



## Predicting food-web structure with metacommunity models

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Synthesis

Metacommunity theory aims to elucidate the relative influence of local and regional-scale processes in generating diversity patterns across the landscape. Metacommunity research has focused largely on assemblages of competing organisms within a single trophic level. Here, we test the ability of metacommunity models to predict the network structure of the aquatic food web found in the leaves of the northern pitcher plant *Sarracenia purpurea*. The species-sorting and patch-dynamics models most accurately reproduced nine food web properties, suggesting that local-scale interactions play an important role in structuring *Sarracenia* food webs. Our approach can be applied to any well-resolved food web for which data are available from multiple locations.

The metacommunity framework explores the relative influence of local and regional-scale processes in generating diversity patterns across the landscape. Metacommunity models and empirical studies have focused mostly on assemblages of competing organisms within a single trophic level. Studies of multi-trophic metacommunities are predominantly restricted to simplified trophic motifs and rarely consider entire food webs. We tested the ability of the patch-dynamics, species-sorting, mass-effects, and neutral metacommunity models, as well as three hybrid models, to reproduce empirical patterns of food web structure and composition in the complex aquatic food web found in the northern pitcher plant *Sarracenia purpurea*. We used empirical data to determine regional species pools and estimate dispersal probabilities, simulated local food-web dynamics, dispersed species from regional pools into local food webs at rates based on the assumptions of each metacommunity model, and tested their relative fits to empirical data on food-web structure. The species-sorting and patch-dynamics models most accurately reproduced nine food web properties, suggesting that local-scale interactions were important in structuring *Sarracenia* food webs. However, differences in dispersal abilities were also important in models that accurately reproduced empirical food web properties. Although the models were tested using pitcher-plant food webs, the approach we have developed can be applied to any well-resolved food web for which data are available from multiple locations.

Food-web structure and dynamics play important roles in maintaining species diversity and functioning of ecosystems (Lawler and Morin 1993, Dunne et al. 2002, Duffy et al. 2007). Variation in food-web structure has been linked to habitat size (Post et al. 2000, Gotelli and Ellison 2006, Baiser et al. 2012), productivity (Winemiller 1990, Kaunzinger and Morin 1998), disturbance (McHugh et al. 2010), species interactions (Paine 1969), assembly history (Piechnick et al. 2008), and dynamical constraints such as the instability of longer food chains (Pimm 1982). Although individual drivers such as ecosystem size are highly correlated with certain measures of food-web structure (Post et al. 2000), variation in food-web structure results from context-dependent interactions among these (and other) drivers operating at both local and regional scales (Holt 2002, Post 2002, McHugh et al. 2010).

Ecologists have studied food webs at local scales to understand how biotic and abiotic factors in a particular

location influence food-web structure and composition (Winemiller 1990, Martinez 1991, Polis 1991). For example, competitive exclusion and resource exploitation can result in local species losses, whereas keystone predation can facilitate co-existence of species at lower trophic levels (Paine 1969, Cochran-Stafira and von Ende 1998). Habitat size and productivity influence species richness, composition, and trophic position through species–area and productivity–diversity relationships (Holt et al. 1999, Mittlebach et al. 2001) and species richness is strongly correlated with food-web structure across a variety of well-studied food webs (Riede et al. 2010).

Increasingly, regional-scale factors that drive spatial dynamics are being recognized as important determinants of local food-web structure (Holt 2002, Amarasekare 2008, Pillai et al. 2010). Dispersal among patches intersects with, for example, heterogeneity in ecosystem size, productivity, and disturbance regimes to influence food-web

structure and dynamics (Holt 2002, Holt and Hoopes 2005, Amarasekare 2008, Gouhier et al. 2010). Dispersal can influence food-web structure by stabilizing or destabilizing predator–prey dynamics through spatial subsidies (Holt 2002, Gouhier et al. 2010), determining the number of suitable patches that consumers can colonize (Calcagno et al. 2011, Gravel et al. 2011), providing rescue effects for species that are over-exploited by predators (Holyoke 2000), and providing refuges that allow over-exploited prey species to persist on a regional scale (Huffaker 1958). Moreover, the spatial scale of dispersal can influence food-web structure (Pillai et al. 2011) and habitat heterogeneity can directly affect colonization and extinction dynamics, altering food-web structure across the landscape (Holt 2002).

