

The phylogenetic component of food web structure and intervality

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Abstract Despite the exceptional complexity formed by species and their interactions in ecological networks, such as food webs, regularities in the network structures are repeatedly demonstrated. The interactions are determined by the characteristics of a species. The characteristics are in turn determined by the species' phylogenetic relationships, but also by factors not related to evolutionary history. Here, we test whether species' phylogenetic relationships provides a significant proxy for food web intervality. We thereafter quantify the degree to which different species traits remain valuable predictors of food web structure after the baseline effect of species' relatedness has been removed. We find that the phylogenetic relationships provide a significant background from which to estimate food web intervality and thereby structure. However, we also find that there is an important, non-negligible part of some traits, e.g., body size, in food webs that is not accounted for by the phylogenetic relationships. Additionally, both these relationships differ depending if a predator or a prey perspective is adopted. Clearly, species' evolutionary history as well as traits not determined by phylogenetic relationships shapes

predator-prey interactions in food webs, and the underlying evolutionary processes take place on slightly different time scales depending on the direction of predator-prey adaptations.

Keywords Ecological networks · Food web · Interspecific · Phylogenetic correction · Taxonomy · Traits

Introduction

Food webs describe who eats on whom in ecological communities, and complex networks can be formed with the species as nodes and the feeding relationships as edges. Despite the complexity arising when species-rich communities are described, several regularities in their network structure have been demonstrated (Briand and Cohen 1984; Martinez 1992), and simple models for food web structure have been proposed in order to capture and mechanistically explain these regularities (Cohen and Newman 1985; Williams and Martinez 2000; Cattin et al. 2004; Stouffer et al. 2005; Allesina et al. 2008). One such regularity is intervality: if a food web is fully interval, each predator feeds upon a contiguous range of prey species such that there are no gaps within that range (Cohen 1977, 1978; MacDonald 1979; Sugihara 1982, 1984). Interspecific can also be described in the other direction, namely that each prey is predated upon by a contiguous range of predators (Zook et al. 2011). Several studies have analyzed intervality in food webs, and it has been demonstrated that empirical food webs show a strong bias toward intervality (Stouffer et al. 2006; Zook et al. 2011; Stouffer et al. 2011) despite not being fully interval (Williams and Martinez 2000; Cattin et al. 2004).

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The degree of intervality of a food web is directly related to the number of niche dimensions (Hutchinson 1957) in a community since the interactions in a fully interval web could, by definition, be explained using a single dimension. Moreover, the number of dimensions required to describe an ecological community can clearly be coupled to species traits (Rohr et al. 2010; Rossberg et al. 2010; Eklöf et al. 2013). The trait most often suggested to represent the first dimension in ecological interaction networks is body size (Warren and Lawton 1987; Neubert et al. 2000; Petchey et al. 2008). However, organizing species based on body size does not induce perfectly-interval diets (Stouffer et al. 2011) and also does not reproduce the maximum possible intervality when ordering the species in one dimension (Zook et al. 2011). Given that more than a single ecological factor or trait is required, it is therefore likely that the single niche dimension in large, interval webs is actually the combination of several, more or less correlated, variables (Eklöf et al. 2013).

The question of which traits provide the strongest predictor of network architecture (Eklöf et al. 2013) or of ecosystem function (McGill et al. 2006; Messier et al. 2010) is also of interest because these traits themselves are determined by coevolutionary dynamics among species (Forbes 1887; Thompson 1994). Moreover, closely-related species are also more likely to share similar traits than are distantly-related ones (Felsenstein 1985; Garland and Ives 2000; Blomberg et al. 2003). As such, similar species are more likely to consume and/or be consumed by similar species (Cattin et al. 2004; Rezende et al. 2009; Eklöf et al. 2012; Stouffer et al. 2012). Species' phylogenetic relationships therefore provide the foundation that most to all trait-based analyses and conclusions are built on top of, and this is as true for food webs as with any other key ecological process (Cadle and Greene 1993; Cavender-Bares et al. 2009).

