

**IDEA AND  
PERSPECTIVE**

## Effects of trophic similarity on community composition

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### Abstract

Understanding how ecological processes determine patterns among species coexisting within ecosystems is central to ecology. Here, we explore relationships between species' local coexistence and their trophic niches in terms of their feeding relationships both as consumers and as resources. We build on recent concepts and methods from community phylogenetics to develop a framework for analysing mechanisms responsible for community composition using trophic similarity among species and null models of community assembly. We apply this framework to 50 food webs found in 50 Adirondack lakes and find that species composition in these communities appears to be driven by both bottom-up effects by which the presence of prey species selects for predators of those prey, and top-down effects by which prey more tolerant of predation out-compete less tolerant prey of the same predators. This approach to community food webs is broadly applicable and shows how species interaction networks can inform an increasingly large array of theory central to community ecology.

### Keywords

Clustering, community assembly, dispersion, food webs, interaction networks, metacommunity, phylogenetics.

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### INTRODUCTION

Ecologists have long been interested in the processes responsible for patterns of species coexistence within local communities. This interest is reflected in classic debates about whether community assembly is dominated by random (Connor & Simberloff 1979; Strong *et al.* 1979), competitive (Diamond 1975; Gilpin & Diamond 1982), environmentally-driven (Chase & Leibold 2003), or dispersal processes (Hubbell 2001). Much research in this area hinges on the concept of the niche (Grinnell 1917; Elton 1927; Hutchinson 1957) including the distinction between the fundamental and the realised niche, that is the conditions under which a species can and does exist, respectively (Hutchinson 1957).

A classic approach to exploring the role of species' niches in community composition has been to investigate the ecological similarity between coexisting species (MacArthur & Levins 1967). When species coexisting in a given community are found to be unusually dissimilar, researchers explain this pattern by invoking processes of competition whereby species with similar niche requirements exclude each other from the community (Elton 1946). Alternatively, if coexisting species are unusually similar, processes of environmental filtering are often invoked whereby aspects of the environment such as temperature or the presence of specific resources restrict

coexisting species to those that are similarly adapted to the environment of that community (but see e.g. Mayfield & Levine (2010) for different interpretations).

Directly measuring species' ecological similarity is challenging. Instead, ecologists often measure it indirectly by assuming that more easily observed measures such as habitat preference, morphology and, more recently, phylogenies can be used to effectively estimate similarity in how species interact among themselves and their environment (Webb *et al.* 2002; Emerson & Gillespie 2008; Kraft *et al.* 2008; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012). Habitat preferences and traits associated with these preferences emphasise the role of Grinnellian niches (Grinnell 1917). In comparison, traits associated with Eltonian niches – those defined by consumer–resource interactions (Elton 1927), such as mouth size – are less often measured. Such avoidance of more direct consideration of trophic interactions may misrepresent the roles of food availability and, more broadly, the 'trophic environment' (or 'biotic interaction milieu', McGill *et al.* 2006) in determining community composition. For example, poor understanding of who eats whom within communities may obscure the roles of food availability and predator diversity relative to the roles of tolerance to abiotic conditions in shaping species' coexistence. More direct assessments of how trophic similarity affects community assembly are especially important given the powerful

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roles that feeding relations play in species' evolution, distribution and abundance (Pascual & Dunne 2005).

Here, we use food webs – networks of who eats whom among a set of species – to quantify trophic similarity and explore patterns of species coexistence. We measure species' similarity in terms of which species they eat and which species they are eaten by. We analyse the extent to which the trophic similarity among coexisting species deviates from null models of community assembly. Our framework helps, e.g. to measure the strength of filtering by the 'trophic environment' and food-mediated interspecific competition in determining community composition. We apply our framework to 50 Adirondack lake food webs (Havens 1992) and discuss key findings and several limitations of our approach.