Metacommunity theory posits that spatially distinct assemblages are linked through the dispersal of multiple interacting species; it provides a framework for assessing simultaneously the roles that local and regional-scale dynamics play in generating diversity patterns across the landscape (Leibold et al. 2004, Holyoke et al. 2005). So far, metacommunity models and empirical studies have largely focused on assemblages of competing organisms within a single trophic level (Louge et al. 2011). Studies focusing on multi-trophic metacommunities are predominantly restricted to models of simplified webs and trophic motifs (Holt and Hoopes 2005, Amarasekare 2008, Gouhier et al. 2010, Pillai et al. 2010, Calcagno et al. 2011, Gravel et al. 2011, Massol et al. 2011), but some recently have been extended to complex species-rich webs (Calcagno et al. 2011, Gravel et al. 2011, Pillai et al. 2011). The study of entire food webs in a metacommunity context represents a large gap in our understanding of metacommunities (Louge et al. 2011).

Here, we begin to fill this gap by testing the ability of metacommunity models to reproduce empirical patterns of species richness, composition, and network structure of aquatic food webs inhabiting the water-filled leaves of the northern pitcher plant, *Sarracenia purpurea*. We built

metacommunity models based on ‘patch dynamics’, ‘species sorting’, ‘mass effects’ and ‘neutral dynamics’, each of which makes different assumptions about the relative importance of dispersal, habitat heterogeneity, and species interactions in structuring communities (Table 1; Leibold et al. 2004, Holyoke et al. 2005, Louge et al. 2011). We used these models to explore whether the incorporation of regional-scale processes in a metacommunity framework yielded better predictions of *Sarracenia* food-web structure than do correlations of food-web structure with geographic and climatic variables, which explain at most 40% of the variation in food-web structure (Buckley et al. 2003, 2010, Baiser et al. 2012).

We used a combined empirical and modeling approach in which we: 1) determined regional species pools and estimated dispersal probabilities (i.e. the probability of a species being drawn from a regional species pool and introduced into a local food web) from empirical *Sarracenia* metacommunities; 2) simulated local food-web dynamics using Lotka–Volterra equations; 3) dispersed species from regional pools into local food webs based on the assumptions of each metacommunity model; 4) tested the relative fit of each metacommunity model to observed food-web structure (Fig. 1).

## Study system and empirical data

### The *Sarracenia* food web

*Sarracenia purpurea* is a long-lived, perennial, carnivorous plant that inhabits nutrient-poor bogs and seepage swamps along the coastal plain of eastern North America, and in bogs and poor fens across the upper Midwestern states and across Canada (Buckley et al. 2010). The plant possesses tubular leaves that open during the growing season, fill with rainwater, and subsequently capture invertebrate prey that serves as the resource base of a food web

Table 1. Metacommunity models (Leibold et al. 2004) that were used to simulate the assembly of *Sarracenia* food webs. Italics indicate how we met each metacommunity assumption in our pitcher plant model.

Model	Characteristic		
	Patch similarity	Species interactions	Time-scale of regional and local dynamics
Patch dynamics	Similar <i>– pitchers share identical resource levels (i.e. have the same prey capture function)</i>	Competition-colonization tradeoff <i>– better dispersers have higher (less negative) competition coefficients (<math>a_{ij}</math>) (Eq. 7)</i>	Local > regional <i>– one dispersal event per 25 iterations of population dynamics</i>
Species sorting	Dissimilar <i>– pitchers differ in resource levels (i.e. have different prey capture functions)</i>	Species perform differently in different habitats <i>– species either increase (Eq. 8) or decrease (Eq. 9) their competitive ability (<math>a_{ij}</math>) as a function of resource levels</i>	Local > regional <i>– one dispersal event per 25 iterations of population dynamics</i>
Mass effects	Dissimilar <i>– pitchers differ in resource levels (i.e. have different prey capture functions)</i>	Species perform differently in different habitats <i>– species either increase (Eq. 8) or decrease (Eq. 9) their competitive ability (<math>a_{ij}</math>) as a function of resource levels</i>	Local = regional <i>– one dispersal event per one iteration of population dynamics</i>
Neutral	Similar <i>– pitchers share identical resource levels (i.e. have the same prey capture function)</i>	All species are assumed to have identical fitness <i>– population dynamics are not simulated – species composition is solely the result of random draws from the regional species pool</i>	No local dynamics <i>– population dynamics are not simulated – species composition is solely the result of random draws from the regional species pool</i>

Table adapted from Holyoak et al. 2005.