In this paper, we test whether knowledge of species' shared evolutionary history—based on their taxonomic classification—provides a significant proxy for food web intervality. In doing so, we test the crucial *a priori* hypothesis that intervality is intimately linked to the community's pattern of species' relatedness. We then quantify the degree to which different species traits remain valuable predictors of food web structure after the baseline effect of species' relatedness has been removed. This step allows us to determine whether or not previous conclusions about the importance of different traits (Eklöf et al. 2013; Petchey et al. 2008; Stouffer et al. 2011) can be more parsimoniously argued on the basis of the phylogenetic relationships underneath.

Materials and methods

Empirical data

For our analyses, we used a data set consisting of six well-resolved marine food webs: the St Marks Seagrass system within Goose Creek Bay of St. Marks National Wildlife Refuge, St. Marks, Florida, USA (Christian and Luczkovich 1999); the Ythan Estuary, which is a small shallow estuary that flows into the North Sea about north of Aberdeen on the east coast of Scotland (Cohen et al. 2009); the Caribbean Reef network which includes the shelf of the American Virgin Islands, the British Virgin Islands and Puerto Rico (Optiz 1996); the arctic Kongsfjorden area which is an archipelago situated at the boundary of the European Arctic and is a glacial fjord on the northwest corner of the Svalbard archipelago (Jacob et al. 2011); Lough Hyne which is a semi-enclosed marine sea lough in the south-west of Ireland (Riede et al. 2010, 2011); and the high Antarctic Weddell Sea food web on the eastern Weddell Sea shelf and slope region (Jacob 2005; Jacob et al. 2011).

For each food web, the empirical data consists of an adjacency matrix that describes the presence and absence of interactions between species. In addition, all species in the food webs have been characterized based on one continuous trait, body mass, and five categorical traits with four or five distinct classes each: habitat preference, feeding type, foraging mode, metabolic category, and mobility. The first of the six traits, body mass (BM), is measured as the species' weight in grams. The next trait, metabolic category (MC), divides the species into four classes: *Primary producer*, *Invertebrate*, *Endotherm vertebrate*, and *Ectotherm vertebrate*.

A species' feeding mode (FM) describes the species' feeding strategy, and it has five classes. (1) *Predator*—A consumer who feeds upon prey species it has killed directly, either via an active hunt or via a sit-and-wait strategy for prey to approach within striking distance. Note that a consumer does not need to consume the whole prey (consuming only part is sufficient) to fall into this category; parasites, for example, do not necessarily kill their hosts. (2) *Scavenger*—A consumer who, in at least some of their feeding interactions, feeds upon prey that has already been killed by some previous event. As with predators, the whole prey does not need to be consumed during this interaction. (3) *Grazer*—A consumer that feeds by grazing. In the process, they may either kill their prey (like zooplankton species preying on unicellular algae) or merely damage it (as in the case of herbivorous urchins preying on a small part of benthic macroalgae). (4) *Filter feeder*—A consumer that

actively or passively filters their prey species out of the water column, i.e., a suspension feeder. (5) *None*—Species that are not consumers (e.g., primary producers).

A species' feeding type (FT) describes the type of consumer and has five classes: (1) *Herbivore*—A consumer that feeds on plant material only; (2) *Carnivore*—A consumer that feeds exclusively on other animals; (3) *Omnivore*—A consumer that feeds both animals and plants and therefore interact with more than one trophic level; (4) *Detritivore*—A consumer that feeds on dead animals and plants and/or dissolved organic matter only; (5) *Primary producer*—Species that are not consumer species of any kind but instead are producers.

A species' mobility (MB) distinguishes the various mechanisms for maintaining position and moving around in the (aquatic) environment. Each species was assigned to one of four mobility categories: *Sessile or passive floater*, *Crawler*, *Facultative swimmer*, and *Obligate swimmer*.

Lastly, the trait habitat (HB) describes the physical position of a species within the environment. Here, species are described as one of four categories: *Benthic*—the species lives on the seafloor; *Pelagic*—the species lives close to the surface; *Benthopelagic*—the species moves between and links both environments; *Land-based*—the consumer is not aquatic but feeds predominantly in the marine realm; *Reef-associated*—species that live in close relation to coral reefs.

