

# The role of body mass in diet contiguity and food-web structure

Daniel B. Stouffer<sup>1\*</sup>, Enrico L. Rezende<sup>2</sup> and Luís A. Nunes Amaral<sup>3,4,5</sup>

<sup>1</sup>*Integrative Ecology Group, Estación Biológica de Doñana-CSIC, c/ Américo Vespucio s/n, 41092 Sevilla, Spain;*

<sup>2</sup>*Departament de Genètica i de Microbiologia, Facultat de Biociències, Edifici Cn, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain;* <sup>3</sup>*Howard Hughes Medical Institute, Northwestern University, Evanston, IL 60208, USA;*

<sup>4</sup>*Department of Chemical and Biological Engineering, Northwestern University, Evanston, IL 60208, USA; and*

<sup>5</sup>*Northwestern Institute on Complex Systems (NICO), Northwestern University, Evanston, IL 60208, USA*

## Summary

1. The idea that species occupy distinct niches is a fundamental concept in ecology. Classically, the niche was described as an  $n$ -dimensional hypervolume where each dimension represents a biotic or abiotic characteristic. More recently, it has been hypothesised that a single dimension may be sufficient to explain the system-level organization of trophic interactions observed between species in a community.

2. Here, we test the hypothesis that species body mass is that single dimension. Specifically, we determine how the intervality of food webs ordered by body size compares to that of randomly ordered food webs. We also extend this analysis beyond the community level to the effect of body mass in explaining the diets of individual species.

3. We conclude that body mass significantly explains the ordering of species and the contiguity of diets in empirical communities.

4. At the species-specific level, we find that the degree to which body mass is a significant explanatory variable depends strongly on the phylogenetic history, suggesting that other evolutionarily conserved traits partly account for species' roles in the food web.

5. Our investigation of the role of body mass in food webs thus helps us to better understand the important features of community food-web structure and the evolutionary forces that have led us to the communities we observe.

**Key-words:** complex networks, food webs, intervality, niche dimension, species phylogenetics

## Introduction

Food webs are a description of who eats whom in an ecosystem (Cohen, Briand & Newman 1990; Pimm 2002; Pascual & Dunne 2006). Recently, multiple studies have helped to quantify food-web structure by revealing a number of statistical regularities within the data (Camacho, Guimerà & Amaral 2002a,b; Dunne, Williams & Martinez 2002; Cattin *et al.* 2004; Stouffer *et al.* 2005; Beckerman, Petchey & Warren 2006; Stouffer, Camacho & Amaral 2006; Camacho, Stouffer & Amaral 2007; Stouffer *et al.* 2007; Allesina, Alonso & Pascual 2008; Petchey *et al.* 2008). Instrumental in the understanding of these statistical patterns has been the development of models that attempt to explain their origin (Cohen & Newman 1985; Williams & Martinez 2000; Cattin *et al.* 2004; Loeuille & Loreau 2005; Stouffer *et al.* 2005, 2006; Allesina *et al.* 2008; Petchey *et al.* 2008; Williams & Martinez 2008).

'Niche space' is a fundamental concept in these models (Cohen 1978).

Hutchinson (1957) originally defined niche space as an ' $n$ -dimensional hypervolume' where each dimension accounts for a distinct biotic or abiotic characteristic. A species' role or position within its community is thus conditioned by a set of  $n$  factors acting upon it. To determine a species' niche, one must quantify all  $n$  factors and determine those which are most relevant. More recently, the ecological niche has been reinterpreted as the minimum set of species attributes that explains some ecological phenomena (Cohen 1978; Warren & Lawton 1987). This latter formulation of the niche has proven an integral assumption of current static models of food-web structure (Cohen & Newman 1985; Williams & Martinez 2000; Stouffer *et al.* 2005, 2006; Allesina *et al.* 2008; Williams & Martinez 2008) and provides a testable criterion – something that the ' $n$ -dimensional hypervolume' does not – to study which and how many variables may describe species' niches in an ecosystem.