## A GENERAL FRAMEWORK TO UNDERSTAND COMMUNITY ASSEMBLY USING TROPHIC SIMILARITY

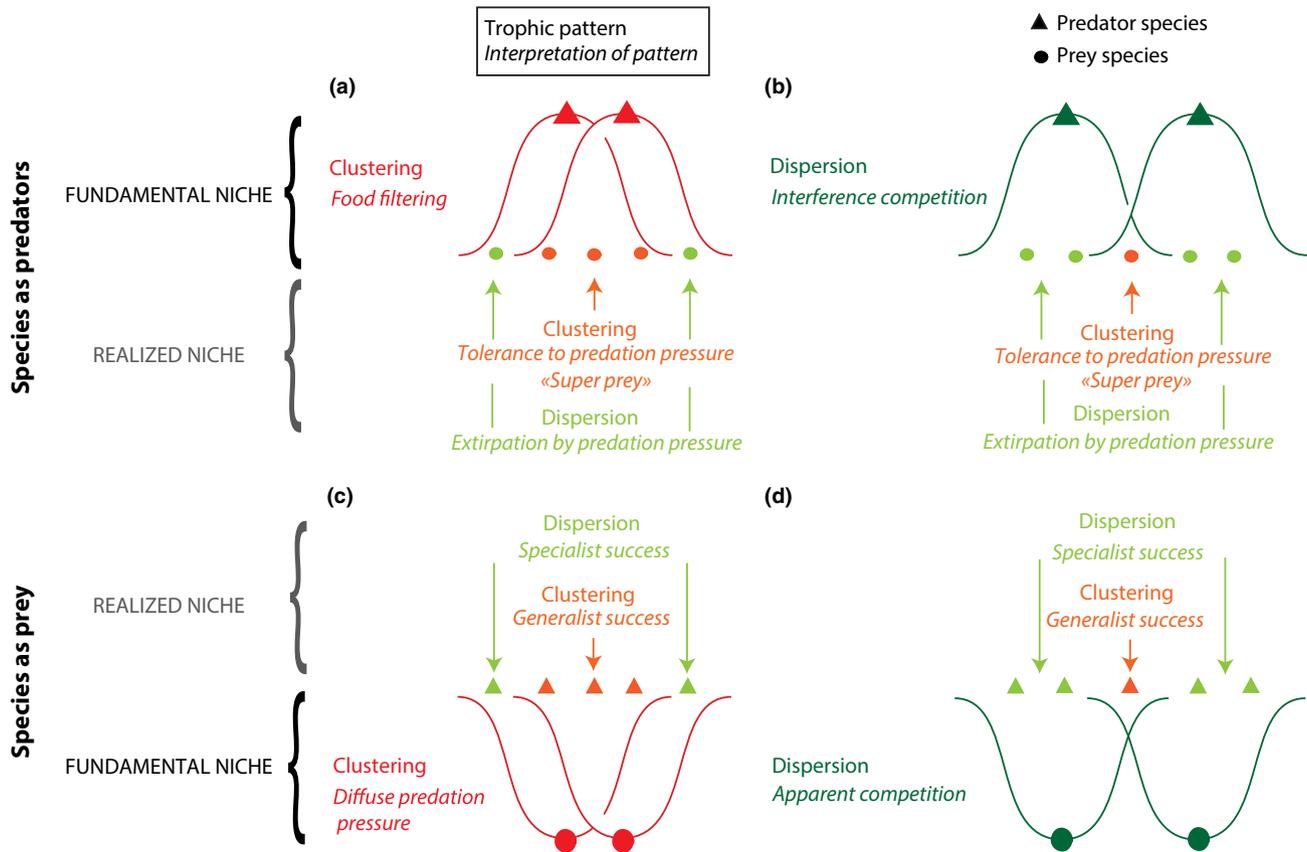
### General framework

Our framework applies concepts, methods and mechanistic inferences associated with analyses of the phylogenetic structure of communities that builds on much of the above research on niche structure of communities (Webb *et al.* 2002; Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012) to analyse the trophic structure of communities (Pascual & Dunne 2005). Similar to community analyses of niche structure, community phylogeneticists often compare the phylogenetic diversity of local communities to that of 'null' communities obtained by randomly drawing the observed number of species from a regional species pool. Deviations from null expectations are then interpreted in terms of community assembly processes. In practice, the regional species pool is obtained by combining all local scale communities. Various measures of phylogenetic diversity are used. Popular measures include the mean pairwise phylogenetic distance (MPD, Webb *et al.* 2002) and the mean nearest phylogenetic taxon distance (MNTD, Webb *et al.* 2002; Kraft *et al.* 2007; Kembel 2009). Both are calculated based on pairwise phylogenetic distances between species. The phylogenetic distance between two species is an estimate of the time of evolutionary divergence between the two species and is computed as the branch-length separating these species on the phylogenetic tree. Assuming niche conservatism, phylogenetic distance is presumed to reflect the ecological dissimilarity between two species (Losos 2008).

Rather than assuming such ecological niche conservatism here, we more directly measure a key aspect of ecological similarity between two species as the overlap between two species' sets of predator and prey species (Martinez 1991). We consider 'predator similarity' to be the similarity between predators based on their prey (i.e. how many prey species two species have in common) and 'prey similarity' to be the similarity between prey species based on their predators (i.e. how many predator species two species have in common). Considering these two aspects of pairwise trophic similarity is close in spirit and complementary to previous approaches that have investigated asymmetry in interaction sets, including asymmet-

ric structure in mutualistic and trophic networks (Bascompte *et al.* 2006; Thébault & Fontaine 2008; Joppa *et al.* 2009). We use 'predators' and 'prey' throughout because these familiar terms reasonably describe the feeding relationships we analyse in the pelagic area of lakes where consumers typically engulf and kill individuals that they eat. However, while predator and prey may be intuitive and relatively appropriate for pelagic species, our framework employs these terms to more generally refer to categories of consumers and resources that include feeding relationships such as parasitism, herbivory, etc. Measures of trophic similarity are particularly meaningful among species within a trophic level whose set of predators and prey are more comparable than species among different trophic levels. Therefore, we perform our analyses on the following three trophic levels: primary producers (species without prey, hereafter referred to as basal species), herbivores (species that eat only basal species) and carnivores (all other species including omnivores). We use the Jaccard index, which divides the number of predator and/or prey species that two species have in common by the total number of both species distinct predator and/or prey species. We use the average (Martinez 1991) and maximum (Williams & Martinez 2000) values of this index across all species at a given trophic level to calculate ecological similarity at that trophic level. Average similarity is analogous to the MPD (Webb *et al.* 2002) and equals the mean pairwise trophic similarity between all pairs of species within a trophic level. Maximum similarity is analogous to the MNTD (Webb *et al.* 2002; Kraft *et al.* 2007) and is obtained by averaging the similarity between each species and its most similar species across all species within the trophic level considered.

We consider both 'fundamental' and 'realised' measures of trophic similarity. Unlike the independence of phylogenetic distance between two species on the community in which the species are found, species' trophic distance depends on the pool of species considered. Species' diets are determined not only by morphological and physiological attributes constrained by processes such as evolutionary history, but also by the availability of prey that vary among places and over time. In niche theory, this is the well-known difference between fundamental and realised niches (Hutchinson 1957). The realised trophic niche of a species includes all the prey species it actually feeds upon in a given community, which is inherently community-dependent. The fundamental trophic niche of a species includes all the prey species it could feed upon if they were available. This potential is considered a more evolutionarily derived and relatively intrinsic characteristic of the species independent of the community in which it is found. We estimate the fundamental trophic niche using the regional 'metaweb' comprised of all species present in the various local communities (i.e. the regional species pool or metacommunity) and of their potential feeding interactions. The metaweb contains links between species that may never co-occur in the local communities but would trophically interact if they did co-occur, e.g. in a feeding experiment. Our estimates – which are based on a regional species list – fall short of the full fundamental niche. Still, they are closer to the fundamental niche than estimates based on local webs.



**Figure 1** Inferring processes of community assembly and species' coexistence from patterns of trophic clustering and dispersion. The bell curves represent the fundamental trophic niches of predator (top row) or prey (bottom row) species with clustered niches on the left in red and dispersed niches on the right in green. In the top row, dots represent prey species within predator fundamental niches occurring in a given community. In the bottom row, triangles represent predator species within prey fundamental niches occurring in a given community. The occurrences of prey (top row) and predator (bottom row) species within a given community determine the realised niche of predators and prey respectively. Red and green arrows point from the pattern and the inferred process labeled in the same color towards which prey (top row) or predator (bottom row) species create the pattern by being overrepresented in clustered and dispersed realised niches respectively. The processes (in italics) inferred from the patterns named just above the processes are described in the text (section *General Interpretation of patterns*).