Approximating the phylogeny

For the set of food webs analyzed here, the full phylogeny of species is not available. We therefore estimated the “approximate” evolutionary relationships between species based on their taxonomic classifications. Following an earlier approach (Eklöf et al. 2012), the species list for each food web was used to search the Integrated Taxonomic Information System online database (www.itis.gov). For all of the following analyses of each web, we kept only the species for which we could recover a full valid taxonomy (kingdom, phylum, class, order, family, and genus). This taxonomic classification is what we base our “phylogenetic orderings” and “phylogenetically corrected trait values” on. Some of the food webs were quite heavily simplified from this filtering process, i.e., between 7 and 30 % of the species had to be removed based on lack of taxonomic information (Table S1). This could potentially have an effect on the results if species from certain trait classes were to be more often removed compared to others. However, analyses of the distribution of traits among the removed species does not reveal any strong bias (see SI).

Phylogenetic contiguity

We first aimed to determine whether there is a common, phylogenetically consistent ordering of species that is compatible with significant contiguity of prey (or predators). To do so, we followed an earlier approach (Stouffer et al. 2006; Stouffer et al. 2011) which minimized a community-wide cost function of the form

$$\mathcal{G}_{\text{gen}}(\mathcal{O}_k) = \sum_{i=1}^S \sum_{j=1}^{\gamma_i} g_{ij|k}, \quad (1)$$

where $\mathcal{G}_{\text{gen}}(\mathcal{O}_k)$ is the total number of “generality” gaps in the whole web ($\mathcal{G}_{\text{vul}}(\mathcal{O}_k)$ is the same for “vulnerability” gaps). With gaps, we refer to the potential discontinuities in the predators' feeding ranges and preys' predator ranges, respectively. In addition, S is the number of species in the web, \mathcal{O}_k is an ordering of those species, γ_i is the number of gaps in the prey (or predators) of species i given ordering \mathcal{O}_k , and $g_{ij|k}$ is the number of species in the j th gap. The core idea of food web intervality is that there should be at least one ordering for which $\mathcal{G}_{\text{gen}}(\mathcal{O}_k)$ or $\mathcal{G}_{\text{vul}}(\mathcal{O}_k)$ are much smaller than would be expected at random (Stouffer et al. 2006).

In general, there are $S!/2$ possible orderings for a food web with S species that, for reasons of symmetry, could lead to unique intervality values. However, when maintaining the phylogenetic relationships between species, there can be far fewer permissible orderings. Specifically, for a tree with n interior nodes, there are $\frac{1}{2} \prod_{i=1}^n (d_i!)$ unique orderings, where d_i is the number of direct descendants of node i . A full binary tree with 7 species and 6 interior nodes, for example, will have just 32 orderings that do not violate the tree structure (which stands in stark contrast to the total of 2520 possible when ignoring the tree). Note that, for the same number of species, fully binary trees will always have fewer orderings possible than multifurcating trees where each internal node can have more than two direct descendants. This is particularly relevant in the present case since trees based on taxonomic classification are typically multifurcating.

Considering the above, we used a stochastic optimization method to search for an optimal ordering \mathcal{O}_k that minimized \mathcal{G}_{gen} (following Eq. 1) while respecting the pattern of relatedness between species. In this optimization process, we started with a random, but phylogenetically consistent ordering of species. We then calculated the changes in \mathcal{G}_{gen} corresponding to a rotation of the tree at each internal node; in all instances, we followed the principle of steepest descent and rotated the tree at the node that provided the

greatest reduction in total number of gaps. We then repeated this procedure until no further reduction was possible at which point we obtained a candidate ordering \mathcal{O}_k . Note that we also performed this optimization when minimizing \mathcal{G}_{vul} .

We used steepest descent here as opposed to other methods (e.g., simulated annealing (Stouffer et al. 2006; Stouffer et al. 2011) or genetic algorithms (Zook et al. 2011)) because of the considerable computational cost associated with this process. Recognizing, however, that this method provides no guarantee of finding an absolute global optimum, we repeated the procedure 100 times for each food web and selected the best overall ordering as the basis of our results. To demonstrate that our results are robust to this decision and to determine whether our optimal, phylogenetically-consistent ordering leads to significant intervality, we also compared our best orderings to an ensemble of 100 random orderings of each community.

