 2005). Strong (1992) proposed that trophic cascades are unlikely in terrestrial ecosystems as omnivory "predisposes damping and subdivision of consumer influence," with food webs forming a "trophic tangle" where "consumption cannot tumble down in a ladder-like unified fashion." This suggests that terrestrial systems have more omnivory than aquatic systems where taxa tend to occupy integer trophic positions.

Two recent syntheses of published food webs have come to differing conclusions whether omnivory is a prevalent feature in natural ecosystems. In a review of published food webs Arim and Marquet (2004) found that between 58% and 87% of taxa fed on more than one trophic level. Williams and Martinez (2004) found somewhat lower rates in four food webs, finding that 54% of taxa could be "unambiguously assigned to a discrete trophic level." The question remains whether trophic levels can accurately or usefully characterize real food webs despite the presence of omnivory. If omnivory is frequent, does it predominate in particular ecosystem types? We compared the distribution of trophic positions in the real webs with those from randomizations of the food web matrices to ask three questions: (1) Are species' trophic positions distributed

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continuously or in an aggregated fashion about integer values? (2) Does the frequency of omnivory vary among ecosystems? and (3) Is omnivory more common among taxa at higher or lower trophic positions? We employ two null models where all animal taxa (null model 1) and all non-herbivores (null model 2) feed randomly throughout the web to ask whether real webs show more aggregation of trophic positions than expected in the absence of any biological constraints.

#### MATERIAL AND METHODS

We tested whether organisms' trophic positions tended to be aggregated around discrete trophic levels by analyzing 58 food webs containing between 18 and 200 taxa. The webs came from four different ecosystems: marine/estuarine (10 webs), terrestrial (14 webs), streams (28 webs), and lakes (six webs; Appendix). These webs were chosen as the most complete currently available in the literature based on degree of taxonomic resolution (at least 50% identified to species) and number of taxa included (at least 20 taxa). Topological maps of feeding interactions in food webs have been widely criticized on a number of grounds (e.g., Paine 1988, Pimm and Kitching 1988, Closs 1991, Cohen et al. 1993). Many webs show low levels of taxonomic resolution, particularly at low trophic positions. Webs are also not constructed using standard criteria for assigning links and may therefore include rare interactions or ignore important ones. We acknowledge all of these criticisms and urge caution in interpreting patterns observed in topological food webs. While the utility of binary food webs has been challenged (Paine 1988), studies using well resolved food webs have shown that they can meaningfully quantify ecological processes such as invasion, and changes in productivity and disturbance (Hall and Raffaelli 1991, Martinez 1991, Woodward and Hildrew 2001, Thompson and Townsend 2004). Since the webs were constructed using a range of approaches, common patterns across webs will indicate that similar forces shape the distribution of trophic position. All of the webs we analyzed were constructed based on extensive and thorough analysis of diet contents of a wide range of taxa, and are therefore useful for elucidating patterns among species and ecosystems.

Trophic positions (TP) were calculated for every taxon based on its position in the food web using the "prey-averaged technique" (Williams and Martinez 2004). This metric is based on the TP of all prey in the diet of a consumer, where primary producers are assigned a TP = 0, and assumes that all links are quantitatively equivalent (each taxon eats the same amount of every prey). TP is calculated for taxon  $i$  from the binary matrix of trophic interactions as

$$TP_i = \frac{\sum_j TP_j}{n_i} + 1$$

where  $n_i$  is the total number of prey taxa consumed by

taxon  $i$ , and  $TP_j$  represents the trophic position of all prey items ( $j$ ) of taxon  $i$ . Prey-averaged TP provides a good estimate of the more informative "flow-based TP" (Williams and Martinez 2004) based on the quantitative contribution of each prey item to the diet of the consumer. Prey-averaged and flow-based TP are highly correlated although the former technique tends to overestimate trophic position and is more variable than flow based techniques (Williams and Martinez 2004). Food webs selected for analysis all had a high level of taxonomic resolution (at least 60% to genus or species), and include cases interpreted by the original investigators as having a strong representation of omnivory; Coachella desert (Polis 1991), Ythan Estuary (Hall and Raffaelli 1991), and Broadstone Stream (Woodward and Hildrew 2001).

