

Niche Evolution, Trophic Structure, and Species Turnover in Model Food Webs

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ABSTRACT: The features that govern the stability and persistence of species interaction networks, such as food webs, remain elusive, but recent work suggests that the distribution and strength of trophic links play an important role. Potential omnivory-stability relationships have been investigated and debated extensively, but we still have a relatively poor understanding of how levels of omnivory relate to the stability of diverse food webs. Here, we use an evolutionary assembly model to investigate how different trade-offs in resource use influence both food web structure and dynamic stability during the assembly process. We build on a previous model by allowing speciation along with the evolution of two traits: body size and feeding-niche width. Across a wide range of conditions, the level of omnivory in a food web is positively related to its dynamic instability (variability and species turnover). Parameter values favoring omnivory also allow a wider range of phenotypes to invade, often displacing existing species. This high species turnover leaves signatures in reconstructed phylogenies, with shorter branches connecting extant species in more omnivorous food webs. Our findings suggest that features of the environment may influence both trophic structure and dynamic stability, leading to emergent omnivory-stability relationships.

Keywords: omnivory, trophic levels, evolutionary assembly model, niche width, trade-offs, phylogenies.

Introduction

A considerable challenge facing community ecologists is to understand the causes of variation in trophic structure among ecosystems and the consequences for food web dynamics. Species' foraging behavior and dietary niche breadths strongly influence food web structure (Kondoh 2003; Beckerman et al. 2006). Food webs can consist of a few discrete trophic levels when most consumers specialize on a small number of trophically similar prey species, or the presence of many omnivores can lead to food webs

with complex trophic structure. Recent meta-analyses have shown that virtually all food webs include both omnivores and species at discrete trophic levels but that the relative prevalence of omnivory and trophic levels varies across ecosystem types (Williams and Martinez 2004; Thompson et al. 2007).

The presence of omnivores affects trophic structure in ways that may influence the stability of food webs. Omnivory-stability relationships have been the subject of considerable research and occasional controversy (Vandermeer 2006). Early theory suggested that omnivory decreases the probability of stable equilibria and therefore should be rare in nature (e.g., Pimm and Lawton 1978; Pimm 1982). This prediction appeared to be supported by early empirical data (Pimm 1980), but later studies with improved resolution showed many species feeding on multiple trophic levels (e.g., Polis 1991; Goldwasser and Roughgarden 1993). More recent analytical models have identified conditions under which omnivory stabilizes food webs both by conferring a stable equilibrium and by reducing the probability of extinctions (McCann and Hastings 1997; Vandermeer 2006).

Most current models consider only small modules of a few interacting species, making their implications for complex natural food webs unclear. Omnivory may stabilize large food webs by reducing the likelihood that strong predator-prey interactions will drive population cycles or trophic cascades (strong top-down effects across more than two trophic levels). Fagan (1997) provided experimental support for this hypothesis by showing that arthropod assemblages with omnivores were more resilient to disturbance. Bascompte et al. (2005) indirectly demonstrated a stabilizing role of omnivory by showing that food chains with consecutive strong interactions (where trophic cascades are likely) were underrepresented in a large marine food web. When they occurred, consecutive strong interactions tended to include an omnivorous link between the top and basal species, suggesting that omnivory acts as a buffer against strong top-down control.

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While omnivory may have direct effects on food web stability, we suggest that omnivory and aspects of stability may be related if they are influenced by the same environmental features. Theory predicts that omnivory is most likely to be stabilizing if trophic interactions are weak, consistent with other links between weak interactions and food web stability (McCann et al. 1998; Emmerson and Yearsley 2004). However, while a preponderance of weak interactions may favor the persistence of a food web, it may also increase community invasibility (Case 1990). Omnivory may therefore have a complex relationship with the overall stability of a food web, favoring the maintenance of a stable trophic structure but facilitating turnover through species invasions and extinctions. To our knowledge, no studies have yet considered the relationship between levels of omnivory and components of food web stability such as invasibility and species turnover.

We explore patterns of trophic structure and stability that arise through speciation-extinction dynamics, using an evolutionary assembly model modified from Loeuille and Loreau (2005, 2006). Evolutionary assembly models allow food webs to emerge from the evolution of traits that affect fitness via species interactions (e.g., Caldarelli et al. 1998; Yoshida 2003; McKane 2004; Rossberg et al. 2005; Guill and Drossel 2008), in contrast to stochastic descriptive models of food webs (e.g., Cohen and Newman 1985; Williams and Martinez 2000; Cattin et al. 2004). In an attempt to directly link the assembly process to a measurable characteristic of species, Loeuille and Loreau devised a model based on the evolution of a single measurable trait, body size. In Loeuille and Loreau's model, body size determines each species' metabolic rates as well as the identity of its predators, prey, and competitors. Loeuille and Loreau's model produced either complex networks of omnivores or food webs with all species at distinct trophic levels, depending largely on whether species can eat a wide or narrow range of prey (i.e., their dietary niche width). Loeuille and Loreau's model assumes that all species have identical niche widths, which may limit the model's predictive ability, given the marked variability in dietary generality in real food webs. The evolution of niche width is likely to have implications for both the fitness of species and the structure and stability of the food web as a whole.

Here, we extend Loeuille and Loreau's (2005) model by allowing niche width to evolve under a variety of trade-off scenarios. We assess the conditions that favor different types of trophic structure and consider how the assembly process may lead to emergent relationships between omnivory and the dynamic stability of food webs.