\*Correspondence author. E-mail: stouffer@ebd.csic.es

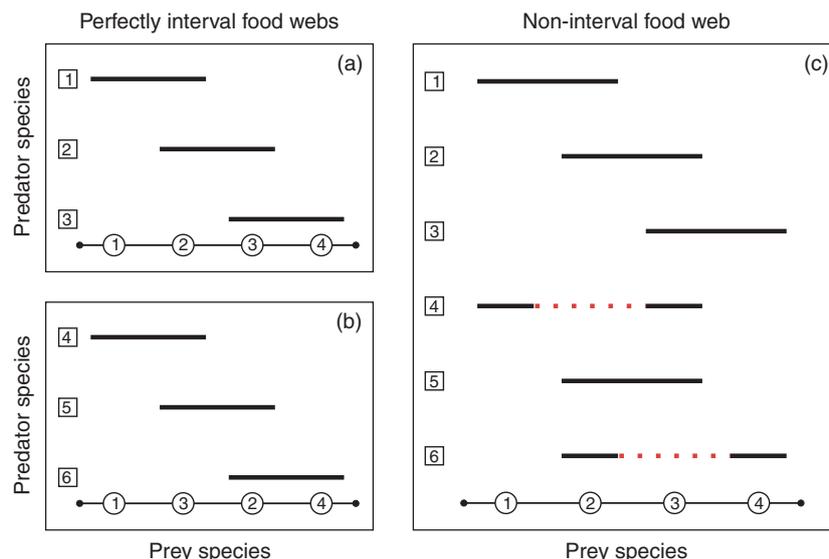
One case of particular interest is the set of variables necessary to explain the organization of the interactions within food webs. Cohen & Newman (1985) hypothesized that intermediate species and top predators in an ecosystem can be ranked based upon a single characteristic, i.e. assigned an ordered set of 'niche-values' (Stouffer *et al.* 2005). This concept of a trophic ordering is very closely tied to that of 'food-web intervality' (Cohen 1977, 1978; MacDonald 1979; Sugihara 1982, 1984; Fig. 1). According to the original definition, a food web is interval if its interactions are constrained such that diets can be represented as contiguous segments in the same single-dimensional set-up as the trophic ordering (Cohen 1977). It has been observed that empirical food webs are not strictly interval (Williams & Martinez 2000). Nevertheless, it was recently demonstrated that they exhibit a strong tendency toward intervality (Stouffer *et al.* 2006) and toward empirically observed diet contiguity (Williams & Martinez 2000; Stouffer *et al.* 2006; Allesina *et al.* 2008; Williams & Martinez 2008; Fig. 2). Remarkably, this is true for food webs from a variety of environments. Intriguingly, a number of robust, empirically observed patterns in food-web structure arise as a direct consequence of diet contiguity (Williams & Martinez 2008); these include the over/under-representation of food-web motifs (Stouffer *et al.* 2007) and food-web compartmentalization (Guimerà *et al.* 2010). These structural patterns in turn mediate the response of an ecosystem to threats, such as extinctions or invasive species (Srinivasan *et al.* 2007; Romanuk *et al.* 2009).

Determining which variables account for both trophic ordering and diet contiguity is therefore of paramount importance to understand food-web structure and dynamics. The identity of a true empirical proxy, however, has

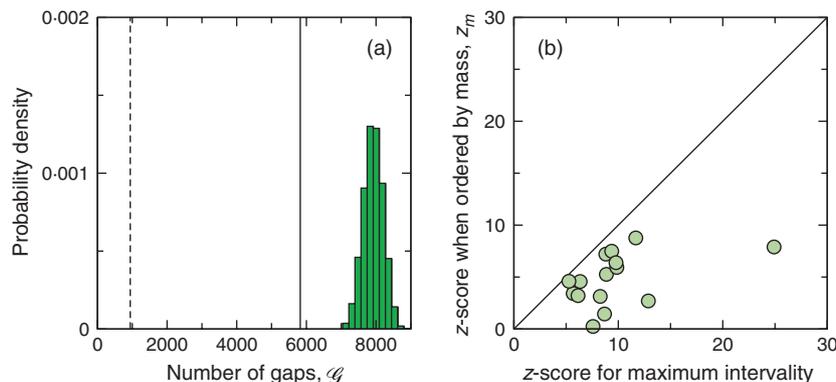
remained elusive, although multiple alternative hypotheses have been suggested (Neubert *et al.* 2000; Layman *et al.* 2005; Jonsson, Cohen & Carpenter 2005; Woodward *et al.* 2005; Allesina *et al.* 2008). In particular, a number of authors have suggested that species' mass or body size provides the most suitable mapping of the species in a food web along a single dimension (Warren & Lawton 1987; Cohen 1989; Lawton 1989; Cohen *et al.* 1993; Neubert *et al.* 2000; Woodward & Hildrew 2002; Cohen, Jonsson & Carpenter 2003; Brose *et al.* 2006; Barnes *et al.* 2010; Zook *et al.* 2011).

Here, we examine the role of species mass in explaining empirically observed diet contiguity. We choose to examine the explanatory power of body size not because of convenience (Berlow, Brose & Martinez 2008), but because of its long-recognized importance. Hutchinson proposed that body sizes could directly explain the coexistence of different species within an ecosystem (Hutchinson 1959). Body size is correlated with many descriptors of species ecology (Whittfield 2004; Berlow *et al.* 2008; Bersier & Kehrli 2008), such as species abundances (Cohen *et al.* 2003; Jonsson *et al.* 2005), and even leads to finely structured communities at an intra-specific level (Buston & Cant 2006; Kohda *et al.* 2008). Body size has also been shown to be an important indicator of mammals' vulnerability to extinction (Davidson *et al.* 2009), for example. Moreover, there is a rich history of the interactions between body size and ecological networks (Woodward *et al.* 2005). The strength of its explanatory power is fortunate as 'measuring body size provides a relatively simple means of encapsulating and condensing a large amount of biological information' (Woodward *et al.* 2005).

Our manuscript is organized as follows. First, we test whether species mass not only provides species a hierarchy



**Fig. 1.** Visualizing food-web intervality. Potential prey species (circles, oriented horizontally) are placed in a single dimension called the resource axis. For every predator (squares, oriented vertically), a line is placed above the prey that it consumes. (a), The food web is interval because there exists an ordering of the prey species,  $\mathcal{O} = \{1, 2, 3, 4\}$ , for which all predators have contiguous diets. (b), This food web is also interval because the ordering,  $\mathcal{O} = \{1, 3, 2, 4\}$ , corresponds to contiguous diets. (c), The food web consisting of the predator species from both (a) and (b) is not interval because there is no way to reorder the prey species such that all diets are contiguous. Note the 'gaps' in the diets of predators 4 and 6.