To determine whether TPs in real webs were significantly aggregated around integer values, we compared the distribution of TPs for each web with null models based on 1000 randomizations of the original feeding matrix. Two types of randomized models were generated: (1) all non-herbivores randomized, where the number of herbivores and their links were held constant, but links to all other animal taxa were randomized and (2) all randomized, where all animal taxa were randomized. In both types of model, the number of basal taxa and top predators was held constant, and the total number of taxa and directional links between taxa was conserved, with the additional constraint that each taxon had to have the same number of incoming and outgoing links as the original food web. Trophic position distributions generated without the latter constraint bore little resemblance to the original webs. Our random webs were generated using a Monte Carlo algorithm. On each step, two random trophic links were chosen and the destinations of the links are swapped. The procedure was repeated 1000 times the number of edges to ensure that the new web was properly randomized. Our measure for calculating TP is highly sensitive to loops in the network which tend to inflate the TP. We constrained our program to only go around loops once, and rejected food webs with multiple loops (loops within loops) that are computationally intractable. While this may favor food webs that are more hierarchically organized, multiple loops were rare in the real webs (two cases) and may carry relatively little energy (Thompson and Townsend 2004). The null models represented situations where (1) all consumers and (2) all non-herbivorous animals lacked any biological tendency to feed on prey items with particular TPs. Since the randomized webs retain a number of features of the original webs (the number of basal taxa and top predators), our statistical test regarding the frequency of omnivory is conservative.

For each real food web and each of the two types of randomized models, we generated frequency distributions of the number of taxa in TP classes at 0.1 intervals (i.e., 0–0.05, 0.05–0.15, 0.15–0.25, and so on). Frequency distributions for the two null models were the average of