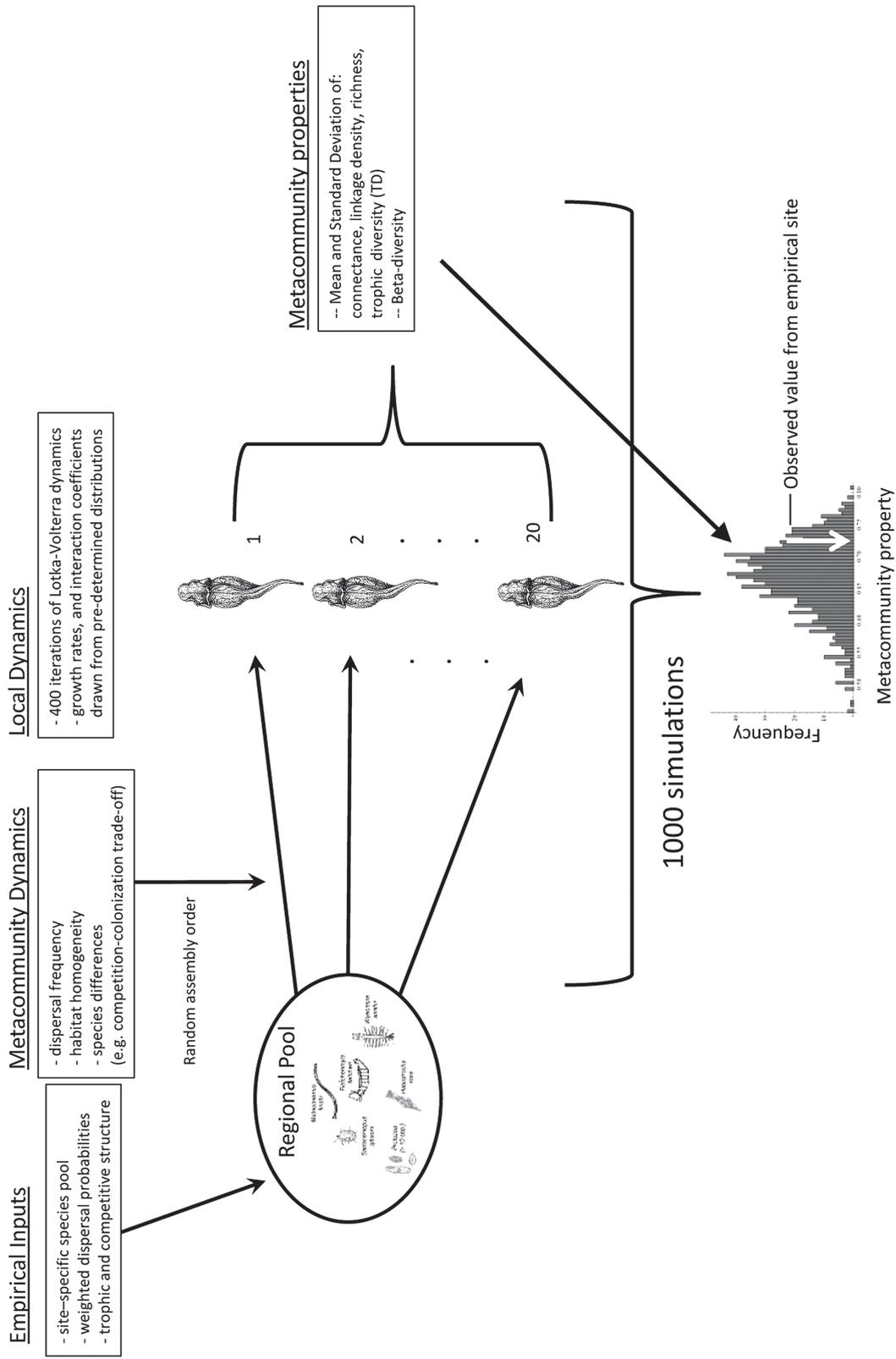


Figure 1. Schematic diagram of *Sarracenia* metacommunity models. We collected empirical data from 20 pitchers (19 at the Georgia site [GEO]) to construct regional species pools and species specific dispersal probabilities. Dispersal rates, habitat (pitcher) homogeneity, and species differences varied among the seven different metacommunity models we examined (Table 1). We simulated local dynamics with Lotka–Volterra equations for 20 (or 19) pitchers and calculated food web properties after 400 iterations of local dynamics ( $n = 40$  days). We ran each type of model ( $n = 7$ ) for each site ( $n = 3$ ) for a total of 21 models; each model was simulated 1000 times, providing likelihood distributions of food-web structural characteristics against which we could compare the values observed at each site.

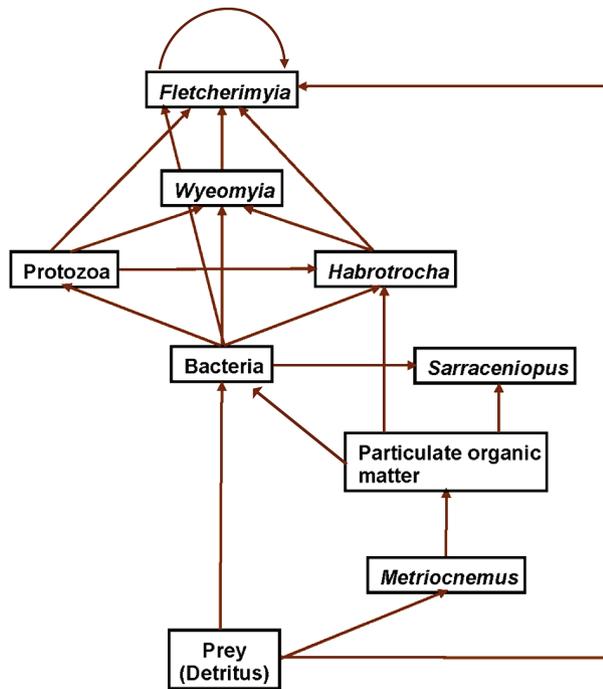


Figure 2. Main components of the *Sarracenia* food web. Captured prey is shredded by both midge *Metriocnemus knabi* and flesh fly *Fletcherimyia fletcheri* larvae into particulate organic matter (POM) and directly decomposed by Bacteria. Bacteria also feed on POM along with mites (*Sarraceniopus gibsoni*) and rotifers (*Habrotrocha rosa*). Bacteria is consumed by protozoa, and rotifers (which also prey on protozoa), all of which are preyed upon