**Fig. 2.** Comparison of intervalty for mass-ordered and randomly ordered food webs. (a), The probability of observing a particular number of gaps for the Caricaie Lakes food web. The histogram shows the distribution of gaps for random orderings of species, the solid black line indicates the empirical value  $G_m$  obtained using the ordering provided by the empirical masses, and the dashed line indicates the best-estimate minimum number of gaps  $\hat{G}$  for the empirical food web. We find  $z_m = 7.89$  corresponding to  $P < 0.001$  while the  $z$ -score for  $\hat{G}$  is 24.90. (b), We compare the  $z$ -score for intervalty according to species mass with the same but compared to maximum diet contiguity for the 15 empirical food webs studied. Differences between the two can be regarded as the fraction of potential contiguity that is unexplained by body mass.

but can also significantly explain diet contiguity. Second, we present a novel means to quantify the degree of diet contiguity of individual species within a food web. This measure allows us to then test whether species mass can significantly explain individual diet contiguity. Finally, we use tools from community phylogenetics to investigate how intervalty varies across the species found within empirical food webs.

## Materials and methods

For a food web with  $S$  species, there are  $S!/2$  possible orderings of species  $\mathcal{O}_k = s_1 s_2 \dots s_{S-1} s_S$ . The diet contiguity of a particular ordering can be computed with a suitable cost function (Stouffer *et al.* 2006). An example of such a function is

$$\mathcal{G}(\mathcal{O}_k) = \sum_{i=1}^S \sum_{j=1}^{\gamma_i} g_{ijk}. \quad \text{eqn 1}$$

Here,  $\gamma_i$  is the number of gaps in the diet of species  $i$ , and  $g_{ijk}$  is the number of species in the  $j$ -th gap in the diet of species  $i$  for the ordering  $\mathcal{O}_k$ .

Given an empirical food web  $\mathcal{F}$ , there exists a specific ordering  $\mathcal{O}_m(\mathcal{F})$  determined by the set of masses  $\{m_1, m_2, \dots, m_{S-1}, m_S\}$  of the 'typical' individual of each of the  $S$  species. We will adopt the convention here of ranking species in order of increasing mass, that is, the species with the smallest mass is assigned rank 1, with the next smallest mass rank 2, and so on up to the species with the largest mass which is assigned rank  $S$ . We compare the number of gaps  $G_m = \mathcal{G}(\mathcal{O}_m)$  to the number of gaps  $\tilde{\mathcal{G}}$  for a random permutation of species<sup>1</sup>. We quantify this comparison with the  $z$ -score

$$z_m = \frac{\langle \tilde{\mathcal{G}} \rangle - G_m}{\sigma_{\tilde{\mathcal{G}}}} \quad \text{eqn 2}$$

where  $\langle \tilde{\mathcal{G}} \rangle$  and  $\sigma_{\tilde{\mathcal{G}}}$  are the average and standard deviation of the number of gaps across the ensemble of random permutations, respectively. In our analysis, we consider an ensemble of 10 000 random

permutations. Note that, because of the inverse relationship between the number of gaps in a food web and its intervalty, we have reversed the traditional order of the numerator in eqn 2. Values  $z_m < -1.96$  therefore imply that diets in a food web ordered by mass are less contiguous than expected at random, values  $z_m > 1.96$  imply that they are more contiguous, and values  $-1.96 < z_m < 1.96$  imply that they are consistent with the random null hypothesis.

By following this methodology, the viability of any alternative hypothesis (Neubert *et al.* 2000; Jonsson *et al.* 2005; Layman *et al.* 2005; Woodward *et al.* 2005; Allesina *et al.* 2008) for an empirical analogue to species' niche value can be directly gauged with its significance. Previous studies of intervalty have instead searched for globally optimum permutations or orderings (Stouffer *et al.* 2006; Mouillot, Krasnov & Poulin 2008). While such studies can describe the existence of a significant pattern of contiguity, focusing only on the best possible ordering could interfere with the ability to detect important and significant patterns by mistakenly regarding them as 'not good enough.' In this study, by concentrating on the ability of a specific variable – here, body mass – to explain contiguity, we can quantify how individual species deviate from the hypothesized pattern. That is, we can measure how the diets of individual species contribute to the intervalty of the community as a whole. We can also directly assess the degree to which species' masses determine the diet of each species.

Recall that every species  $i$  contributes

$$\delta_i = \sum_{j=1}^{\gamma_i} g_{ijk}, \quad \text{eqn 3}$$

gaps from their diet to the overall number of gaps  $\mathcal{G}$ . The value  $\delta_i$  is thus the absolute intervalty of species  $i$  measured as the number of gaps in their diet.