Model Presentation

We modify the model presented by Loeuille and Loreau (2005) by allowing the evolution of both body size and

niche width. All variables and parameter values used in the model are summarized in table B1 in appendix B in the online edition of the *American Naturalist*. Each species i has biomass density N_i and is characterized by two traits: body size (x_i , on a logarithmic axis) and niche width (s_i ; see below). The basal resource N_0 represents the inorganic nutrient pool and is arbitrarily assigned a body size of $x_0 = 0$. Predation is size structured so that predators are always larger than their prey. Each consumer i has an optimum prey size of $x_i - d$, with $d = 2$, following Loeuille and Loreau (2005) and consistent with typical empirical predator-prey size ratios (Brose et al. 2006a, 2006c). Consumers have Gaussian utilization functions with standard deviation (niche width) s_i . The attack rate a_{ij} of consumer i on prey j (where $x_i > x_j$) is

$$a_{ij} = a_0 \left(\frac{\exp\{-c[\ln(s_i/s_0)]^2\}}{s_i\sqrt{2\pi}} \exp\left[-\frac{(x_i - x_j - d)^2}{s_i^2}\right] \right). \quad (1)$$

Here, a_0 scales the maximum attack rate, while c and s_0 describe a trade-off associated with niche width; s_0 is the optimum niche width, at which overall attack rate is highest ($s_0 > 0$), while c is the cost associated with deviating from this optimum ($c \geq 0$). When $c = 0$, s can vary with no intrinsic fitness cost, because the numerator of the first fractional term in equation (1) simplifies to 1 and total attack rate (the integral of eq. [1] over all x_j from 0 to x_i) is independent of niche width (with the minor exception that species with large niche widths have slightly lower total attack rates because they are not permitted to consume species larger than themselves). This produces a commonly employed trade-off where increasing efficiency at exploiting a particular prey size decreases the range of body sizes that can be consumed (e.g., Roughgarden 1972; Slatkin 1980; Taper and Case 1985; fig. 1A). As niche width is unlikely to evolve unconstrained and a review of experimental data shows that costs can be associated with both generalization and specialization (Kassen 2002), we modify the utilization function so that a cost can be imposed to having a nonoptimal niche width (for other approaches to constraining niche width evolution, see Yoshida 2003; Ackermann and Doebeli 2004). We assume a cost to having niche width either higher or lower than the optimum s_0 , allowing us to explore the effect of varying the optimum to give specialists or generalists an intrinsic advantage. As the cost c increases, the total attack rate decreases more rapidly when s differs from s_0 (fig. 1B); conceptually, this scales down the utilization curve in figure 1A so that the area under the curve decreases as $|s - s_0|$ increases. We inferred reasonable "narrow" and "wide" optima ($s_0 = 0.5$ and 1.0, respectively) from em-

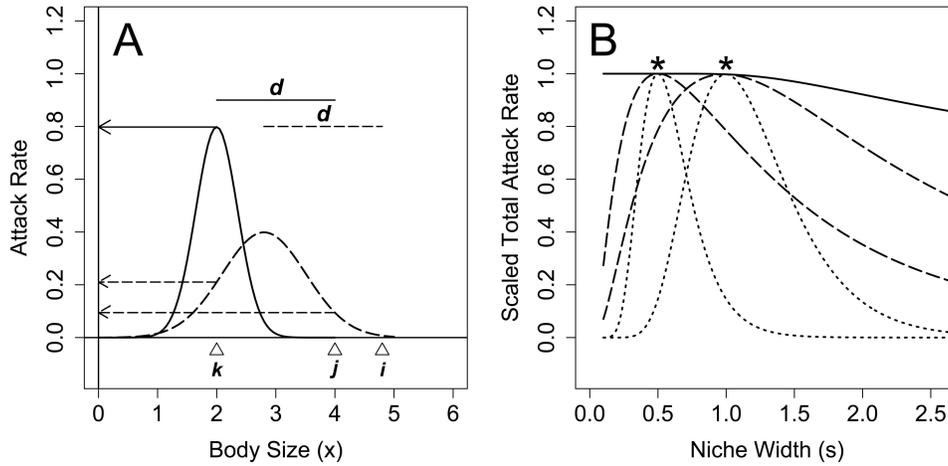


Figure 1: A, Illustration of utilization curves for species differing in body size (x) and niche width (s). Species j ($x_j = 4$, $s_j = 0.5$; solid lines) consumes prey species k ($x_k = 2.0$) with high efficiency, but species i ($x_i = 4.9$, $s_i = 1.0$; dashed lines) can consume both j and k with lower efficiency. B, Effect of a species' niche width and the parameters c and s_0 on total attack rate (i.e., the area under the curve in A), scaled to the maximum value. Curves show the relationships between total attack rate and niche width at three values of the cost parameter c (solid lines: 0; dashed lines: 0.5; dotted lines: 4) and two values of the optimum niche width s_0 (0.5 and 1; asterisks).

pirical consumer-resource body size data (app. A in the online edition of the *American Naturalist*; Brose et al. 2006b; Barnes et al. 2008). We chose values of c to capture its range of behavior ($c = 0, 0.5$, and 4).

We calculate the total amount of each prey j consumed by i by using a flexible functional predator response to prey density that applies to multispecies communities (modified from Drossel et al. 2004):

$$g_{ij} = \frac{a_{ij}N_j}{1 + \sum_k a_{ik}N_k b}. \quad (2)$$

We use a weakly saturating Type II functional response ($b = 0.1$) for simulations presented here and explore Type I ($b = 0$) and strongly saturating Type II ($b = 0.5$) functional responses in appendix B.

Like previous evolutionary assembly models, our model requires predator interference to sustain food webs of more than a few species (e.g., Drossel et al. 2004; Loeuille and Loreau 2005; Guill and Drossel 2008). Interference competition promotes diversity in this model by intensifying interactions within species and between species with similar trophic positions. Interference is often incorporated into predator-dependent functional responses, but we follow Loeuille and Loreau (2005) by making the simplifying assumption that interference occurs on the basis of body size. Interference may therefore occur either during foraging (as similar-sized species will have common prey) or in competition for other resources, such as territories (Oksanen et al. 1979; Bowers and Brown 1982). We use

a Gaussian competition function so that competition is strongest between equally sized species and declines as the size difference increases:

$$\alpha_{ij} = \left\{ \frac{\alpha_0}{\sigma_\alpha \sqrt{2\pi}} \exp \left[-\frac{(x_i - x_j)^2}{\sigma_\alpha^2} \right] \right\}. \quad (3)$$

Here, α_0 determines the overall strength of interference competition and σ_α determines the width of the interference function: both values were assigned small values so that interference is weak relative to predation and occurs only between species with fairly similar body sizes. Loeuille and Loreau (2005) thoroughly explored how the strength of interference competition influences food web structure in this framework, so we do not present the effects of varying α_0 and σ_α here. Consistent with the results of Loeuille and Loreau, we found that when $\alpha_0 = 0$, food webs contain few species and frequently collapse, while higher α_0 tends to disrupt trophic levels and lead to a more uniform distribution of body sizes.