Correcting traits for phylogenetic relatedness

Many analyses of ecological data can be confounded because of non-independence of species (Felsenstein 1985; Garland Jr. and Ives 2000; Rohlf 2001, 2006). To account for this fact in our analysis, we follow a statistical approach here that allows us to estimate species' *phylogenetically corrected* trait values based on what would be expected given their shared evolutionary history (Butler et al. 2000). To do so, we first estimate the matrix V of covariances that are expected as a result of phylogeny (Sokal and Rohlf 1962; Cavalli-Sforza and Piazza 1975) using the function “vcv” in the R-package “ape” (Paradis et al. 2004). Note that the form of V is a function of the evolutionary process (Grafen 1989). For simplicity, we assume here that the trait have evolved according to Brownian motion (Felsenstein 1985), though this method can be adapted to other microevolutionary models (Hansen and Martins 1996).

The next step builds from the theory underlying generalized least-squares (GLS) regression which is an extension of ordinary least-squares regression that controls for known (or expected) correlation between observations (Rao 1965; Rao et al. 2010). In particular, to convert the values of any continuous trait X with correlations to their corrected values U with zero correlations (Rao 1965), we perform a phylogenetic GLS transformation $U = V^{-1/2}X$, where $V^{-1/2}$ is the Cholesky decomposition of V^{-1} (Butler et al. 2000) and was computed using the function “chol” in R (R Development Core Team 2014).

The procedure we follow for categorical traits is similar and builds on the way in which such traits would be treated in comparable regression analyses and is widespread in regression models (Rao et al. 2010; Zuur et al. 2009).

Specifically, we first convert each categorical trait C with c distinct classes to c different dummy variables D that can take the values 0 or 1 that indicate whether that class is “on” or “off” for that particular species (Quinn and Keough 2002). Given this set of dummy variables, we can then apply the same transformation described above to calculate their corrected values.

Predicting interactions based on phylogenetically corrected trait values

We next analyzed how and whether network structure could be explained on the basis of species-specific traits. The methodology here follows the procedure as that outlined by Eklöf et al. (2013) with the important difference that the traits are corrected for the phylogenetic relationship present between species (see section above). In that way, we can explicitly quantify how much structure is not captured by the phylogenetic relationships but is rather due to the traits themselves.

We tested all phylogenetically-corrected traits one by one as well as all possible combinations of the six traits. For all networks and each combination of traits, we measured the proportion of correctly predicted connections. As a representative example, suppose we use three traits to describe a food web: body size, metabolic category, and mobility. In the empirical data, represented by the adjacency matrix A , all the prey of predator i have size in the interval $[1, 3]$ cm, are *invertebrates* and have *high* or *medium* mobility. Based on this information, we can construct a new interaction matrix A' in which i preys upon all the species that simultaneously satisfy all three of these conditions. A' will necessarily contain all of the interactions present in the original matrix A , but potentially contains additional, erroneous connections (species that satisfy the requirements on body size, metabolism, and mobility but are not actually consumed by the predator). If E is the number of erroneous connections and L the number of empirically observed connections, we can estimate the performance of this combination of traits by computing $p = L/(L + E)$, the proportion of correctly predicted links, the overlap (Petchey et al. 2008; Allesina 2011; Eklöf et al. 2013).

In a web with original trait values (i.e., values that have not been corrected for the phylogenetic relationships), a high overlap implies that the information in the trait data is sufficient to correctly reproduce or predict a large proportion of the interactions. However, since we use traits here whose values have been phylogenetically corrected, the proper interpretation is modified slightly. Namely, a trait that is strongly phylogenetically conserved would be expected to exhibit relatively low additional explanatory power after its values have been corrected. This would therefore correspond to a low overlap value since most of the