Just as with community intervalty, we can compare these species-specific contributions to their equivalent in the ensemble of random permutations of species. This means that, in addition to understanding how intervalty of the community compares to the random null hypothesis, we can quantify the degree to which individual species do as well. We first calculate  $d_i$ , the number of gaps in the diet of species  $i$  when species are ordered by their mass. As before, we compare the number of gaps  $d_i$  to the number of gaps  $\tilde{\delta}_i$  for a random permutation of species (10 000 permutations). We again quantify this comparison with the  $z$ -score

<sup>1</sup>Note that due to the resolution of the empirical data, two or more empirical species could be recorded to have the same mass. Should this occur, we report the largest value  $G_m$  encountered over multiple realizations where the equivalent species are permuted randomly.

$$z_i = \frac{(\bar{\delta}_i) - d_i}{\sigma_{\delta_i}} \quad \text{eqn 4}$$

where  $(\bar{\delta}_i)$  and  $\sigma_{\delta_i}$  are the average and standard deviation, respectively, of the number of gaps in the diet of species  $i$  across the ensemble of random permutations. The value  $z_i$  measures the relative intervality of species  $i$  and relative explanatory power of body mass on the diet of species  $i$ .

We estimate the role of evolutionary history on diet contiguity by measuring the phylogenetic signal – i.e. the tendency of close relatives to resemble each other – on species' mass  $m_i$ , number of prey  $n_i$  (degree of generalization or specialization) and relative intervality  $z_i$ . In each community, we first construct the phylogenetic tree using species' taxonomic classifications and branch lengths that best fit the observed distribution of body mass (Appendix S2). With this tree, we analyse whether species attributes show significant phylogenetic signal by employing a randomization procedure in which species' attributes are shuffled across the phylogeny, destroying any signal that may have been present (Blomberg, Garland & Ives 2003).

## Results

We examine 15 empirical food webs for which both trophic interaction data and species masses have been tabulated (see Appendix S1 for original references): Benguela, Broadstone Stream, Scotch Broom, Capinteria, Caribbean Reef, Caricaie Lakes, Coachella Valley, EcoWEB41, EcoWEB60, Grasslands, Mill Stream, Sierra Lakes, Skipwith Pond, Tuesday Lake and Ythan Estuary.

We first obtain the set of orderings  $\{O_m\}$  for the 15 empirical food webs and compare their properties with those of random orderings (see Methods). Here, we find that the

**Table 1.** Comparison of orderings based on species' masses with random species permutations. Using eqn 1, we compute the number of gaps in all diets in the empirical food web  $G_m$  given the ordering according to the masses of the individual species. We perform the same computation for an ensemble of random species permutations and from this calculate the  $z$ -score that measures the number of standard deviations away from the expected value under the random null hypothesis. The more positive the value, the more species' masses can account for empirically observed diet contiguity. For only two empirical food webs, Broadstone Stream and Grasslands, would we reject this hypothesis at a 95% confidence level

Food web	$G_m$	$\langle \bar{G} \rangle$	$\sigma_{\bar{G}}$	$z$ -score
Benguela	102	283	39	4.56
Broadstone Stream	76	90	10	1.44
Broom	326	770	127	3.40
Capinteria	702	1472	147	5.24
Caribbean Reef	5425	7656	377	5.92
Caricaie Lakes	5825	8087	286	7.89
Coachella	154	235	26	3.14
EcoWEB41	19	108	20	4.58
EcoWEB60	146	289	45	3.21
Grasslands	545	569	70	0.23
Mill Stream	516	2134	224	7.21
Sierra Lakes	42	162	14	8.76
Skipwith Pond	939	1122	68	2.70
Tuesday Lake	344	1587	164	7.49
Ythan	1124	2783	259	6.38

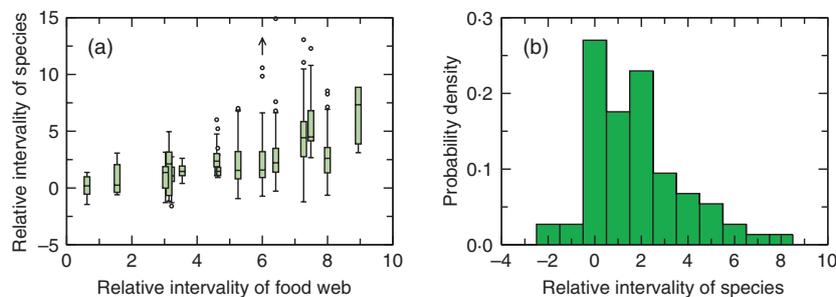
number of gaps  $G_m$  is consistent with the random null hypothesis for only two of the 15 food webs (Table 1). This implies that species' masses have significant explanatory power not only for a one-dimensional niche space but also for contiguity of diets. Moreover, we find that the rejection of the random hypothesis is independent of the food web's size (Kruskal–Wallis,  $P = 0.54$ ) and number of links (Kruskal–Wallis,  $P = 0.45$ ).

We also find that the ability of species' masses to explain food-web intervality and dietary contiguity appears to be largely independent of environment (Chase 2000), something which has also been observed for other food-web properties (Dunne, Williams & Martinez 2004; Stouffer *et al.* 2005; Stouffer *et al.* 2007; Dunne *et al.* 2008; Williams & Martinez 2008). The differences are not significant if we classify the webs as freshwater, marine and terrestrial (Kruskal–Wallis,  $P = 0.10$ ). If, on the other hand, we classify food webs more coarsely as aquatic and terrestrial, we find that aquatic food webs are significantly more interval (Kruskal–Wallis,  $P = 0.037$ ), indicating a more important role of size structuring across aquatic systems. The two food webs, Broadstone Stream and Grasslands, for which we cannot reject the random null hypothesis are from freshwater and terrestrial ecosystems, respectively.