We calculate population dynamics by using a system of discrete-time recursion equations, in which species i 's growth rate depends on its total prey assimilation and losses due to mortality, predation, and interference competition:

$$\begin{aligned}
N_i(t + \Delta t) = & N_i(t) + \Delta t \times N_i(t) \\
& \times \left(f_0 x_i^{-0.25} \sum_{j=0}^{i-1} N_j g_{ij} - m_0 x_i^{-0.25} \right. \\
& \left. - \sum_{j=i+1}^n N_j g_{ji} - \sum_{j=1}^n N_j \alpha_{ij} \right). \quad (4)
\end{aligned}$$

Here, f_0 and m_0 are basal metabolic parameters (mass-specific production efficiency and mortality rates, respectively) that are scaled as an exponent of body size (Kleiber 1947; Peters 1983), and the other terms are as described above. The dynamics of the basal inorganic resource N_0 are identical to those used by Loeuille and Loreau (2005):

$$\begin{aligned}
N_0(t + \Delta t) = & N_0(t) + \Delta t \\
& \times \left(I - eN_0 + \nu N_{\text{recycled}} - \sum_{i=1}^n N_i N_0 g_{i0} \right), \quad (5)
\end{aligned}$$

where

$$\begin{aligned}
N_{\text{recycled}} = & \sum_{i=1}^n m_0 x_i^{-0.25} N_i + \sum_{i=1}^n \sum_{j=1}^n N_i N_j \alpha_{ij} \\
& + \sum_{i=1}^n \sum_{j=1}^n (1 - f_0 x_i^{-0.25}) N_i N_j g_{ij}, \quad (6)
\end{aligned}$$

I is the nutrient inflow at each time step, e is the rate of nutrient outflow, and ν is the rate of nutrient recycling from higher trophic levels. We use a step size $\Delta t = 0.2$ that balances low numerical instability with quick computation time (Drossel et al. 2001).

New species are introduced to the system by stochastic speciation events, with concurrent mutations in trait values. Speciation occurs with probability 0.005 in each generation, with one extant species randomly selected as the parent. This constant, community-wide speciation rate is convenient because it supplies new variants at a constant rate regardless of species richness. Our results are qualitatively unchanged when we use a constant per-lineage speciation rate for greater consistency with macroevolutionary theory (Nee 2006; see app. C in the online edition of the *American Naturalist*). The body size and niche width of the new species are randomly drawn from normal distributions around the parent species' traits, with standard deviations σ_x and σ_s and no correlations between mutations in x and s . We present simulations in which mutations in both traits have either larger ($\sigma_x = 0.5$ and $\sigma_s = 0.25$) or smaller ($\sigma_x = 0.2$ and $\sigma_s = 0.1$) standard deviations. If

undefined values of either trait are selected (x or $s \leq 0$), both trait values are rejected and new values are drawn from the same distribution. Species are introduced at a low density ($N_i = x_i \times 10^{-8}$), also the threshold density below which species are considered extinct and removed from the community. If new species have nonnegative population growth, they successfully establish in the community; otherwise, they immediately become extinct.

We initialize each simulation with a single species that consumes the basal resource, with its x and s randomly drawn from normal distributions with expectations d and s_0 and standard deviations σ_x and σ_s , respectively. Each simulation lasts 10^6 time steps, typically long enough for the food web to reach a dynamic equilibrium state where the number and type of species present undergoes little further directional change (see fig. 3). We record species richness every 1,000 generations and track ancestor-descendent relationships among species. For the results presented here, we varied three parameters, simulating food webs with small and large optimum niche widths ($s_0 = 0.5$ and 1.0 , respectively); no costs, weak costs, and strong costs to deviating from the optimum ($c = 0, 0.5$, and 4 , respectively); and large and small trait mutations ($\sigma_x = 0.5, \sigma_s = 0.25$ and $\sigma_x = 0.2, \sigma_s = 0.1$, respectively). We replicated each of these 12 parameter combinations 20 times to assess the consistency of the resulting food web structures. Simulations were carried out with code written in C, and subsequent data manipulations were performed in the R environment (R Development Core Team 2008).

Analyses

We began by characterizing the trophic structure of food webs produced by our model. We then assessed food webs' dynamical stability, using a measure of variability and species turnover and a component of phylogenetic tree shape. Finally, we evaluated whether structure and stability are related across a range of simulated food webs.

Food Web Structure

Our analysis of food web structure focused on the distribution of trophic positions and levels of omnivory. We calculated trophic position (TP) and a measure of omnivory for each species, following Levine (1980). A species' TP is the expected number of trophic steps separating it from the base of the food web (the basal resource, with $TP = 0$), while the trophic height of a food web is the maximum TP of any species (TP_{max}). Each species' omnivory is the weighted variance of the trophic positions of its prey,

$$\sigma_{TP_i}^2 = \sum_{j=1}^n (TP_j - TP_i - 1)^2 p_{ij}, \quad (7)$$

where TP_j are the trophic positions of species i 's prey, $TP_i - 1$ is the average TP_j , and p_{ij} is the proportion of each species j in the diet of species i (Levine 1980). We calculated the level of omnivory in a food web as the mean σ_{TP}^2 of all species present. As an alternative measure of trophic structure, we calculated the proportion of species occupying integer (± 0.05) TPs (Thompson et al. 2007).