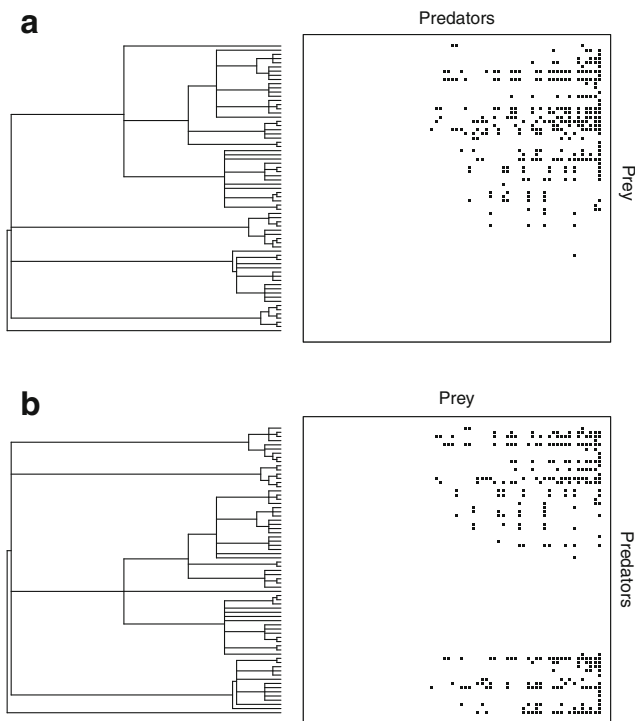


Fig. 1 Visualizing phylogenetic food web intervality. Here, we show the optimal phylogenetically consistent orderings of species in the Ythan Estuary food web (Cohen et al. 2009) when maximizing **a** the collective contiguity of all species' prey and **b** the collective contiguity of all species' predators. The trees to the left show the relationships between species in the two optimal orderings, and the graphical “matrices” to the right show the ordered predator-prey interactions with the black squares indicating observed interactions. In addition, predators' positions in **a** are in order of increasing generality from left to right, whereas the position of prey in **b** is in order of increasing vulnerability

“structure” predicted by that trait is embedded in the phylogeny. As one might expect, the opposite should be true for traits that are less phylogenetically conserved or not phylogenetically conserved whatsoever.

Table 1 The number of generality or vulnerability gaps in different food webs when species' prey and predators, respectively, are ordered according to their phylogenetic relatedness

Food web	Generality gaps			Vulnerability gaps		
	$G_{\text{gen}}^{\text{phylo}}$	$\langle G_{\text{gen}}^{\text{random}} \rangle$	z -score	$G_{\text{vul}}^{\text{phylo}}$	$\langle G_{\text{vul}}^{\text{random}} \rangle$	z -score
Kongsfjorden	3811	11,433.57	−15.19	5634	18,157.31	−7.99
Loughhyne	12,575	37,355.63	−20.51	24,307	64,070.88	−13.29
Caribbean Reef	4713	7961.83	−8.84	13,993	30,240.78	−5.76
St. Marks	887	3660.89	−11.13	1002	2349.63	−10.19
Weddell	20,690	63,592.43	−33.55	48,274	96,944.58	−23.53
Ythan Estuary	451	1625.94	−7.87	441	1223.58	−8.13

We identified a phylogenetically consistent ordering which minimized Eq. 1, and compared the number of gaps $G_{\text{gen}}^{\text{phylo}}$ and $G_{\text{vul}}^{\text{phylo}}$ with the same value across an ensemble of random orderings. From this comparison, we calculated the z -score which measures the number of standard deviations away from the expected value under the random null hypothesis. The more negative the value, the more that species' phylogenetic relationships are consistent with intervality and therefore can account for observed contiguity of species' prey or species' predators

For comparison, we also calculated the “overlap” based on the optimal phylogenetic ordering of the species (see section “Phylogenetic contiguity”). In this case, we counted the gaps in the optimal orderings as erroneous connections E , and the overlap would then be computed in the same manner as for the traits: $p = L/(L + E)$.

Phylogenetic diversity measures

The food webs analyzed differ in diversity—in terms of the number of species—as well as their degree of phylogenetic diversity. Since this may impact our earlier results, we calculated the phylogenetic species variability (PSV) for each web using the function “psv” in the R-package “picante” (Helmus et al. 2007). PSV summarizes the degree of relatedness among a group of species and, importantly, should be independent of species richness (Helmus et al. 2007).