We compare observed trophic similarity measures to null expectations using a set of community food webs found within a region. These expectations emerge from randomly drawing species from the regional species pool in a way that creates connected food webs with identical numbers of species at each trophic level for each community. We first randomly draw the empirically observed number of basal species. Then, we randomly draw the empirically observed number of herbivorous species among only those that eat at least one previously chosen basal species. Finally, we draw the empirically observed number of carnivorous species among only those that eat at least one non-basal species already in the web. Webs containing basal species with no predators are ignored. This matching of empirical levels of diversity at several trophic levels connected to other species in the community is conservative in that it minimises differences between modelled and observed similarities. For example, the null requirement for community membership (i.e. the presence of suitable prey in that community) institutes strong trophic filtering, which suggests that significantly stronger filtering in empirical data is an ecologically important signal. On the other hand, our assembly procedure restricts quite considerably how many

different food webs can be generated. We addressed this restriction by evaluating how many of unique webs were generated by our assembly procedure.

Our null model formalises the trophic-dependence hypothesis of Holt *et al.* (1999) and is similar to Piechnik *et al.*'s (2008) and Gravel *et al.*'s (2011) trophic models of island biogeography, except that we constrain the number of basal, herbivore and carnivore species in each local web. Our initial null models that constrained only the total number of species rather than the number at each trophic level created webs that greatly over-represented basal species due to the high ratio of regional to local diversity of phytoplankton among the lakes relative to the same ratio at higher trophic levels. Other stochastic food web models (Cohen & Newman 1985; Williams & Martinez 2000; Cattin *et al.* 2004; Allesina *et al.* 2008) have highlighted general rules underlying food web structure. Our model follows this tradition but focuses on rules underlying species' co-occurrence with more emphasis on trophic niche overlap than on rules responsible for overall food web structure.

We compare observed communities to null expectations using 'P-values' representing the quantile of the observed metric vs. null communities, defined as the rank of the

observed metric within null communities, divided by the number of null communities + 1.  $P$ -values  $> 0.5$  indicate that species are more trophically similar than expected by chance (significantly so for  $P > 0.95$ ), whereas  $P$ -values  $< 0.5$  indicate that species are less trophically similar than expected by chance (significantly so for  $P < 0.05$ ). We, respectively, refer to these non-random patterns as ‘trophic clustering’ and ‘trophic dispersion’ by analogy with terminology used in community phylogenetics. All analyses were performed in the R statistical language and environment (R development Core Team 2009), with personal codes and codes adapted from the *picante* package (Kembel *et al.* 2010) and Owen Petchey’s ‘Food webs’ online resources (<https://bitbucket.org/owenpetchey/ttl-resources>).

### General interpretation of patterns

The tendency of co-occurring species to be more or less trophically similar than expected under a random assembly model can be interpreted in terms of community assembly processes, such as how competitive exclusion may structure community composition (Fig. 1). Combining analyses of fundamental and realised niche enables inferences about community structure that would not be possible by analysing either fundamental or realised niches in isolation. Realised trophic similarity is computed from local community composition data, and reflects a combination of the fundamental niche of species and current community composition. For example, the processes of evolving to eat similar food and preferential dispersal to locations where similar food persists would result in a clustering among fundamental predator niches. This clustering combined with preferential extinction of the prey species within predators’ fundamental niche overlap may result in the dispersion of realised predator niches. In other words, predators’ fundamental niches could be clustered in the same community where their realised niches are dispersed. Such findings can corroborate richly articulated hypotheses of community assembly. More generally, considering predator niches, patterns in fundamental niches reflect relationships between species’ broadly considered feeding behaviours, whereas patterns in realised niches describe which prey persist among those relationships. Considering prey niches, patterns in fundamental niches reflect relationships between species’ broadly considered vulnerability to predation (in terms of how many predator species prey upon the species), whereas patterns in realised niches describe which predators are actually present among those relationships (Fig. 1).

More specifically, trophic clustering of predator species’ fundamental niches (Fig. 1a) indicates that co-occurring predator species appear adapted to consume more similar prey species than expected by chance. This suggests that their local coexistence may be explained by ‘food filtering’ whereby food availability beyond the single prey species required by our null model attracts the predators to a community. This process may be particularly strong under certain types of facilitation such as interspecific cooperation of predators in hunting prey (e.g. that of tuna and dolphins preying on schools of fish) or the ability of plant volatiles resulting from herbivory to attract multiple species of the herbivore’s predators (Amo

*et al.* 2013). In both cases, trophic clustering is consistent with the trophic environment in terms of prey species composition driving community assembly. This would contradict more conventional expectations that interference competition (Skalski & Gilliam 2001), intraguild predation (Polis *et al.* 1989) and competitive exclusion – by which predators may extirpate other predators of their prey – would force co-occurring predators to share relatively few species, leading to trophic dispersion (Fig. 1b). Trophic clustering of predator species’ realised niches indicates that prey species manage to coexist while being preyed upon by many predators (‘super prey’ in Fig. 1a). This would contradict more conventional expectations that high predation pressure would lead to the extirpation of the prey (‘extirpation by predation pressure’ in Fig. 1a). Overall, expectations of community assembly via food filtering and extirpation due to predation pressure would result in clustering of fundamental predator niches and dispersion of realised predator niches.

Niche overlap in terms of species’ predators that focuses on species as prey (Fig. 1c and d) has been studied much less than overlap of species’ prey. Trophic dispersion of prey species’ fundamental niches indicates that co-occurring prey species share relatively few predators (Fig. 1d). This pattern may be driven by apparent competition by which the prey more able to sustain predation increases the predator’s population resulting in the extirpation of the species less able to sustain predation (Holt 1977). Trophic clustering of prey species’ fundamental niches (Fig. 1c) indicates that prey species with shared predators are relatively frequent within a local community. This is consistent with facilitation among prey whereby trophically similar prey species may diffuse the pressure imposed by mutual predators. Such facilitation may emerge from prey exhibiting out of phase oscillations when predators may adaptively forage on abundant prey species leaving rare prey species relatively free from predation.