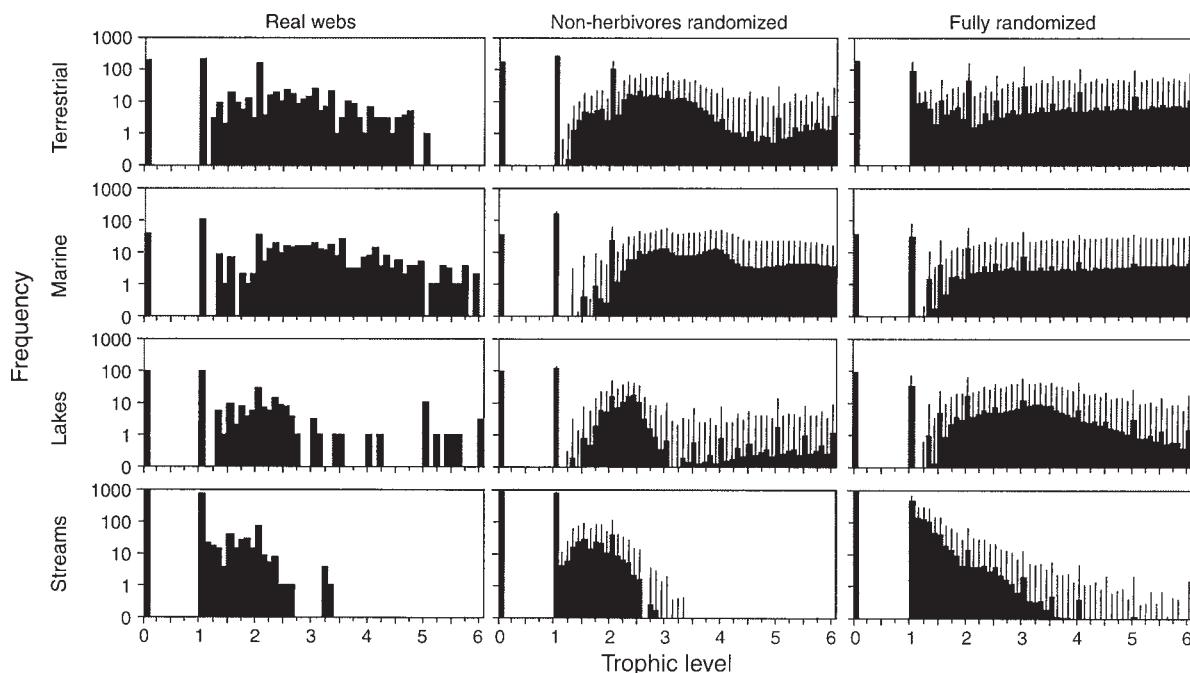


FIG. 1. Frequency histograms of taxa in different trophic position classes in food webs from four ecosystem types. Trophic positions can be interpreted as follows: 0, primary producers (plants, algae, detritus); 1, herbivores and detritivores; >2, predators. Data are shown for real food webs (left panels), for randomized food webs with non-herbivore and non-plant taxa randomized (middle panels), and with all non-plant taxa randomized (right panels). For randomized food webs, each class frequency is the mean of 1000 iterations with 95% confidence intervals.

the 1000 iterations. Each frequency distribution was converted into the percentage of taxa for that web that occurred in each class. Taxa occurring in any of the classes centered on an integer (i.e., 0.95–1.05, 1.95–2.05) were considered to be non-omnivorous and occupy a discrete trophic level.

To test whether integer TPs were more common in different ecosystem types and in real food webs as opposed to the two types of randomized models, repeated-measures ANOVA was used (JMP-In 4.0.3; SAS Institute, Cary, North Carolina, USA). The total percentage of taxa in each food web with an integer TP was calculated and arcsine transformed for normality. Ecosystem type (stream, marine, lake, terrestrial), model type (real, non-herbivores randomized, all-randomized), and food webs were used as main factors, with ecosystem as a fixed term, model type a repeated factor, and food webs nested within ecosystem. Effect sizes were calculated as per Sall and Lehman (1996), with the food web (ecosystem) MS used as denominator when calculating  $F$  to compare ecosystems and ecosystem  $\times$  model interactions, and the residual error mean square used for comparing model types. Tukey's hsd post hoc tests were used to analyse pairwise differences for significant tests.

#### RESULTS

Fig. 1 shows the distribution of TP for all non-basal taxa in the food webs by ecosystem type for the real food

webs and the two classes of randomizations. In the real food webs, 64.4% of taxa had integer TPs clustered around the values 0 and 1 (indicating plants and herbivores). There was also a peak associated with TP 2, although this was less clearly defined. The randomized food webs produced longer food chains and very high TPs (maximum 15), although this data is curtailed in Fig. 1. Food webs produced by randomizing non-herbivores only or by full randomization of the animals in the food webs, also showed clearly defined peaks associated with TPs 0, 1, and 2, and less clearly with TP 3 (mainly in the lake and stream ecosystems).

The number of taxa where TP was an integer differed significantly between the real and the two classes of randomized food webs (Table 1). Integer TPs were more frequent in real food webs than in fully randomized food webs, but food webs where only non-herbivores were randomized showed the same degree of trophic structuring as real food webs (Fig. 2). There was clear evidence that integer trophic positions were less common among taxa higher up in food webs (Fig. 1). When basal and herbivore categories (TPs 0 and 1) were excluded from the analysis, the remained a significant difference between the different model types (Table 1), with real food webs having more species with integer trophic positions than fully randomized food webs. However, post hoc tests could not distinguish a significant difference between food webs constructed

TABLE 1. Repeated-measures ANOVA testing for an effect of different classes of model (R, real; H, herbivores randomized; A, all taxa randomized) and ecosystem type (M, marine; T, terrestrial; L, lakes; S, streams) on the proportion of taxa occupying integer trophic positions.