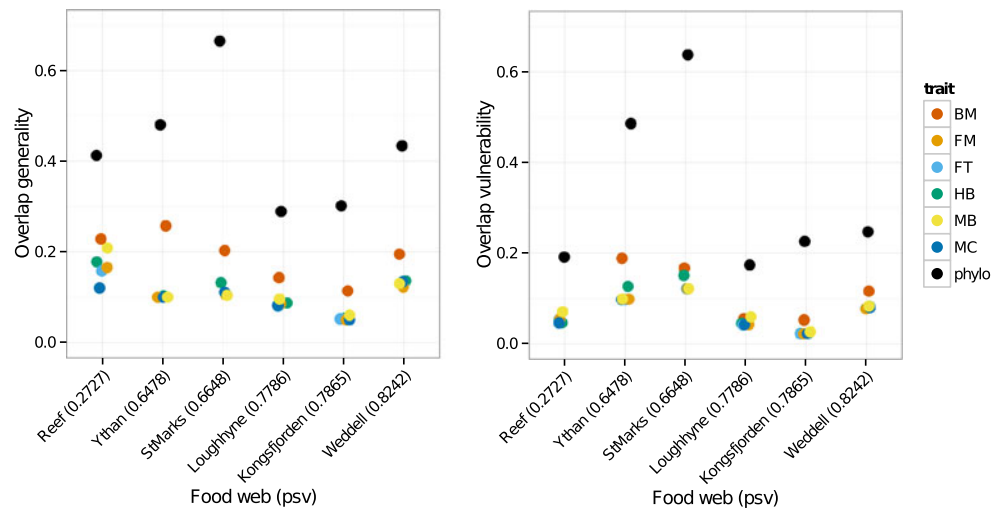
Data and code availability

All of the food web matrices are available from their original sources, whereas the trait data is available upon request (data owner U. Jacob). All code, and additionally a sample R-script and a set of sample data files, is available in a R-package which can be found at <http://github.com/stoufferlab/phyloint>.

Results

We first obtained the set of optimal orderings of prey and predators for the six empirical food webs and compared their properties with those of random orderings (Fig. 1). Here, we found that the number of generality gaps $G_{\text{gen}}^{\text{phylo}}$ and the number of vulnerability gaps $G_{\text{vul}}^{\text{phylo}}$ are always

Fig. 2 The overlap for the best ordering based on phylogeny (“phylo,” *black dots*) and the different traits after being corrected for phylogeny (*colored dots*) for the different food webs. In parenthesis is the phylogenetic species variability (PSV) value presented. Trait identifiers: *BM* body mass, *FM* feeding mode, *FT* feeding type, *HB* habitat, *MB* mobility, and *MC* metabolic category. Note that the webs are ordered based on their PSV, but the x-axis is not scaled accordingly



significantly less than would be expected given the random null hypothesis (Table 1). These results indicate that phylogeny provides a significant background from which to estimate contiguity of prey and/or of predators. In general, we also observed that phylogeny provides a better approximation for diet contiguity than predator contiguity in five of the six empirical webs (Table 1).

Alternatively, the observed number of gaps when the single dimension is represented by phylogeny can be seen as erroneous interactions, i.e., interactions that are wrongly predicted by the phylogenetic relationships. When viewed from this perspective, we find similar results as those for diet and predator contiguity (Fig. 2). Specifically, when considering the optimal species’ orderings are dictated by their

phylogeny, the average generality overlap across the six networks is $0.43 (\pm 0.14)$; likewise, the average vulnerability overlap is $0.33 (\pm 0.19)$. Interestingly, these values compare quite favorably to the overlap for uncorrected traits found in an earlier study (Eklöf et al. 2013); there the mean of the best performing single trait for the generality case was $0.19 (\pm 0.053)$ and $0.22 (\pm 0.25)$ for the vulnerability case.