Trophic clustering of prey species’ realised niches (Fig. 1c and d) simply indicates that co-occurring predators prey on more of the same prey species than expected by chance. These predators have to prey on at least two prey and clustering in this situation could arise from an insurance effect in an instable trophic environment whereby an at least somewhat general predator species can switch from a food source to another depending on availability. On the other hand, dispersion in prey’s realised niches (Fig. 1c and d) indicates that the predators of co-occurring prey are specialised on relatively few prey species, a situation thought to be more likely in more stable environments.

Perhaps, the pattern most consistent with the largest body of ecological theory is dispersed fundamental and realised predator niches (Fig. 1b, green). According to the considerations above (and summarised in Fig. 1), dispersed fundamental predator niches are expected if competitive exclusion prevents predators with high overlap from locally coexisting. We would expect the realised predator niches to also be dispersed if these predators preferentially extirpate the few species within the predators’ relatively small diet overlap. However, in contrast to such intolerance of predation pressure by multiple predator species, the predators’ realised niches could be clustered if prey species within the small over-

lap preferentially persisted, perhaps if their growth or dispersal rates overcompensated for the prey species' high vulnerability.

The complementarity provided by multiple niche perspectives (both fundamental and realised niches as well as predator and prey niches) is further enhanced by focusing on adjacent trophic levels individually (basal species, herbivores and carnivores) and then combined for a fuller picture of the niche space of entire communities. This full picture is illustrated by the following analysis of 50 lake food webs found in a mountainous region of the US state of New York.

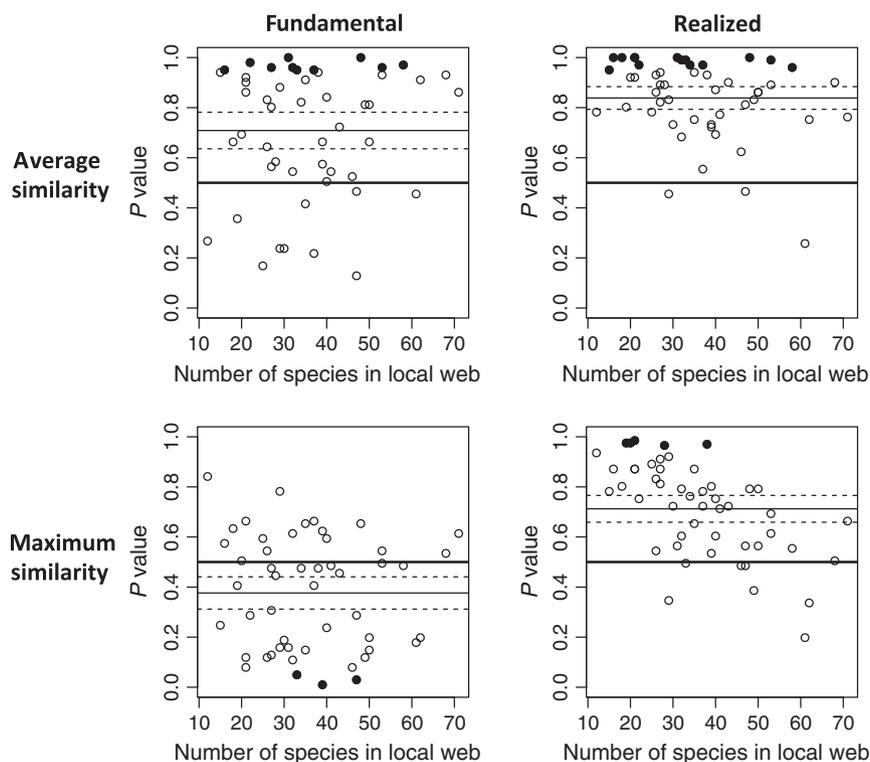
## ILLUSTRATION: COMMUNITY ASSEMBLY IN THE ADIRONDACK LAKES

### Data and random web assembly

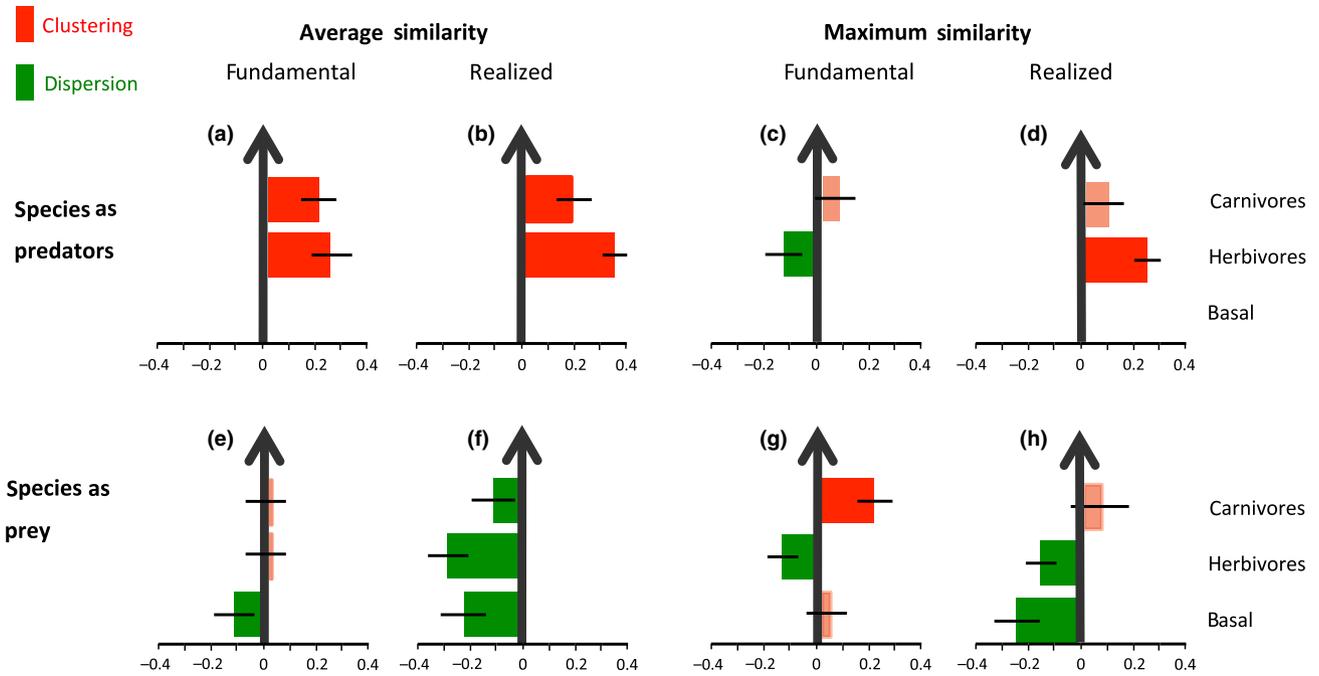
We applied our framework (Fig. 1) to the pelagic food webs found in 50 Adirondack lakes with 12–71 species and 18–487 feeding links in each lake (Table S1, Havens 1992). When Havens first described the feeding links in these lakes in 1992, he took what he called a 'cumulative web' approach by which he first considered all the species collected in the lakes, then used the expert knowledge available to him rather than restricting consideration to, e.g. observations of locally col-