If we 'zoom in' to the level of individual species, we reach similar conclusions as for whole food webs. Indeed, the diets of a majority of species are more contiguous than would be expected at random (Fig. 3 and Methods). This implies that species mass has explanatory power not just at the food-web level but also at the level of individual species' diets. Not surprisingly, we find that as the intervality of a food web increases so does the diet contiguity of its constituent species. Nevertheless, and despite the general agreement of species' diets with orderings based on species mass, we do observe deviations from this pattern (Fig. 3). We next ask whether there is a common thread that helps us understand why mass has strong explanatory power for some species but lacks explanatory power for others.

Specifically, we ask whether the degree to which species mass explains species-level intervality is related to species' evolutionary history, that is, to the species' phylogenetic relationship. We quantify the phylogenetic relationship between species via their individual taxonomic classification. Note that detailed taxonomic information is only available for eight of the 15 empirical food webs we have examined up to this point: Broadstone Stream, Scotch Broom, Caribbean Reef, Caricaie Lakes, Grasslands, Mill Stream, Skipwith Pond and Tuesday Lake. Therefore, all phylogenetic analyses and conclusions are restricted to this subset of webs.

First, we examine whether species that are phylogenetically related species tend to have similar body mass. We indeed find a significant phylogenetic signal on species' mass for every food web under consideration, that is, closely related species tend to have similar body masses (Appendix S2). Note, however, that similarity in body mass in no way implies similarity of the species' diets or how their diets fit into the overall pattern of community intervality.



**Fig. 3.** Comparison of food-web and species-level intervality. (a), The degree of food-web intervality, as measured by the  $z$ -score, compared to the degree of intervality of its constituent species, also measured by their  $z$ -score. All measurements quantify intervality when the species are ordered by their mass. As expected, species-level intervality increases significantly with increasing food-web intervality. However, we observe that the intervality of species in a food web can vary substantially. The arrow shown indicates points which fall outside of the visible area. (b), The probability distribution of species-level relative intervality in the Caricaie Lakes food web. A majority of all predator species are significantly interval (62% have relative intervality  $z_i > 1.96$ ).

**Table 2.** Phylogenetic signal on species attributes. For the eight webs for which we have detailed taxonomic information, we tabulate the number of species  $S$  and the  $P$ -values associated with phylogenetic signal on species body mass  $m_i$ , species number of prey  $n_i$  and species relative intervality  $z_i$ . We observe strong evidence for a phylogenetic signal on each of these species-specific attributes across the various food webs studied. The phylogenetic signal on species number of prey implies that phylogenetically similar species tend to exhibit similar degrees of specialization. The signal on relative intervality implies that body mass plays a similar role in the organization of the diets of phylogenetically similar species

Food web	$S$	$P$ -value, $m_i$	$P$ -value, $n_i$	$P$ -value, $z_i$
Broadstone Stream	28	< 0.001	0.201	0.332
Broom	68	< 0.001	< 0.001	< 0.001
Caribbean	200	< 0.001	0.036	0.011
Caricaie Lakes	149	< 0.001	0.039	0.016
Grasslands	65	< 0.001	0.227	0.906
Mill Stream	76	< 0.001	0.002	0.012
Skipwith Pond	71	< 0.001	0.402	0.999
Tuesday Lake	71	< 0.001	< 0.001	< 0.001

To quantify the role of phylogeny on species diets, we examined in detail its relationship with two additional species attributes: (i) species' number of prey  $n_i$  and (ii) species' relative intervality  $z_i$ . We summarize the results of these analyses in Table 2. Notably, we find frequent, significant correlations between phylogenetic similarity and each of these species-level attributes across the different food webs (Fig. 4). In particular, we find a lack of phylogenetic signal on relative intervality in only three food webs, Broadstone Stream and Grasslands – the two webs for which we observed no relation between species mass and food-web intervality – and Skipwith Pond. The correlations observed in the remainder of the food webs imply that, in these ecosystems, species' evolutionary history helps to explain their roles within a food web – i.e. specialist or generalist predator – and also the manner in which their diet fits within the larger organization of the community.

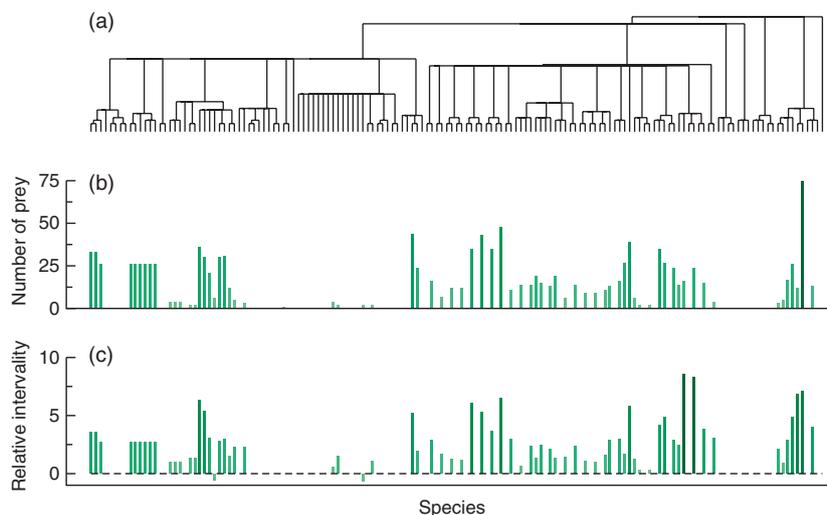
To better understand these results, we examine whether species that have large relative intervality tend to have large

body masses as well, or vice versa. We also take into consideration species' number of prey, species' number of predators and species' total number of interactions (Appendix S3). We find no evidence from which to conclude that species whose diets are strongly interval also tend to have large body masses (or small), tend to be generalized predators (or specialized) or tend to have many interactions (or few). Overall, our analysis supports the idea that species need not be the most generalist predator or be found 'high up' in the trophic hierarchy for body mass to have played an important role in the evolution of their diet. We did find, however, that species with non-interval diets tend to have many predators ( $P = 0.034$ ), indicating a possible link between vulnerability and diet contiguity.