Source	SS	F	df	P	Tukey's post hoc
A) All trophic positions					
Model	1.559	44.630	2, 108	<0.001	R > A, H > A
Food web[Ecosystem]†	4.000	4.242	54, 108	<0.001	
Ecosystem	1.450	27.668	3, 54	<0.001	L > M, S > L, S > M, S > T, T > M
Ecosystem × model	0.183	1.743	6, 108	0.118	
B) TP > 1 only					
Model	0.046	6.637	2, 108	0.002	R > A, H > A
Food web[Ecosystem]†	0.873	4.718	54, 108	<0.001	
Ecosystem	0.161	15.366	3, 54	<0.001	S > L, S > M, S > T
Ecosystem × model	0.034	1.639	6, 108	0.144	

Notes: Significant Tukey's post hoc tests are shown. The analysis is carried out for (A) all trophic positions and (B) excluding trophic positions 0 and 1.

† Nominated as a random term.

by randomizing non-herbivore animals and the real webs (Table 1B).

There were also significant differences in the prevalence of integer trophic positions between ecosystems (Table 1). Omnivory (indicated by lower proportions of species with integer trophic positions) was most prevalent in marine pelagic systems, rarest in streams, and intermediate in lakes and terrestrial systems (Fig. 2). Tukey's post hoc tests identified significant differences between stream and marine ecosystems and the other ecosystems (Table 1). There was no evidence of a split in the prevalence of omnivory between terrestrial and aquatic systems. Some webs had high degrees of omnivory while others were highly aggregated into trophic levels. For example, in the marine food web from Monterey Bay, only 20% of taxa could be placed into a discrete trophic level. In contrast, many stream food webs had between 90% and 100% of taxa with integer trophic positions. Systematic variation in the occurrence of omnivory was not due to difference in food web size: there was no relationship between

number of taxa and degree of omnivory ( $r^2 = 0.001$ ,  $P = 0.801$ ).

DISCUSSION

We found evidence of a discontinuous distribution of trophic positions in food webs with distinct clustering of taxa to form trophic levels. However this clustering was only evident among lower trophic levels. When plants and herbivore numbers were held constant, randomizations of food webs had as many integer TPs as real food webs. Constraints on the randomizations meant that even fully randomized food webs showed high frequencies of taxa at integer trophic positions. Food webs where only taxa with trophic positions above plants and herbivores are randomized show no more omnivores than the real webs. In biological terms, this means that while there are constraints on species to be exclusively grazers and producers, trophic omnivory predominates above the herbivore trophic level. This is a function in part of network topology, as the probability of being a trophic omnivore increases the higher a taxon occurs in a food

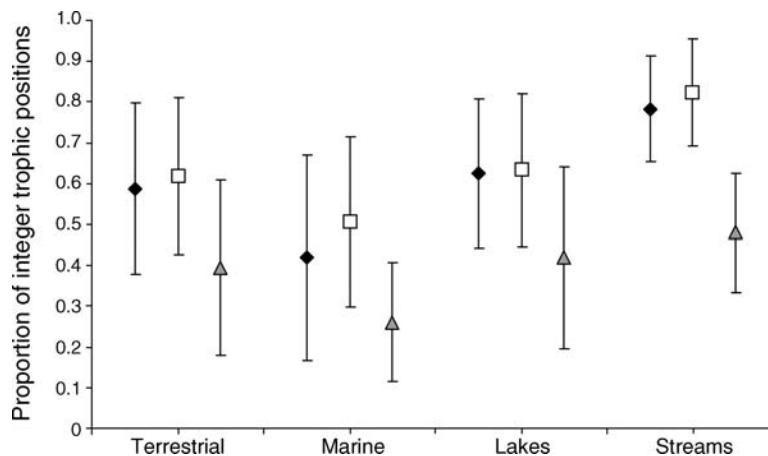


FIG. 2. Mean proportions ( $\pm$ SD) of non-basal taxa with trophic positions that were integers for the four ecosystems. Data are shown for real food webs (black diamonds), randomized food webs that randomize secondary and higher consumers (white squares), and all non-plant taxa randomized (gray triangles).

chain). A food web with only two trophic levels will show less omnivory because taxa have a higher probability of feeding at a single trophic level. In contrast, when food webs have long food chains, taxa have a higher potential to encounter prey items with a range of trophic positions. The food webs analysed here can be characterised as linear collections of chains when food chains are short, but resemble tangles in environments with longer food chains. Food chains may tend to lengthen in response to higher productivity or ecosystem size (Pimm 1982, Kaunzinger and Morin 1998, Post et al. 2000, Thompson and Townsend 2005). Given these patterns, it follows that more productive or larger systems would be expected to have more omnivores, although theory predicts that omnivores should persist only at intermediate productivity (Holt and Polis 1997, Diehl et al. 2000).