lected gut contents, to construct a cumulative matrix of all likely predator–prey interactions assuming coexistence of all species. Finally, individual matrices for the 50 lakes were derived from the rows and columns corresponding to the species actually present in each lake (Havens 1992). His cumulative web is the analogue to our metaweb. However, the originally considered cumulative web is no longer available (Havens, personal communication), whereas data on the individual webs are still available. Given the unavailability of the original cumulative web and more than 20 years of further research on these intensely studied organisms' feeding behaviour and preferences (e.g. Havens 2002), Havens (personal communication) provided us with a revised metaweb. The new metaweb includes 3485 realised and potential feeding links among the 216 distinct species resulting in a metaweb connectance of 0.075. For comparison, the regional web used by Gravel *et al.* (2011), which included all links from the 50 individual webs and excluded links thought to be likely among non-co-occurring species if they speculatively co-occurred had 210 species, 2020 links and a connectance of 0.045.

Other categories of food not typically thought of as species including benthic detritus, periphyton, nanoflagellates, fish eggs and fish fry were included in the food webs and in measuring trophic similarity. Benthic detritus, periphyton and



**Figure 2** Trophic niche similarity among herbivores' diets in 50 Adirondack lakes. Each of the 50 data points depicts the number of species in each lake vs. the *P*-value of herbivores diet similarity within each lake (see also Table S2). Points falling above and below the thick black line indicate trophic clustering and dispersion, respectively, with filled data points indicating statistical significance within individual lakes. The thin plain and dashed lines represent, respectively, the estimated mean *P*-value (z-score) among communities and the 95% Confidence Interval around this estimate, computed as  $CI = \bar{z} \pm t^{n-1}_{0.975} \times \frac{sd(\bar{z})}{\sqrt{n}}$ , where *n* is the number of observed communities (*n* = 50 here) and  $t^{n-1}_{0.975}$  is the 0.975 quantile of the Student distribution with *n*-1 degrees of freedom). CIs that exclude the thick black line depict statistically significant niche clustering or dispersion among lakes. See also Table S3–S6 and Fig. S1–S4 for results of similar tests but other aspects of the trophic niche.



**Figure 3** Trophic clustering and trophic dispersion in the Adirondack lakes. Each bar summarises  $P$ -values observed among communities. Results are arranged in each panel from bottom to top to depict results for basal species, herbivores and carnivores. The direction and length of the coloured bars correspond to the difference between the average  $P$ -value across lakes (thin black horizontal line in Fig. 2 and Fig. S1–S4) and 0.5, which corresponds to an absence of trophic structure (thick black horizontal line in Fig. S1–S4). The black bars are CIs. Red bars indicate trophic clustering. Green bars indicate trophic dispersion. Dark colours indicate that the CI of the estimated mean  $P$ -value does not contain 0.5, suggesting a significantly nonrandom pattern across communities.

nanoflagellates were present in all the lakes, whereas fish eggs and fish fry only were present in all the lakes where there were fish. We accounted for these nuances by invariably including benthic detritus, periphyton and nanoflagellates in the first step of randomly assembling food webs and including fish eggs and fish fry in any assembled web in whichever step happened to include fish in the web. We excluded the very few simulated webs that required more species at a given trophic level than were available in the pool of species that ate at least one species already in the web. Despite the constraints imposed by our random assembly rules, we found that of 100 random webs, all were unique for the 46 lakes with more than 18 species, and at least 90 were unique for four lakes with 18 or less species (results not shown, see Table S2–S6 for the number of unique ‘random’ similarity values generated).

## RESULTS

The trophic structure of lake communities taken in isolation is largely within random expectations, regardless of the trophic level of species (basal, herbivores, carnivores), their trophic role (prey or predators), as well as the niche (fundamental or realised) and similarity measure (average and maximum similarity) considered (Fig. 2 & Fig. S1–S4). However, results for the minority of communities outside random expectations are largely consistent with the relatively strong and significant trophic clustering or dispersion that emerged among lake communities as a group. Given this consistency between individual and general patterns, we focus on the broad patterns here (Fig. 3).

Before discussing broad patterns among the fundamental and realised niches of carnivores, herbivores and basal species in detail, we note some key generalities among these broad patterns. These generalities include the surprising tendency for the predator niches of carnivores and herbivores (Fig. 3a–d, Figs S1 and S3) to be significantly clustered, whereas the prey niches of herbivores and basal species (Fig. 3e–h, Figs S2 and S4) tend to be significantly dispersed. This clustering and dispersion is strongest in the average similarity of realised niches (Fig. 3b and f, Figs S1 and S2) and relatively weaker in the maximum similarity of fundamental niches (Fig. 3c and g, Figs S3 and S4) where the only statistically significant contradiction of these generalities occurs: the dispersion in herbivores’ maximum similarity of their fundamental niche as predators (Fig. 3c). Otherwise, the average similarity of fundamental niches (Fig. 3a and e) and the maximum similarity of realised niches (Fig. 3d and h) usually support, and never significantly contradict, the general clustering of carnivores’ and herbivores’ predator niches and the dispersion of herbivores’ and basal species’ prey niches. Overall, these generalities are stronger and most consistent among realised niches (Fig. 3b, d, f and h) than among fundamental niches (Fig. 3a, c, e and g), which may corroborate the hypothesis that interactions within communities constrain trophic structure more strongly and consistently than does dispersal to these communities.