## Discussion

Since the cascade model of Cohen & Newman (1985), mechanistic food-web models have relied upon a conceptual 'niche-value' to provide a species ordering. Because of a lack of strong evidence, the underlying, but often unstated, assumption was that body mass provided the best proxy for these models' niche-values (Cohen *et al.* 1993; Neubert *et al.* 2000). Our results strongly support the hypothesis that species' masses explain both the ordering of trophic links (Warren & Lawton 1987; Cohen 1989; Lawton 1989; Cohen *et al.* 1993, 2003; Neubert *et al.* 2000) and empirically observed diet contiguity (Williams & Martinez 2000; Stouffer *et al.* 2006; Allesina *et al.* 2008; Williams & Martinez 2008).

In our examinations at the species-specific level, we again find strong evidence that body mass can explain individual species' diet contiguity. The degree to which this takes place, however, is significantly modulated by the phylogenetic history of the community. These results imply that there is a phylogenetic component to how each species fits within the larger organization of their community. Importantly, our results are also consistent with previous studies that have documented the importance of phylogenetic history in understanding additional aspects of food-web structure (Cattin *et al.* 2004; Rezende *et al.* 2009).



**Fig. 4.** Phylogenetic signal and species' diet contiguity. (a), The phylogenetic tree for the Caricaie Lakes food web, built using species' taxonomic classifications. (b), The number of prey of each species ordered according to their phylogenetic similarity. (c), The relative intervality of each species ordered according to their phylogenetic similarity. To facilitate visual clarity, the colour of the bars is proportional to the value from low values (light green) to high values (dark green). We observe a significant phylogenetic signal for both number of prey ( $P = 0.039$ ) and relative intervality ( $P = 0.016$ ). Visually, this means that species that are closer together in the phylogeny have a greater than expected probability of having similar numbers of prey and similar relative intervalities.

We find that food webs are highly size-structured, in agreement with earlier results (Beckerman *et al.* 2006; Petchey *et al.* 2008). Furthermore, our analyses provide insight into the role that body mass has played in the evolutionary history of the individual species under consideration. Phylogenetic effects on diet contiguity suggest that other factors, apart from body mass, likely account for species' contributions to the food-web structure. Indeed, this is in close agreement with recent analyses, which suggest that interactions in a food web are predicted with increased accuracy by models that include two latent traits in addition to body mass (Rohr *et al.* 2010). Interestingly, these variables, that describe species foraging intensity and vulnerability, also appear to show significant phylogenetic signal.

The pervasiveness of phylogenetic signal across variables and food webs provides unequivocal evidence that closely related species often have similar niches in the community. Even though phylogenetic signal is expected from shared ancestry and very simple evolutionary models, it is also possible that the structure of the food web – and the selective pressures inherent to size-structured interactions – contributes to this pattern, resulting in phylogenetic niche conservatism due to selection (Losos 2008). Importantly, these alternatives are by no means mutually exclusive, and the interplay between phylogenetic and ecological factors in shaping species' niches may be strikingly different across taxa or trophic levels within a single food web (Rezende *et al.* 2009).

It is widely acknowledged that some of the species making up empirical food webs result from the aggregation of individuals across size and ontogeny (Werner & Gilliam 1984; Martinez 1991; Solow & Beet 1998; Rudolf 2007). For example, it has previously been observed that taxonomic aggregation in Broadstone Stream – one of the food webs for which

we cannot reject the random null hypothesis – has created a food web that no longer reflects the size of the individuals that actually interact (Woodward & Warren 2007; Woodward *et al.* 2010). We therefore find the general nature of the patterns that we observe to be all the more intriguing. Were food webs more highly resolved, to the level of individuals and not just individual species, we would expect the signal to be even stronger. Similarly, we have focused on food webs that are largely free of parasitic interactions, despite their recognized importance (Lafferty, Dobson & Kuris 2006; Lafferty *et al.* 2008; Beckerman & Petchey 2009). Here, we have treated all antagonistic interactions – predatory or parasitic – as equivalent when parasites or parasitoids are present (e.g. Broom and Grasslands). It will be interesting to see how this assumption holds up for future data sets with parasitism incorporated in greater quantity.

In the present manuscript, we provide statistical methods and results that allow us to link species body mass to the concepts of intervality and diet contiguity. This does not, however, imply that these factors represent sufficient or necessary ingredients in any model that aims to explain empirical food-web structure (Cohen & Newman 1985; Williams & Martinez 2000; Stouffer *et al.* 2006; Allesina *et al.* 2008; Williams & Martinez 2008). Nevertheless, any such model will likely need to incorporate the observed, phylogenetically related, non uniform variation across species. The challenge remaining, then, will be to definitively link the results presented here to a mechanistic model of food-web structure.