by the top predators the larvae of the mosquito *Wyeomyia smithii* and the sarcophagid fly *F. fletcheri*. *Fletcherimyia* larvae are cannibalistic and also prey upon on 1st- and 2nd-instar *W. smithii* larvae.

(Fig. 2) that includes bacteria, protozoa, the bdelloid rotifer *Habrotrocha rosa*, and a suite of obligate arthropods: the mite *Sarraceniopus gibsoni*, and aquatic larvae of the pitcher-plant mosquito *Wyeomyia smithii*, the midge *Metriocnemus knabi* and the sarcophagid fly *Fletcherimyia fletcheri* (Addicott 1974, Heard 1994, Bledzki and Ellison 2003). Less common members of this food web include loricate rotifers, cladocerans, copepods, amphipods, nematodes and multicellular algae (Addicott 1974, Harvey and Miller 1996, Bledzki and Ellison 2003). Feeding interactions in the *Sarracenia* food web center on a detritus 'processing chain' (Heard 1994). Prey items that are captured by the plant are shredded by the midge and the sarcophagid fly into particulate organic matter (POM). Bacteria directly decompose prey items and also consume POM. Bacteria are preyed upon by a suite of intraguild predators including protozoa, rotifers, *W. smithii* and *F. fletcheri*. *Wyeomyia smithii*, and late-instar *F. fletcheri* also consume protozoa, rotifers, and each other, and are the top predators in this five-level food web (Fig. 2).