In common with recent reviews of smaller data sets (Arim and Marquet 2004, Williams and Martinez 2004), we found that while omnivory was common in food webs, the majority of taxa fell near integer trophic position. This is a product of the fact that most taxa in ecosystems are plants and herbivores. There is no support in these food webs for defined trophic levels 2 or 3 (primary or secondary consumers) across a range of ecosystems and locations, but particularly in stream and lake systems. The trophic tangle representation of food webs becomes appropriate higher in food webs where omnivory is the norm. Strong clustering of trophic positions may emerge from evolutionary assembly of food webs. A size-structured model developed by Loeuille and Loreau (2005) found that omnivory evolved when niche width and competition intensity were both high. Under those conditions, continuous size distributions emerged and packing into trophic levels was not observed. Loeuille and Loreau's (2005) models showed characteristics consistent with those we found here, namely the emergence of integer peaks in trophic position when food chain lengths were relatively short (compare our Fig. 1 to Loeuille and Loreau's [2005] Fig. 2). Another emergent property of their models was the observation that strong competitive interactions between species favoured omnivory. A recent analysis of a large marine food web (Bascompte et al. 2005) also suggested that omnivory is associated with the presence of strong feeding links. These models suggest processes which may explain the variability in degree of omnivory present in our data, and generate clear predictions for the situations under which this may evolve.

We found variability in omnivory between ecosystems but no evidence for differences in the degree of omnivory between aquatic (collectively) and terrestrial ecosystems. This suggests that trophic complexity cannot account for the tendency for stronger trophic cascades in aquatic systems (Strong 1992, Shurin et al. 2002). The observation that top-down control of producers by predators is stronger in some aquatic systems may therefore be explained by differential vulnerability to grazing between systems, higher nutritional quality or faster turnover

times of aquatic producers (Shurin et al. 2006). The underlying phylogenetic and ecological factors that predispose some systems to higher levels of omnivory are poorly understood. The high omnivory webs in our set came from all four ecosystem types and displayed a range of food web sizes and primary energy sources. However, we did find contrasts in the importance of omnivory among systems. Streams in particular showed little omnivory, perhaps reflecting the small size and short food chains in lotic environments.

As our understanding of food webs has increased, so too has our awareness of their complexity. To simplify these networks, taxa have been aggregated into super-taxonomic groups such as trophic levels. This practice has been criticized for ignoring ontogenetic or behavioral variability, and neglecting groups such as parasites (Cousins 1987, Burns 1989, Polis and Strong 1996, Thompson et al. 2005). These are important phenomena, and future food web studies should seek to address them (as has been attempted for parasites [Huxham et al. 1996, Thompson et al. 2005]). Our results show that while integer trophic positions can be attributed to the majority of taxa in real food webs, the evidence for defined trophic levels in predatory taxa is relatively sparse. For consumers other than herbivores, taxa were no more likely to occupy an integer trophic position in most of the real food webs than they were in randomized webs. In systems where longer food chains predominate and secondary consumers are abundant, trophic levels are an inaccurate abstraction. Thus we may expect that top down effects such as trophic cascades will be most evident where food chains are relatively short. As food chains lengthen, omnivory becomes increasingly prevalent, potentially diffusing the effects of changes in top predators across trophic networks. These results both generate testable hypotheses for the next generation of trophic cascade studies and studies of the food web dynamic consequences of omnivory.

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#### APPENDIX

Food webs included in the analysis (*Ecological Archives* E088-040-A1).