## Acknowledgements

We thank S. Allesina, J. Bascompte, P.M. Buston, M.A. Fortuna, R. Guimerà, R.D. Malmgren, P. McMullen, M. Sales-Pardo, G. Woodward and A.E. Zook

for stimulating discussions and helpful suggestions. D.B.S. acknowledges a CSIC JAE Postdoctoral Fellowship. E.L.R. is a Ramón y Cajal fellow of the MICINN, Spain. All figures were generated with PyGrace (<http://pygrace.sourceforge.net>).

## References

- Allesina, S., Alonso, D. & Pascual, M. (2008) A general model for food web structure. *Science*, **320**, 658–661.
- Barnes, C., Maxwell, D., Reuman, D.C. & Jennings, S. (2010) Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology*, **91**, 222–232.
- Beckerman, A.P. & Petchey, O.L. (2009) Infectious food webs. *The Journal of Animal Ecology*, **78**, 493–496.
- Beckerman, A.P., Petchey, O.L. & Warren, P.H. (2006) Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 13745–13749.
- Berlow, E.L., Brose, U. & Martinez, N.D. (2008) The ‘Goldilocks factor’ in food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4079–4080.
- Bersier, L.F. & Kehrli, P. (2008) The signature of phylogenetic constraints on food-web structure. *Ecological Complexity*, **5**, 132–139.
- Blomberg, S.P., Garland, Jr., T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.
- Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L., Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G. & Cohen, J.E. (2006) Consumer-resource body-size relationships in natural food webs. *Ecology*, **87**, 2411–2417.
- Buston, P.M. & Cant, M.A. (2006) A new perspective on size hierarchies in nature: patterns, causes, and consequences. *Oecologia*, **149**, 362–372.
- Camacho, J., Guimerà, R. & Amaral, L.A.N. (2002a) Analytical solution of a model for complex food webs. *Physical Review E, Statistical, Nonlinear, and Soft Matter Physics*, **65**, art. no. 030901.
- Camacho, J., Guimerà, R. & Amaral, L.A.N. (2002b) Robust patterns in food web structure. *Physical Review Letters*, **88**, art. no. 228102.
- Camacho, J., Stouffer, D.B. & Amaral, L.A.N. (2007) Quantitative analysis of the local structure of food webs. *Journal of Theoretical Biology*, **246**, 260–268.
- Cattin, M.F., Bersier, L.F., Banašek-Richter, C., Baltensperger, R. & Gabriel, J.P. (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature*, **427**, 835–839.
- Chase, J.M. (2000) Are there real differences among aquatic and terrestrial food webs? *Trends in Ecology & Evolution*, **15**, 408–412.
- Cohen, J.E. (1977) Food webs and the dimensionality of trophic niche space. *Proceedings of the National Academy of Sciences of the United States of America*, **74**, 4533–4536.
- Cohen, J.E. (1978) *Food Webs and Niche Space*. Princeton University Press, Princeton, NJ.
- Cohen, J.E. (ed.) (1989) *Ecologists’ Co-Operative Web Bank, version 1.0*. Rockefeller University, New York, NY.
- Cohen, J.E., Briand, F. & Newman, C.M. (1990) *Community Food Webs: Data and Theory*. Springer-Verlag, Berlin.
- Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 1781–1786.
- Cohen, J.E. & Newman, C.M. (1985) A stochastic theory of community food webs I. Models and aggregated data. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **224**, 421–448.
- Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. (1993) Body sizes of animal predators and animal prey in food webs. *The Journal of Animal Ecology*, **62**, 67–78.
- Davidson, A.D., Hamilton, M.J., Boyer, A.G., Brown, J.H. & Ceballos, G. (2009) Multiple ecological pathways to extinction in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 10702–10705.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002) Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 12917–12922.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2004) Network structure and robustness of marine food webs. *Marine Ecology Progress Series*, **273**, 291–302.
- Dunne, J.A., Williams, R.J., Martinez, N.D., Wood, R.A. & Erwin, D.H. (2008) Compilation and network analyses of cambrian food webs. *PLoS Biology*, **6**, e102.
- Guimerà, R., Stouffer, D.B., Sales-Pardo, M., Leicht, E., Newman, M. & Amaral, L. (2010) Origin of compartmentalization in food webs. *Ecology*, **91**, 2941–2951.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, **93**, 145–159.
- Jonsson, T., Cohen, J.E. & Carpenter, S.R. (2005) Food webs, body size, and species abundance in ecological community description. *Advances in Ecological Research*, **36**, 1–84.
- Kohda, M., Shibata, J.Y., Awata, S., Gomagano, D., Takeyama, T., Hori, M. & Heg, D. (2008) Niche differentiation depends on body size in a cichlid fish: a model system of a community structured according to size regularities. *The Journal of Animal Ecology*, **77**, 859–868.
- Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., Leo, G.D., Dobson, A.P., Dunne, J.A., Johnson, P.T.J., Kuris, A.M., Marcogliese, D.J., Martinez, N.D., Memmott, J., Marquet, P.A., McLaughlin, J.P., Mordecai, E.A., Pascual, M., Poulin, R. & Thielges, D.W. (2008) Parasites in food webs: the ultimate missing links. *Ecology Letters*, **11**, 533–546.
- Lafferty, K.D., Dobson, A.P. & Kuris, A.M. (2006) Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 11211–11216.
- Lawton, J.H. (1989) Food webs. *Ecological Concepts* (ed. J. Cherratt), pp. 43–78. Blackwell Scientific, Oxford, UK.
- Layman, C.A., Winemiller, K.O., Arrington, D.A. & Jepsen, D.B. (2005) Body size and trophic position in a diverse tropical food web. *Ecology*, **86**, 2530–2535.
- Loeuille, N. & Loreau, M. (2005) Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 5761–5766.
- Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995–1003.
- MacDonald, N. (1979) Simple aspects of foodweb complexity. *Journal of Theoretical Biology*, **80**, 577–588.
- Martinez, N.D. (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs*, **61**, 367–392.
- Mouillot, D., Krasnov, B.R. & Poulin, R. (2008) High intervality explained by phylogenetic constraints in host-parasite webs. *Ecology*, **89**, 2043–2051.
- Neubert, M.G., Blumenshine, S.C., Duplisa, D.E., Jonsson, T. & Rashleigh, B. (2000) Body size and food web structure: testing the equiprobability assumption of the cascade model. *Oecologia*, **123**, 241–251.
- Pascual, M. & Dunne, J.A. (eds) (2006) *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, Oxford, UK.
- Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4191–4196.
- Pimm, S.L. (2002) *Food Webs*, 1st edn. University of Chicago Press, Chicago, IL, USA.
- Rezende, E.L., Albert, E.M., Fortuna, M.A. & Bascompte, J. (2009) Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters*, **12**, 779–788.
- Rohr, R.P., Scherer, H., Kehrli, P., Mazza, C. & Bersier, L.F. (2010) Modeling food webs: exploring unexplained structure using latent traits. *The American Naturalist*, **176**, 170–177.
- Romanuk, T.N., Zhou, Y., Brose, U., Berlow, E.L., Williams, R.J. & Martinez, N.D. (2009) Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **364**, 1743–1754.
- Rudolf, V.H.W. (2007) Consequences of stage-structured predators: cannibalism, behavioral effects, and trophic cascades. *Ecology*, **88**, 2991–3003.
- Solow, A.R. & Beet, A.R. (1998) On lumping species in food webs. *Ecology*, **79**, 2013–2018.
- Srinivasan, U.T., Dunne, J.A., Harte, J. & Martinez, N.D. (2007) Response of complex food webs to realistic extinction sequences. *Ecology*, **88**, 671–682.
- Stouffer, D.B., Camacho, J. & Amaral, L.A.N. (2006) A robust measure of food web intervality. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 19015–19020.