Given these baseline values provided by phylogeny alone, we next sought to determine the degree to which different species traits provided further explanatory power when controlled for the phylogenetic-correlation inherent in those traits. Among the traits tested here, we found that body mass was always the trait adding most additional explanatory

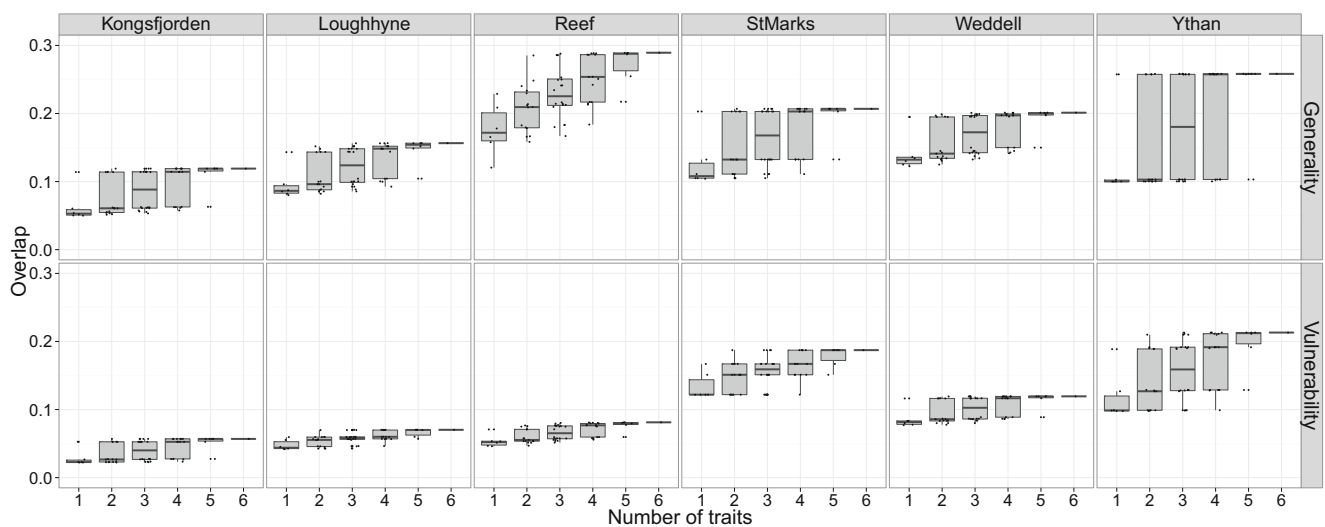


Fig. 3 Boxplots showing the overlap for the different combinations of traits, for all food webs in the generality direction (*top row*) and vulnerability direction (*bottom row*). In all panels, the box covers the 25th–75th percentiles, the *middle line* marks the median, and the

maximum extent of the whiskers are the 5th and 95th percentiles. The *black points* correspond to the empirical data and have been lightly shifted horizontally for visibility

tory power (i.e., produced a higher overlap) when tested in isolation (Fig. 2). In general and in line with the expected effect of correcting for phylogenetic relatedness, the additional explanatory power provided by single traits is rather limited; in fact, it is less than 20 % in almost all cases and considerably less for traits other than body size.

Within these trait-based results, we found a strong divergence between the overlap produced depending if one adopts the predator or prey perspective. The generality overlap produced by any phylogenetically corrected trait ($overlap_{gen}$) is generally higher than the vulnerability overlap ($overlap_{vul}$). This is true for all webs except the St. Marks food web, which shows the opposite relationship for all traits except body mass. Overall, these differences indicate that phylogenetic signal is lower in the traits of the resources compared to consumers.

This divergence can also be seen in the overlap produced by combining several traits, where the joint overlap is lower for the vulnerability overlap (Fig. 3). From these computations, it is also evident that the phylogenetic signal is correlated within the traits since combining traits in most cases rapidly shows diminishing marginal returns (Fig. 3). However, this is not very clear in the Ythan Estuary food web where the spread in the calculated overlap is high. This is due to the high overlap produced by body size (0.2575) compared to the other traits ([0.1000–0.1028]).

How phylogenetically diverse the different food webs are could potentially influence the role phylogeny has for structure. Here, we measured the phylogenetic diversity as phylogenetic species variability (PSV) (Helmus et al. 2007). There is no clear trend in the relationship between a food web's PSV and the overlap produced by phylogenetic ordering or traits. However, the three webs showing the highest phylogenetic diversity (Loughhyne, Kongsfjorden, and Weddell) do show significantly lower overlap for the best phylogenetic ordering compared to the webs with lower psv (Fig. 3).