We also calculated measures of trophic structure for five empirical food webs, with estimates of link strengths that allow them to be compared with the model output. These include four marine webs—(1) Chesapeake Bay (species richness $S = 33$; Baird and Ulanowicz 1989), (2) Cantabrian Sea ($S = 28$; Sánchez and Olaso 2004), (3) Caribbean Shelf ($S = 248$; Opitz 1996), and (4) Florida Seagrass ($S = 48$; Christian and Luczkovich 1999)—and one terrestrial web, (5) Saint Martin ($S = 44$; Goldwasser and Roughgarden 1993). We calculated mean σ_{TP}^2 and the percentage of species at integer TPs for each of these empirical food webs; these values are displayed in figures 3 and 5, with the empirical food webs identified by the numbers 1–5, as listed above.

Assembly Dynamics and Stability

We used a variety of methods to investigate assembly dynamics in our simulations. Evolutionary assembly models simulate adaptive radiations as species evolve to occupy new trophic niches. By tracking speciation and extinction over time, we can construct a community phylogeny and investigate relationships between phylogenetic tree shape and ecological factors affecting species interactions. We examined the effects of varying the niche width trade-off (c and s_0) and the rates of trait evolution (σ_x and σ_s) on an aspect of food web stability and on phylogenetic tree shape.

Food web stability has been defined in many ways, including analytical stability (tendency for all species to return to a stable equilibrium after slight perturbations; e.g., May 1973) and robustness (e.g., numbers of secondary extinctions following species removal; e.g., Dunne et al. 2002). One component of stability that is of particular relevance to evolving food webs is the temporal stability of food web structure and the degree to which species turn over (invade via speciation and become extinct) through time. We focus on the temporal variability of a key feature of food webs: species richness. Food webs tended to reach a “quasi-equilibrium” state fairly rapidly, with no further directional change in richness or trophic structure. However, in a few cases, species richness continued to show

directional change later in the simulation, making variation around a mean (e.g., the coefficient of variation [CV] of species richness) unsuitable. Instead, we calculated Δ_s : the mean absolute change in species richness between successive censuses (1,000-generation intervals, excluding the first 1/4 of the run); Δ_s was correlated with CV but was lower in simulations that showed directional trends. It was also highly correlated with other measures, such as the proportion of speciation events that led to a new species establishing in the food web.

We examined patterns in phylogenetic tree shape by using the phylogenies of species alive at the end of each simulation (after pruning out extinct lineages). Temporal patterns of branching events in phylogenies are typically presented as lineage-through-time (LTT) plots of the reconstructed number of lineages (ignoring extinct species) against time. The shape of these LTT plots can be conveniently described using the gamma statistic (Pybus and Harvey 2000), which is negative when most lineages diverge early in the phylogeny and positive when most branching events are recent. This statistic is typically used to test for changes in speciation rate over time (e.g., Phillimore and Price 2008) but has also been used in meta-community simulations to test for effects of ecological parameters on tree shape (McPeck 2008). We use gamma to ask whether branching events separating extant species tend to be early or more recent. We note that our simulations do not satisfy the conditions under which gamma is standard-normally distributed (Pybus and Harvey 2000) but that the statistic remains a useful descriptor of the shape of LTT plots. Positive values of gamma imply that most species in a community are closely related, so gamma also captures a measure of phylogenetic diversity. We calculated gamma for each phylogeny using the function “gammaStat” in the R package APE (Paradis et al. 2004).

Finally, we investigated relationships among response variables of interest across food webs simulated under a range of parameter values. In particular, we considered whether the mean omnivory in a food web was related to its dynamic stability (Δ_s). While this analysis does not demonstrate causality (e.g., that the presence of omnivory increases or decreases stability), it is a useful exploration of relationships that may emerge from repeating the assembly process across a variety of ecological conditions.

Results

Food Web Structure

The distribution of body size and niche width in food webs varied considerably across the parameter space investigated (fig. 2). The size structuring of predation led to a strong correspondence between body size and trophic