We first consider in more detail the traditional view of niches that focuses on how predators’ prey overlap with other predators’ prey (Fig. 1a and b, Fig. 3a–d). Co-occurring herbivores and carnivores are very strongly clustered in terms of

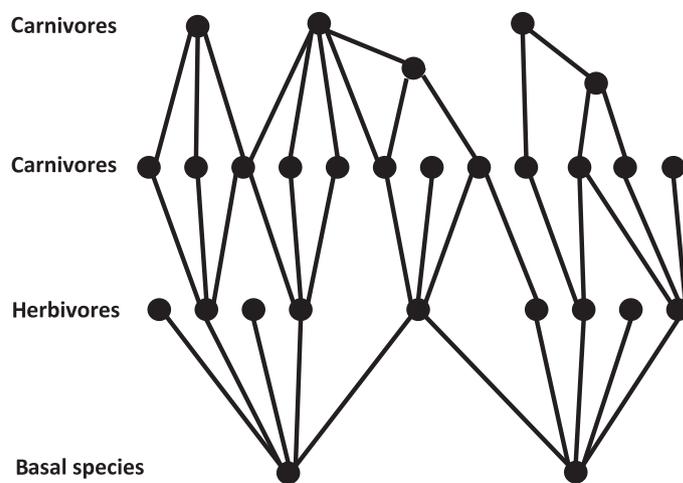
average similarity in both their fundamental (Fig. 3a) and realised (Fig. 3b) predator niches. This indicates that predators that can eat similar prey species are significantly more likely to co-occur in communities than expected by chance and suggests that food filtering is a major factor explaining predators' community composition (Fig. 1). Furthermore, the realised niche results (i.e. clustering of predators' niche, Fig. 3b) show that prey species within the overlaps of predators' fundamental niches are remarkably persistent within communities, as opposed to being extirpated by high top-down pressure (Fig. 1). This finding that predator species with similar potential and realised prey preferentially coexist means that relatively vulnerable prey species consumed by multiple predators tend to occur in the lakes more often than relatively invulnerable prey typically outside overlaps in species' diets. This is confirmed by the relatively high overall vulnerability observed in the lakes compared to random expectations (results not shown).

The maximum similarity of species' predator niches (Fig. 3c and d) is consistently less clustered than their average similarity (Fig. 3a and b). The slight clustering of the maximum similarity of carnivores' fundamental (Fig. 3c) and realised (Fig. 3d) niches is statistically insignificant and, whereas the reduced clustering in maximum (Fig. 3d) compared to average similarity of herbivores' realised niches (Fig. 3b) is still significant, the maximum similarity of herbivores' fundamental niches is significantly dispersed (Fig. 3c). This suggests that the strong clustering more broadly observed among all coexisting species (Fig. 3a and b) is not driven by the fewer number of species within a community that possess the most similar niches. Instead, the maximum similarity of herbivores' fundamental niches is significantly dispersed as expected when community assembly is driven by strong competition between the most similar pairs of predators' species. Apparently, the relatively few prey within the overlap of herbivores' dispersed fundamental niches (e.g. super prey in Fig. 1b) comprise significantly more of these herbivores' diets than expected at random, resulting in the clustering of the maximum similarity of herbivores' realised niches (Fig. 3d). Competition between the most trophically similar species helps explain the insignificant and weaker clustering of carnivores' fundamental and realised niches in terms of maximum similarity (Fig. 3c and d) than in terms of average similarity (Fig. 3a and b). While competition can help explain such details in our results, the strong pattern of clustering in consumers' predator niches (Fig. 1a) contradicts the dispersion (Fig. 1b) expected in communities strongly structured by competition. Instead, this clustering is expected when community assembly is driven by food filtering and community interactions are driven by preferential coexistence of 'super prey' able to sustain multiple predator species (Fig. 1a).

Viewing species as prey rather than predators (Fig. 1c and d, Fig. 3e–h), realised niches of co-occurring species are significantly dispersed both in terms of average (Fig. 3f) and maximum (Fig. 3h) similarity except for maximum similarity among carnivores which is insignificantly clustered. Compared to the relative dispersion of realised niches (Fig. 3f and h), the similarities of fundamental niches (Fig. 3e and g) are consistently less dispersed or more clustered. Only the average simi-

larity of basal species' fundamental niches (Fig. 3e) and maximum similarity of herbivores' fundamental niches (Fig. 3g) are significantly dispersed albeit less dispersed than their realised niches. The maximum similarity of carnivores' fundamental niches (Fig. 3g) is significantly clustered, whereas the maximum similarity of carnivores' realised niches (Fig. 3h) is insignificantly clustered. The dispersion patterns in basal and herbivorous species' fundamental (Fig. 3e and g) and realised (Fig. 3f and h) niches indicate that these species that share few if any predators with other basal or herbivorous species preferentially coexist in local communities. The patterns for carnivores are more mixed. While the average similarity of carnivores' realised niches (Fig. 3f) indicates significant dispersion, their maximum similarity of fundamental niches (Fig. 3g) is significantly clustered and carnivores' other patterns are not statistically significant. These results suggest that for basal and herbivorous species, and only marginally for carnivores, there is a preponderance of specialised predators that eat one or a few persistent prey species that are eaten by few if any other more generalised predators (e.g. successful specialists in Fig. 1d). The largest exception to this suggestion involves the maximum similarity of carnivores' fundamental niches (Fig. 3g), which is significantly clustered indicating that carnivores who can eat similar prey preferentially constitute local communities. However, the insignificant clustering in the maximum similarity of carnivores' realised niches suggests that relatively few of those similar prey of the carnivores persist in these carnivores' local communities.