Discussion

Predators and prey form complex networks via their feeding interactions, and the underlying structure of these networks has been a fruitful venue for ecological research. Of major importance for understanding and practical use of such research is to elucidate the processes underlying any observed patterns. Trophic interactions are formed based on the traits of the interacting species. The traits in turn have been developed during evolution and are therefore to a large extent determined by species phylogenetic relationships. However, other ecological factors independent of the evolutionary process are also of importance for the formation of feeding interactions, but it is not clear to

what degree the two processes matter (Bersier and Kehrli 2008).

We here show that predators have a strong tendency to consume prey species that are phylogenetically related, and that this relatedness is a strong predictor for diet contiguity; we likewise show that prey have a significant tendency to be consumed by related predators. Earlier studies have indeed shown that phylogeny and trophic structure are closely linked (Bersier and Kehrli 2008; Rossberg et al. 2006; Rossberg et al. 2010; Cattin et al. 2004; Eklöf et al. 2012), but in analyses of food web intervality per se the focus has almost always been on traits (i.e., body size) rather than phylogeny (but see Rossberg et al. 2010; Stouffer et al. 2011). Single traits, such as body size, have not been able to produce the level of intervality observed in empirical food webs (Zook et al. 2011; Stouffer et al. 2011) indicating that likely several traits are required. Species phylogeny can therefore be seen as a collection of (more or less correlated) traits, and our results here indicate that phylogeny provides a particularly relevant and appealing candidate for approximating the single dimension consistent with intervality.

We also measured the amount of food web structure explained by single species-specific traits and combinations of traits *after* they were corrected for the species' underlying phylogenetic relationships. One slightly surprising result here is that body size still explains a rather large part of the network structure even after the values have been corrected for phylogeny (Fig. 2). In line with previous research (Naisbit et al. 2012), this suggests that there is an important, non-negligible part of the distribution of body sizes in food webs that is not accounted for by the phylogenetic relationships. Moreover, although it has been shown that body size is phylogenetically conserved (Vamosi and Vamosi 2007; Emerson and Gillespie 2008) there is also evidence that adjustments in body size can occur in relatively short time periods (Köster et al. 2013; Sheridan and Bickford 2011; Gardner et al. 2011)

For the other traits, the overlap is lower compared to body size indicating those traits tended to be more phylogenetically conserved (Butler et al. 2000). Indeed, the traits analyzed here are relatively simple ones defined around coarse-grained classes (e.g., four types of mobility for webs up to almost 500 species), and it is likely evolutionary relationships should capture most to all of the major transitions across the species.

Across nearly all of the food webs, we found evidence that the link between phylogeny and traits differed depending on whether we focused on consumers or resources. As before, this mirrors observations from multiple previous studies (Rossberg et al. 2006; Bersier and Kehrli 2008; Naisbit et al. 2012). One plausible explanation for this discrepancy could be that resources adapt their defense

mechanisms at different evolutionary rates than consumers adapt new strategies for prey capture. Foraging traits seem to evolve considerably faster than resource traits, implying that phylogenetic correlations between resource traits are stronger than between foraging traits (Blomberg et al. 2003; Rossberg et al. 2010; Bersier and Kehrli 2008). This is also what we see here where the resource traits are phylogenetically conserved to a higher degree than consumer traits. Moreover, the evolutionary rate has been suggested to be higher for foraging traits than for resource traits in order to generate food web structures that resemble those seen in nature (Rossberg et al. 2006). The same is true if we return to the original question of food web intervality, where it was previously shown that predators tend to have fewer gaps in their range of prey than prey have in their range of predators (Zook et al. 2011).

Clearly, both species' evolutionary history and their traits allow and prevent predator-prey interactions in food webs. It is also likely that the underlying evolutionary processes take place on slightly different time scales depending on the direction of predator-prey adaptations. This discrepancy in rates imply that phylogenetic relationships alone will never be able to fully predict food web structure, but rather that species-specific traits are needed in addition. Here, we have analyzed a set of relatively simple traits; even though we have demonstrated that they provide significant additional explanatory power more factors remain to play important roles. We therefore conclude that even if ecological research has made substantial progress in this area the full story of unraveling the mechanisms behind food web structure, and the structure of other ecological networks, has yet to be written.

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