- Stouffer, D.B., Camacho, J., Guimerà, R., Ng, C.A. & Amaral, L.A.N. (2005) Quantitative patterns in the structure of model and empirical food webs. *Ecology*, **86**, 1301–1311.
- Stouffer, D.B., Camacho, J., Jiang, W. & Amaral, L.A.N. (2007) Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **274**, 1931–1940.
- Sugihara, G. (1982) *Niche Hierarchy: Structure, Organization, and Assembly in Natural Communities*. Ph.D. thesis, Princeton University, Princeton, N.J.
- Sugihara, G. (1984) Graph theory, homology, and food webs. *Population Biology* (ed. S.A. Levin), pp. 83–101. American Mathematical Society, Providence, RI, vol. 30 of Proceedings of Symposia in Applied Mathematics.
- Warren, P.H. & Lawton, J.H. (1987) Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia*, **74**, 231–235.
- Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology, Evolution, and Systematics*, **15**, 393–425.
- Whittfield, J. (2004) Ecology's big, hot idea. *PLoS Biology*, **2**, e440.
- Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature*, **404**, 180–183.
- Williams, R.J. & Martinez, N.D. (2008) Success and its limits among structural models of complex food webs. *The Journal of Animal Ecology*, **77**, 512–519.
- Woodward, G., Blanchard, J., Lauridsen, R.B., Edwards, F.K., Jones, J.I., Figueroa, D., Warren, P.H. & Petchey, O.L. (2010) Individual-based food webs: species identity, body size and sampling effects. *Integrative Ecology: From Molecules to Ecosystems* (ed. G. Woodward), pp. 211–266. Academic Press, London, UK, vol. 43 of Advances in Ecological Research.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, **20**, 402–409.
- Woodward, G. & Hildrew, A.G. (2002) Body-size determinants of niche overlap and intraguild predation within a complex food web. *The Journal of Animal Ecology*, **71**, 1063–1074.
- Woodward, G. & Warren, P.H. (2007) Body size and predatory interactions in freshwaters: scaling from individuals to communities. In: *Body Size: The Structure and Function of Aquatic Ecosystems* (eds A.G. Hildrew, D. Raffaelli & R. Edmonds-Brown), pp. 98–117. Cambridge University Press, Cambridge, UK.
- Zook, A.E., Eklöf, A., Jacob, U. & Allesina, S. (2011) Food webs: ordering species according to body size yields high degree of intervality. *Journal of Theoretical Biology*, **271**, 106–113.

Received 21 September 2010; accepted 19 January 2011

Handling Editor: Andrew Beckerman

## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Empirical food webs.

**Appendix S2.** Phylogenetic analyses.

**Appendix S3.** Comparison between species attributes.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.