In summary, the strong clustering of the average similarity of carnivores' and herbivores' fundamental and realised pred-



**Figure 4** Food web depicting the community-scale architecture of trophic niche space suggested by our analyses. Nodes represent species and links represent trophic relationships between species with predators at the top of the link feeding on prey at the bottom of the link. The clustering of carnivores' and herbivores' predator niches is illustrated by these species often sharing herbivorous and basal prey respectively. The dispersion of basal species' and herbivores' prey niches is illustrated by these species sharing few herbivorous and carnivorous predators respectively. The prey niches of carnivores are less dispersed. Community-scale empirical food webs are not absolutely structured this way; our results suggest that they are comparatively structured this way, that is, more than webs stochastically sampled from the regional species pool.

ator niches corroborates the hypotheses that the availability of food strongly determines which of these species arrive and persist in ecological communities, and that tolerance to a relatively diverse set of predators strongly determines which of these species' prey persist in the communities (Fig. 1a). The reduced strength of these patterns measured in terms of maximum similarity corroborates the hypothesis that competition may reduce or even reverse this clustering among the most similar carnivores and herbivores. The dispersion of herbivores' and basal species' prey niches, weak in fundamental niches and strong in realised niches, corroborates the hypothesis that apparent competition somewhat restricts which herbivorous and basal species persist in ecological communities to those that have few shared predators and can tolerate predation by specialist predators. The sharing of many prey as suggested by the clustering of carnivores' and herbivores' predators niches (Fig. 1a) could contradict the distinct sets of predators of their presumed herbivorous and basal prey (Fig. 1d) suggested by the dispersed prey niches of these prey. This contradiction may be resolved by multiple distinct guilds each comprised of numerous predators that all consume one or a few species of persistent 'super prey' that share few if any predators of other 'super prey' that comprise different guilds (Fig. 4).

## DISCUSSION

Feeding interactions play a key role in species coexistence and community assembly (Pimm 1982; Pascual & Dunne 2005). Yet, few if any direct community-wide tests of the influence of trophic similarity on coexistence have been conducted. We addressed this shortcoming by developing an approach based on earlier analyses of trophic niche overlaps and inspired by recent research on community phylogenetics that tests for non-random patterns in the trophic similarity of coexisting species. We applied our approach to food webs from lake communities in the Adirondack Mountains of eastern North America. In these lakes, we found a surprisingly frequent occurrence of specialist predators that share highly vulnerable prey. Moreover, these prey with many predators share surprisingly few predators among them. In other words, there appears to be a strongly compartmentalised guild structure within the lake food webs that consist of prey that are consumed by many predators who themselves are consumed by many predators. The compartmentalisation is illustrated by the low overlap we find among these different sets of predators in terms of diet. This compartmentalisation is unlikely to be a bias arising from lower taxonomic resolution at lower trophic levels for at least two reasons. The first is because the phytoplankton – which makes up the vast majority of the lowest trophic level – are very well resolved in the Adirondack lakes data (Srinivasan *et al.* 2007). The second is because low resolution also occurs within our randomly assembled webs, which would tend to obscure patterns by reducing the number of species and therefore statistical power rather than to produce artificial results. The patterns we observed suggest two forces strongly structure the species composition of the lake communities: a bottom-up food filtering effect and a top-down apparent competition mediated by predators. The food

filtering effect increases the number of predator species of each prey compared to random expectations, whereas the apparent competition reduces the number of prey that predators might otherwise share.

The frequent occurrence of vulnerable prey in the Adirondack lakes is surprisingly robust and is reflected both by the strong realised trophic clustering of predators and by the direct measurement of vulnerability. This frequent occurrence of vulnerable prey results in empirical webs that are in general more connected than expected at random. This pattern could be a consequence of enhanced sequential dependence (Holt *et al.* 1999) by which initial colonisers strongly attract predators which themselves attract more predators. Another possible explanation is a defence/colonisation trade-off whereby species that are not good at defending themselves against predation are good at growing and colonising.

Using the same data as the one analysed in our study, Srinivasan *et al.* (2007) found complementary results by looking at the geographical distribution of species among communities. They found that specialist predators preferentially fed on the most widely distributed species, whereas generalist predators preferentially fed on narrowly distributed species. They further explained that widely distributed species thrive in many different environments and are therefore relatively unlikely to go extinct. Such robustness confers a selective advantage to predators that specialise on widely distributed prey species. This, in turn, may release more narrowly distributed and less robust species from predation by specialists thus allowing more predation by generalists. This study suggests that the robust prey species identified by Srinivasan *et al.* (2007) are responsible for the food filtering effect that causes predators to share unusually many prey. In addition, Srinivasan *et al.*'s study helps explain why realised clustering generally exceeds fundamental clustering in our study: the prey species within the overlap of predators' diets are widespread and these robust prey effectively tolerate the predation load imposed by multiple specialist predators.

The bottom-up effect of lower trophic levels determining the composition of higher trophic levels and top-down pressure by higher trophic levels eliminating prey at lower trophic levels via apparent competition that we observed here mirrors patterns observed by De Ruiter *et al.* (1995). In a series of real soil food webs, de Ruiter *et al.* found specific patterns of per capita effects of predators on their prey and of prey on their predators. The authors found strong top-down effects of predators on their prey at lower trophic levels and strong bottom-up effects of prey on their predators at higher trophic levels. This pattern of interaction strengths was shown to play a stabilising role in these communities.

Our findings contradict expectations of dispersed predator niches due to competitive exclusion. Such contradictions have also been found in many community phylogenetic studies that inspired our study. Indeed, while competitive exclusion is generally expected to lead to phylogenetic dispersion (Webb *et al.* 2002; Cavender-Bares *et al.* 2009), a comparative analysis of phylogenetic community structure reported a preponderance of clustered rather than dispersed communities (Vamosi *et al.* 2009). Similarly, the remarkably successful niche model randomly places feeding niches within community niche space

(Williams & Martinez 2000). Further work found that adding repulsion between feeding niches as predicted due to competitive exclusion reduced rather than improved the niche model's fit to food web data. Such findings suggest that competitive exclusion affects community assembly and evolution less than is often assumed. There is also a possibility that predator niche dispersion linked to competition happens at a smaller geographical scale than the one captured here; indeed, empirical studies have shown that dispersion decreases with increasing spatial scale, as the effect of species' interactions is replaced by larger-scale biogeographical processes (Swenson *et al.* 2006, 2007; Cavender-Bares *et al.* 2009). Finally, there is a possibility that competitive exclusion results in a clustering (rather than dispersion) of predator niches if large differences in competitive ability among predators result in the exclusion of trophically similar less competitive predators (Mayfield & Levine 2010).