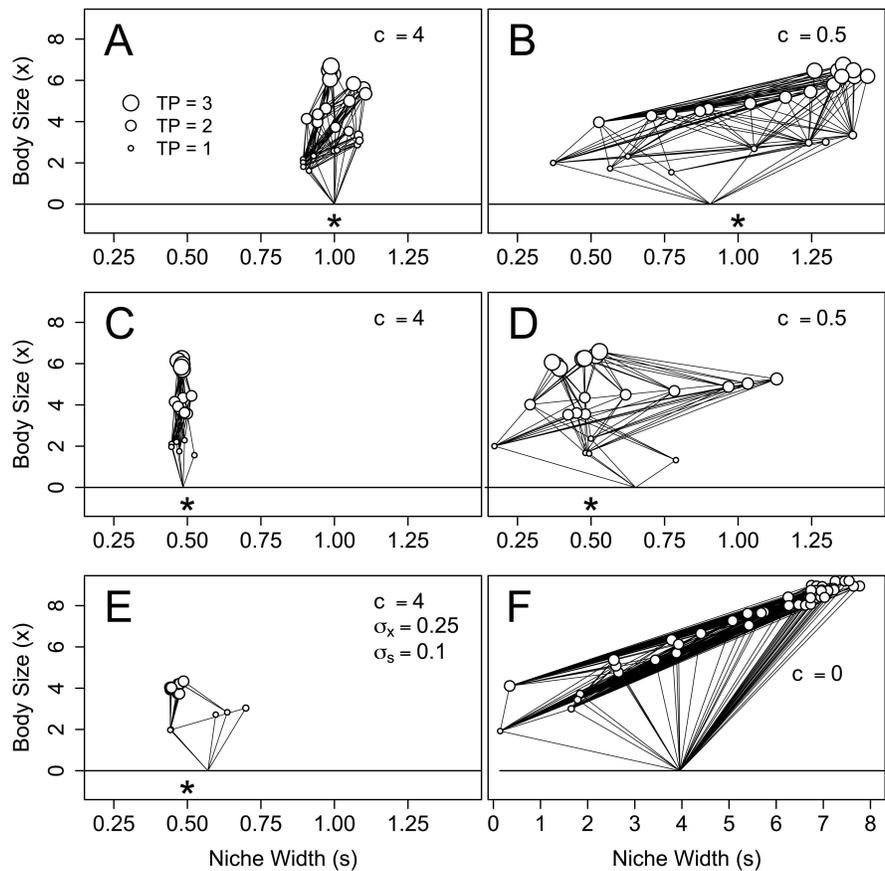


Figure 2: Representative food webs produced by the model under different parameter combinations. Each panel shows body size (x) versus niche width (s), with symbol size indicating species' trophic positions (TP) and lines connecting predators with prey that comprise $\geq 5\%$ of their diet. Mutation size distributions were $\sigma_x = 0.5$ and $\sigma_s = 0.2$ for all panels except *E*. The cost parameter c is shown in each panel, and the optimum niche width s_0 is indicated with an asterisk (except where $c = 0$). Note that the placement of the basal resource on the X-axis is arbitrary, because it has no niche width.

position. In most simulations, integer trophic positions (trophic levels) were occupied by specialists with narrow niches and body sizes close to multiples of the predator-prey size ratio d . These specialists had high densities because of their high rate of consumption of the trophic level below them and were thus able to exclude species with similar body sizes and wider niches through both exploitative and interference competition. However, species with larger niche widths could often persist if their body sizes differed sufficiently from those of the specialists; generalists with intermediate body sizes (between d and $2d$ or between $2d$ and $3d$) experienced less competition and were able to consume prey from two or more trophic levels. When niche width was unconstrained ($c = 0$), some species evolved large body sizes ($x > 9$) and very wide niches ($s > 5$), giving them an almost flat utilization curve that allowed them to feed on all smaller species (and the basal

resource) with low efficiency (fig. 2*F*). These species had relatively low trophic positions despite their large size because much of their diet came from the basal resource. Food webs that evolved without constraints on niche width were highly variable in species trait composition and the number of specialist trophic levels. They also occasionally underwent evolutionary suicide (extinction of all species), which appeared to occur when large predators drove smaller species to extinction and then became extinct themselves when they were unable to persist on the basal resource.

The introduction of a cost of deviating from the optimum niche width reduced the variability in niche width, but when the cost was moderate (e.g., $c = 0.5$; fig. 2*B*, 2*D*), there was still marked variability in niche width that was associated with body size. When the optimum niche width was small, specialists and generalists tended to al-

ternate body sizes over three or four trophic levels, with a characteristic hump-shaped relationship between niche width and body size (fig. 2A, 2D). When the optimum was larger, there was a trend toward increased niche width at higher body sizes and the absence of specialists at upper trophic levels (fig. 2B). As the cost increased further, niche widths were increasingly clustered around the optimum, with either a continuum of body sizes (at large s_0 ; fig. 2A) or a linear food web with all species at integer trophic positions (at small s_0 ; fig. 2C). The combination of high cost and a narrow optimum prevented evolution beyond the second trophic level when the distribution of mutations was small (fig. 2E). In most other cases, the structure of food webs was dictated by the foraging parameters c and s_0 rather than by the evolutionary parameters σ_x and σ_s .

This variability in trait composition led to differences in the trophic structure of food webs simulated under different conditions (fig. 3). Neither species richness nor trophic height varied strongly with the parameters we investigated; most webs had 20–40 species and $TP_{\max} \approx 3.0$ (with the few exceptions described above). Despite these similarities in species richness and trophic height, food webs differed markedly in their distributions of trophic positions and interaction strengths, depending on the values of c and s_0 . Mean omnivory declined with increasing cost (especially from $c = 0$ to $c > 0$) and increased with the optimum niche width. Generally, 40%–100% of species occupied integer (± 0.05) trophic positions, with this percentage increasing with cost when s_0 was small and decreasing with cost when s_0 was large.

Metrics of trophic structure in the five empirical food webs overlapped broadly with the values obtained from our model. Mean omnivory (σ_{TP}^2) varied from 0.07 to 0.24 in the empirical webs, tending to be higher than in food webs composed solely of trophic specialists (e.g., when $c = 4$ and $s_0 = 0.5$) but lower than in many of the food webs simulated with $c = 0$ (figs. 3, 5). The percentage of species at integer trophic positions (± 0.05) was also variable in the empirical food webs (0.11–0.44) and was generally less than or equal to the lowest values produced by the model (fig. 3).

Assembly Dynamics and Stability

The average rate of change of species richness (Δ_s) was influenced by all of the main parameters we varied (c , s_0 , and σ_x and σ_s). The rate Δ_s decreased with increasing cost, particularly from $c = 0$ to $c > 0$. Among simulations with $c > 0$, increasing the optimum niche width increased Δ_s , while increasing the trait mutation sizes decreased Δ_s (fig. 3). Rates of food web assembly were driven largely by the size of trait mutations; for example, regardless of the values

of c and s_0 , food webs reached a second trophic level ($TP_{\max} \geq 2.0$) approximately three times as fast when mutation sizes were high (an average of $\sim 10,000$ vs. $\sim 30,000$ generations).

Phylogenetic tree shape showed relationships with c and s_0 (fig. 4). Gamma was usually negative (indicating an early accumulation of extant lineages) for any simulation with $c > 0$ (fig. 4A–4E), while $c = 0$ led to positive gamma values because of a large recent upturn in the LTT plots (fig. 4F). Gamma decreased with cost when $s_0 = 1$ and increased slightly with cost when $s_0 = 0.5$ (fig. 3). Visual inspections of the LTT plots confirmed that gamma was a useful descriptor of this aspect of tree shape (fig. 4). Gamma was also strongly correlated with Δ_s and other measures of species turnover (such as the proportion of mutants that successfully established in the community), indicating that patterns in phylogenetic tree shape were driven by differences in rates of turnover and community variability and invasibility.