The direct use of a measurable niche, e.g. the trophic niche, may alleviate some limitations inherent to community phylogenetics such as the use of phylogenetic similarity as a proxy for ecological similarity (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012). Using phylogenetic similarity as a proxy for ecological similarity implies that ecological niches are conserved through evolution. While niche conservatism receives some empirical support (Prinzing 2001; Ackerly 2004; Moen *et al.* 2013), cases of ecological niche convergence are widespread enough (e.g. Cavender-Bares *et al.* 2004; Mahler *et al.* 2013) that niche conservatism cannot be assumed (Losos 2008). For this reason, studies measuring niche similarity by means of trait similarity among species have been particularly useful to our understanding of community assembly processes (Ackerly 2004; Cavender-Bares *et al.* 2004; McGill *et al.* 2006; Kraft *et al.* 2008). Food webs provide us with a convenient way to measure similarity in one of the most important aspects of species' niches – the trophic niche (Martinez 1991; Williams & Martinez 2000) – and food web measures of pairwise trophic similarity are increasingly used to measure guild structure (Muñoz & Ojeda 1998) and functional aspects of biodiversity (Martinez 1996; Petchey & Gaston 2002). Our manuscript aims to encourage such analyses further inspired by similar analyses of phylogenetic similarity.

The approach to analysing interaction networks proposed here should improve our understanding of coexistence patterns, yet this approach shares some of the well-known limitations of community phylogenetics (Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012). First, similar community trophic structure can emerge from different assembly processes. Second, we can expect that in many cases, trophic structure will depend on spatial scale (Brose *et al.* 2004). The scale at which the metacommunity is defined is often subjective, and it affects both the species pool and the fundamental trophic similarity of species. This scale sensitivity may render the interpretation of trophic structure delicate; however, it may also provide an opportunity to identify critical scales at which local and regional scales are most important, as has already been noted in the study of phylogenetic community structure (Swenson *et al.* 2006; Cavender-Bares *et al.* 2009). Third, our measure of trophic similarity, based on food web topology, is less direct

than, e.g. gut content analyses which could illuminate subtleties that our measures of similarity are blind to such as quantitative shifts in feeding behaviour driven by competition within trophic overlaps.

Overall, the inferences we made, based on overlaps of fundamental and realised niches, are relatively simple inferences consistent with basic ecological understanding. It would be important to check these inferences with dynamic food web assembly models. Such models could help explore the effects of systematic variations in dispersal ability, interference competition and adaptive foraging on various measures of niche overlap, clustering and dispersion. Such explorations would result in more robust explanations of trophic dispersion and clustering than the inferences described here. There are most likely several explanations consistent with any particular set of results, and analyses based on measures other than trophic overlap may be necessary to distinguish between such hypotheses.

Our framework, illustrated here with the Adirondack lakes, is broadly applicable. This framework is applicable to any set of local scale food webs. An increasing number of food webs are becoming available at different spatial (Poisot *et al.* 2012; Berlow *et al.* 2013) and temporal (Piechnik *et al.* 2008) scales. Applying our framework to these data should provide valuable insights into the relationship between species coexistence and trophic niches. Although we observed general non-random trends in trophic structure across lakes, the trophic structure of individual lakes was very rarely statistically significant. We expect that other ecological systems may show much more trophic structure. Indeed, we know that community structure in the Adirondack lakes is strongly affected by pH (Brose *et al.* 2004); this strong effect of environmental filtering likely weakens the effect of trophic interactions. In communities with less environmental control, the effect of trophic interactions would likely be stronger.

Before general community assembly rules can be drawn from our analyses, it would be necessary to test whether the main results found here in the Adirondack lakes hold across other sets of food webs. The Adirondack data were collected more than 20 years ago and may suffer from various sampling biases. In addition, lakes may greatly differ from benthic and terrestrial ecosystems because of the strongly size structured nature of lake food webs and the relative lack of refugia from predation (Riede *et al.* 2011). If general trends emerge across various food web systems, such results could inform trophic models of community assembly, such as the one developed by Gravel *et al.* (2011).

Our approach could also be applied to other types of interaction networks, which would improve our understanding of species coexistence as it relates to other types of interaction niches. For example, mutualistic and parasite–host networks could be used to investigate the extent to which coexisting species share common vs. distinct partners (Burkle & Alarcón 2011; Griffiths *et al.* 2014). For an even more inclusive consideration of interaction niches, emerging networks integrating non-feeding interactions into food webs could be considered (Olf *et al.* 2009; Kéfi *et al.* 2012; Poccock *et al.* 2012).

We see several ways in which our approach could be expanded. First, paralleling phylogenetic beta-diversity studies

(Graham & Fine 2008; Morlon *et al.* 2011), it could be extended to analyse trophic beta-diversity, that is, the spatial turnover in trophic structure (Poisot *et al.* 2012). Second, the approach would lend itself well to the consideration of combined trophic, trait and phylogenetic data. By considering only trophic data, our analyses cannot currently distinguish, e.g. the direct effect of trophic interactions and the indirect effect of shared physical niche differences in driving associations between predators and prey. Considering similarity in traits associated with abiotic preferences, along with trophic similarity, would improve our understanding of community assembly in light of both the abiotic and the biotic milieu (McGill *et al.* 2006). Phylogenetic data are becoming increasingly available, and are now collected at the scale of entire interaction networks (Ives & Godfray 2006; Rezende *et al.* 2007, 2009; Vacher *et al.* 2008; Stouffer *et al.* 2012). Given that interaction networks, traits and phylogenies provide complementary information regarding species' differences, a framework integrating this combined information, e.g. following Cadotte *et al.* (2013), would further enhance our ability to understand how species assemble in space and time. Given that species interactions play a key role in species' evolution (Ehrlich & Raven 1964; Van 1973), community assembly (Gravel *et al.* 2011; Boulangeat *et al.* 2012) and community spatial turnover (Novotny *et al.* 2007; Pellissier *et al.* 2013), such developments should be particularly fruitful. In particular, they would allow a better integration of evolution, community ecology, spatial ecology and the science of species interaction networks.

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#### AUTHORSHIP

H.M. and N.M. designed the experiment. H.M. performed the experiment and analysed the data. H.M., S.K. and N.M. interpreted the results and wrote the manuscript.

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