Relationships between Food Web Structure and Evolutionary Dynamics

Variability in food webs evolved under different conditions led to emergent relationships between trophic structure and assembly dynamics, especially between levels of omnivory and Δ_s (fig. 5). Across the parameter space explored here, mean omnivory and Δ_s were positively correlated (Pearson's correlation using log-transformed means of 20 replicates at each of 12 parameter combinations: $r = 0.78$, $P = .003$, $df = 10$). This pattern was largely driven by the highly omnivorous and unstable communities that developed when niche width was unconstrained ($c = 0$), but even among simulations with $c > 0$ there was a trend for more omnivorous food webs to have greater turnover.

Discussion

Our simulations show how different forms of foraging trade-off may influence both the structure and the dynamics of food webs. With size-structured interactions, advantages to feeding on a wide or a narrow range of prey sizes promote the assembly of food webs with higher or lower trophic complexity, respectively. These differences in foraging trade-offs—along with the sizes of trait mutations—also affect assembly dynamics, species turnover, and even phylogenetic tree shape. Across a range of conditions, these patterns lead to emergent relationships between food web structure and stability. We find that conditions favoring higher levels of omnivory also tend to increase the variability of food webs and species turnover through time.

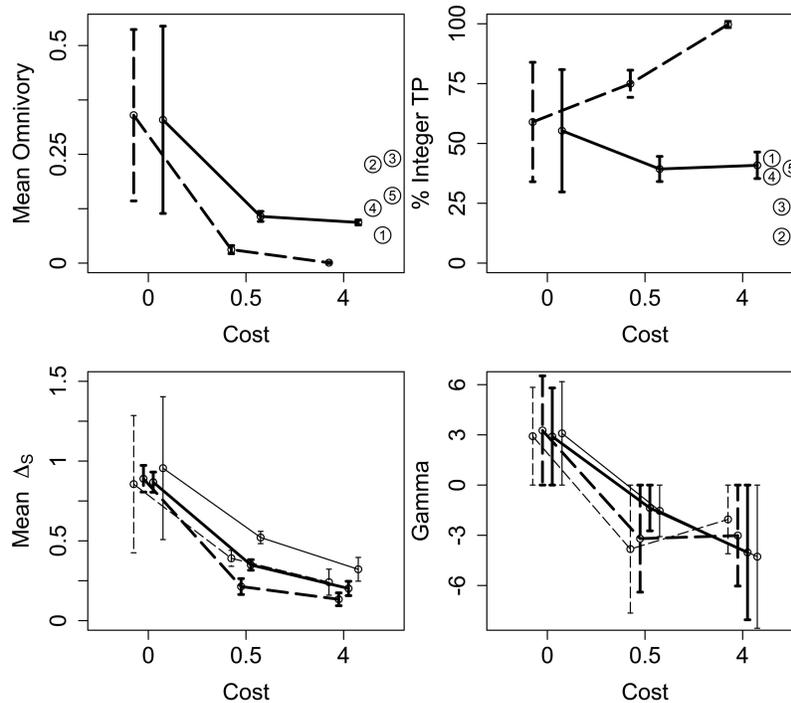


Figure 3: Effects of parameter values on structural (mean omnivory, % integer trophic positions) and dynamic (mean Δ_s , gamma) properties of simulated food webs. The top row shows the effects of varying the cost parameter c (X -axis, offset for clarity) and the optimum niche width s_0 (dashed lines: $s_0 = 0.5$; solid lines: $s_0 = 1.0$). Values calculated from five empirical food webs are shown to the right of the plot for comparison (labeled 1–5; see “Food Web Structure” in “Analyses”). For dynamic properties (bottom), we show the effects of varying c , s_0 (dashed vs. solid lines, as above), and the trait mutation distributions (thin line: $\sigma_x = 0.2$ and $\sigma_s = 0.1$; thick line: $\sigma_x = 0.5$ and $\sigma_s = 0.25$). Error bars show means and standard deviations of replicate runs.

Food Web Structure

The structure of food webs produced by our model depends more on the foraging trade-off parameters—the optimum niche width and the cost of deviating from this optimum—than on evolutionary processes (mutation sizes or the model of speciation; see app. C). Thus, we expect the relationship between food web structure and stability to be similar whether new species arise from speciation or from invasion from a regional pool (see also Loeuille and Loreau 2005). However, in a few cases the dependence on evolutionary assembly constrained the development of complex food webs. Traits associated with omnivory in our simulations (large s and x intermediate between multiples of d) often provided a “bridge” allowing the subsequent evolution of specialists at the next-highest trophic level. Thus, for parameter combinations where these omnivory-associated traits have very low fitness (large c , small s_0) and mutations are small (small σ_x and σ_s), higher trophic levels establish very slowly or not at all over the course of a simulation (e.g., with $\sigma_x = 0.2$, only one in $\sim 10^{22}$ mutants will gain two body size units in a single

step). In addition, when costs are absent, there are often two types of species—small specialists and large generalists—that are so far apart in trait space that the specialists cannot be replaced if they become extinct. In these cases, migration of species from a regional pool could rescue the local food web after extinction of the small specialists.

Our approach investigates how varying foraging trade-offs can lead to emergent relationships between food web structure and stability. This contrasts with previous theoretical investigations of omnivory-stability relationships, which have varied parameter values (e.g., attack rates) within fixed food web configurations (Holt and Polis 1997; Diehl 2003; Vandermeer 2006). In our model, c and s_0 influence the shape of the adaptive landscape: peaks may be steep and concentrated around traits suitable for specialist trophic levels or more diffuse, with a range of trait values able to invade and coexist. The higher variability and species turnover in food webs with omnivory seems to result from the flattened adaptive landscape, which increases the proportion of trait space that can maintain viable populations. In addition, food webs with omnivores

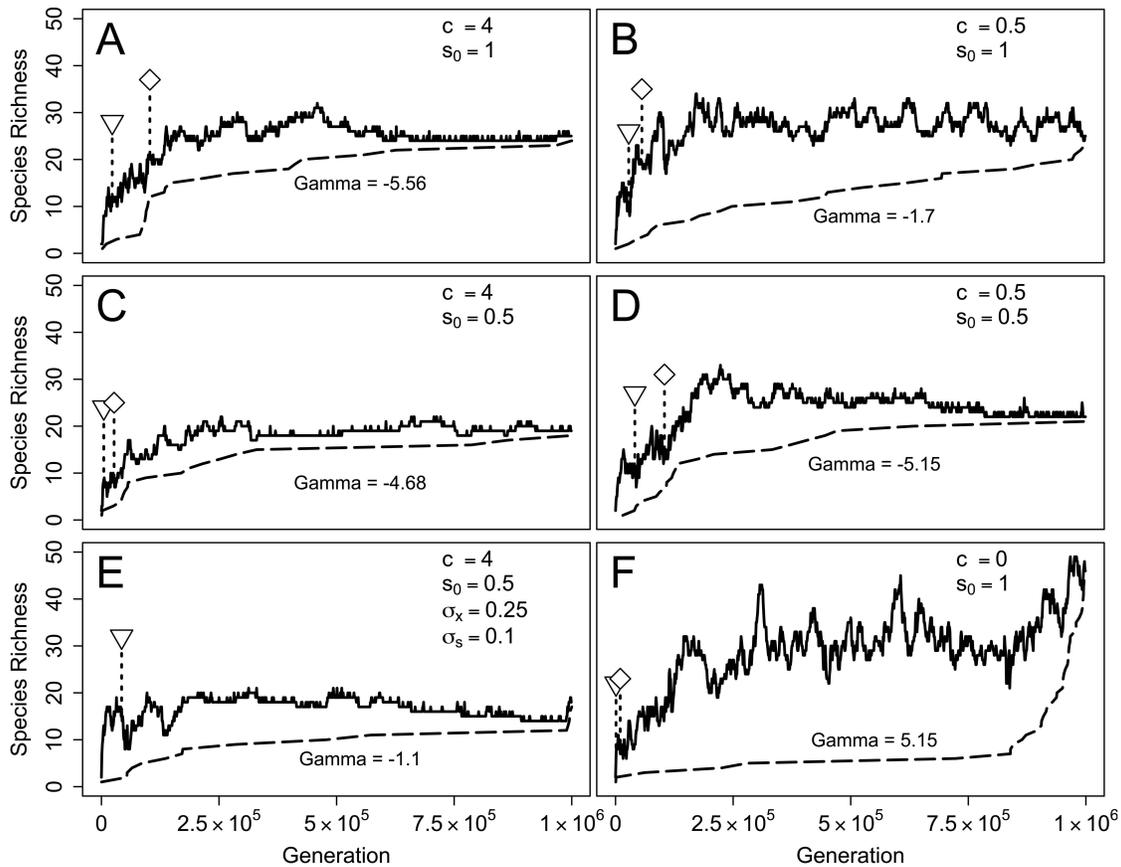


Figure 4: Representative examples of the dynamics of food web assembly under different parameter combinations. Values of c and s_0 are indicated in each panel, and the mutation size distributions were $\sigma_x = 0.5$ and $\sigma_s = 0.2$ for all panels except *E*. The solid line shows species richness at 1,000-generation intervals, while the dashed line is a lineage-through-time plot based on the phylogeny of extant species at the end of the simulation, with its shape described by the gamma statistic (see text). Symbols indicate when the food web first attained a trophic height (TP_{\max}) of 2.0 (triangle) and 3.0 (diamond).

have fewer dominant, strongly interacting species, which may make them more susceptible to invasion (Case 1990). Thus, a positive relationship between omnivory and temporal stability emerges from variation in environmental conditions (trade-off form) and speciation-extinction dynamics.

Previous studies have identified features of food webs that vary among ecosystem types, including incidence of omnivory, trophic height, degree of size structuring, and distribution of biomass among trophic groups (Schoener 1989; Shurin et al. 2006; Thompson et al. 2007; Vander Zanden and Fetzer 2007). The relationship between omnivory and stability in our model depends on variation in environmental features that determine the form of foraging trade-offs. One feature of real ecosystems that might influence such trade-offs is the structural complexity (grain size) of the environment (Ritchie and Olff 1999). If environmental heterogeneity allows size-based parti-

tioning of habitat, consumers may be penalized for foraging on different prey sizes because of the costs of maintaining foraging tactics at multiple spatial scales (i.e., low s_0 and $c > 0$ in our model). On the basis of our results, we would predict that such a community would have relatively low levels of omnivory and high temporal stability. On the other hand, if trophic interactions occur in a well-mixed environment, it may be costly to be size selective (i.e., high s_0 and $c > 0$), leading to more omnivory and potentially greater species turnover. Our examination of empirical body size data suggests that prey size generality (the standard deviation of body sizes of a consumer's prey) varies across ecosystems (app. A). We found prey size generality to be larger in aquatic predators than in terrestrial predators and potentially larger in freshwater than in marine systems (fig. A1 in the online edition of the *American Naturalist*). These patterns suggest that ecosystems vary in prey size generality (roughly corresponding to niche width

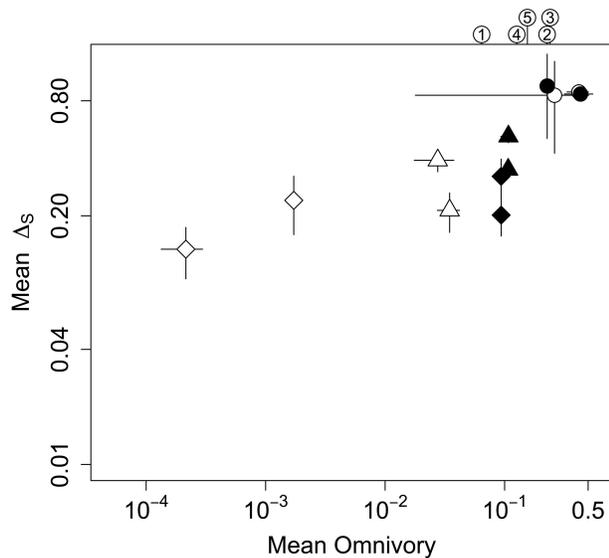


Figure 5: Relationship between omnivory and a measure of stability (mean Δ_s) across food webs simulated with various parameter combinations. Means and standard deviations are shown for 20 replicate simulations at each of 12 parameter combinations (see text). The cost parameter c is indicated by symbol type (circles: $c = 0$; triangles: $c = 0.5$; diamonds: $c = 4$), and the optimum niche width is indicated by shading (open symbols: $s_0 = 0.5$; filled symbols: $s_0 = 1$). Identical symbols indicate the two sets of mutation distributions (σ_x and σ_z) and are not distinguished here for clarity. The numbers 1–5 above the plot show mean omnivory in five empirical food webs (see “Food Web Structure” in “Analyses”).

in our model) and raise the possibility that trade-offs in resource use also vary across systems. Future comparisons across and within ecosystems should allow a more detailed understanding of variation in dietary niche widths and of the implications of this variation for food web structure and dynamics.

Assembly Dynamics and Stability

In our model, a single adaptively radiating lineage diversifies to fill a whole food web, allowing the examination of phylogenetic tree shape in addition to structural and dynamic features of food webs. We found that the shape of reconstructed lineage-through-time plots depended on the values of the ecological trade-off parameters. This pattern results from the differences in dynamic stability already described: the more species turn over, the fewer lineages will persist for long periods of time, and the more closely extant species will be related (Pybus and Harvey 2000). When turnover is lower, lineage accumulation occurs earlier, and the rate of (successful) speciation slows as the community approaches equilibrium. Both of these

situations correspond to early niche filling during adaptive radiation (Gavrilets and Vose 2005), while the variability in tree shape largely comes from whether subsequent turnover “overwrites” the early history of the clade by removing older lineages.

Our analysis of phylogenetic tree shape contributes to a growing interest in interpreting variation in real phylogenies with regard to ecological interactions (McPeck 2008; Phillimore and Price 2008). In a recent metacommunity simulation study, McPeck (2008) showed that clades had negative gamma when speciation was associated with ecological divergence and positive gamma when speciation generated ecologically equivalent species. While all of our speciation events generated differences in trait values, our results are consistent with these findings. Our food webs with high omnivory included more weakly interacting species that likely had very small differences in fitness, similar to the nonecological speciation model used by McPeck (2008). The implication that gamma can be affected by both the mode of speciation (ecological and nonecological) and the specific context of ecological speciation (different trade-off structures in our model) should lead to more detailed investigations into variability in empirical phylogenetic tree shape. Some organisms, especially fishes such as cichlids and salmonids, appear to be prone to diversifying at multiple trophic levels during adaptive radiations (Skulason and Smith 1995; Schluter 2000). When diversification occurs both within and between trophic levels, our results suggest that features of the environment that influence trophic niche evolution may also influence phylogenetic tree shape in adaptively radiating lineages.

Food webs with omnivores are less stable in our model, in terms of species turnover, than those with all species at integer trophic positions. How can this result be reconciled with empirical observations that omnivory is ubiquitous and with theoretical findings that omnivory should often be stabilizing? A possible explanation is that while turnover increases with omnivory, other components of food web stability, such as permanence, may not decrease. In our model, global extinctions of all species rarely occurred; rather, food webs tended to reach a dynamically stable configuration with little structural change despite constant turnover. Omnivory may also contribute to stability by allowing greater resilience to perturbations (such as species loss or changes in nutrient levels). Our model features a constant environment (e.g., nutrient input), and, apart from speciation, all dynamics are deterministic. Incorporating environmental stochasticity and disturbance would be a useful extension to investigate whether omnivory confers stability in a variable environment. Alternatively, omnivory may be common in food webs, despite being associated with instability, if food webs are not stable

entities over the timescales considered here. Much work remains to elucidate the various direct and indirect associations between trophic structure and stability in real food webs.

Our model provides a framework for investigating the simultaneous evolution of body size and niche width in food webs and the resulting development of complex trophic structure. We find that trade-offs in resource use may dictate the amount of omnivory that occurs in food webs and may lead to emergent relationships between omnivory and species turnover, variability, and even phylogenetic tree shape. By exploring how species interactions and foraging constraints contribute to community-wide patterns, we may gain a more thorough understanding of the relationships among community assembly, trait evolution, and food web structure.

Acknowledgments

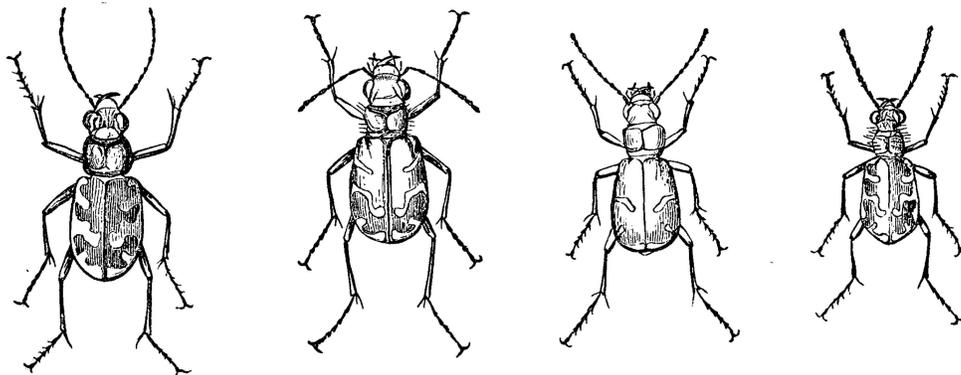
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“The tiger beetle abounds in sunny paths.” From left to right, *Cicindela generosa*, *C. vulgaris*, *C. purpurea*, and *C. hirticollis* from “Natural History Miscellany: Zoology” (*American Naturalist*, 1867, 1:549–555).