*Sarracenia* food webs are an ideal system with which to test metacommunity theory in a food-web context (Miller and Kneitel 2005). Replicate pitchers provide spatially distinct habitat patches that undergo an assembly process consisting of both active and passive dispersal (Ellison et al. 2003, Kneitel and Miller 2003). The resulting food webs vary at both local and regional spatial scales in species

richness, composition, and food-web structure (Buckley et al. 2003, 2004, 2010, Baiser et al. 2012). Dispersal rates (Kneitel and Miller 2003), pitcher size and age (Buckley et al. 2010, Baiser et al. 2012), trophic interactions (Goteli and Ellison 2006, Cochran-Stafira and von Ende 1998), and latitude (Buckley et al. 2003) all are correlated with species richness, composition, and food-web structure.

## Empirical food web and regional pool data

We collected presence/absence data from 20 pitcher-plant food webs at each of two sites and 19 food webs at a third site. The three sites spanned the range of *S. purpurea*, with one site in the southern part of its range in Georgia (GEO, 32°10'N, 81°60'W), one in the northeast, Québec City (QUS, 46°71'N, 71°27'W), and one in the northwest corner of its range in eastern British Columbia (FTN, 58°49'N, 122°54'W). Data from these three sites were collected as part of a larger effort in which we sampled pitchers at each of 39 sites across the range of *S. purpurea* (see Buckley et al. 2003, 2010 for details on site selection, leaf selection, sampling protocol, and a complete list of species found in all food webs).

At each site, we sampled first-year pitchers, each on a different plant, that were 3–6 weeks old. Our sampling protocol adjusted for the influence of leaf age (i.e. we were not comparing a newly opened leaf with a 2nd year leaf), seasonal differences in dispersal (i.e. each leaf was sampled on the same day at a given site) and explicit spatial structure (i.e. leaves on the same plant have more similar communities than leaves on different plants, but spatial location of plants does not explain variation in pitcher plant communities, Buckley et al. 2004). For modeling purposes, therefore, we defined each metacommunity as the 20 (19 in the case of GEO) pitchers that opened on the same day. As a result, we viewed dispersal as a lottery, in which species colonize from a regional pool (Miller and Kneitel 2005). Each site's regional pool consisted of all species found at that site. Within each regional species pool, we quantified the dispersal probability,  $G_i$  (i.e. probability of a species  $i$  being drawn from the regional pool and introduced into a pitcher), as the maximum likelihood estimate of a multinomial distribution based on all species presence across all pitchers. The observed measures of food-web species richness, composition, and network structure from metacommunities at each site were quantified for comparison with food webs generated by our metacommunity models. The three sites in this study contained a total of 25 taxa with bacteria aggregated into a single tropho-species (all data are available from the Harvard Forest Data Archive, data set HF-193 (<<http://harvardforest.fas.harvard.edu/data-archive>>)).

## Models

### Local population dynamics

We simulated local population dynamics within each pitcher using generalized Lotka–Volterra equations, similar to those used to model local dynamics of competitive (Levin 1974,

Wilson 1992) and predator–prey metacommunities (Massol et al. 2011). The equations have the following form:

$$dX_i/dt = X_i (b_i + \sum a_{ij} X_j) \quad (1)$$

where  $dX_i/dt$  is the rate of change in biomass  $X$  for species  $i$ ,  $b_i$  is the intrinsic growth rate of species  $i$ , and  $a_{ij}$  is the per capita effect of species  $j$  on the per capita growth rate of species  $i$ . In this model, consumers cannot establish in a food web in the absence of a prey population, thus  $-0.03 < b_i < 0$ . The dynamics of the basal resource, prey captured by the pitcher plant, is modeled by a prey–capture function (see ‘Dynamics of resource availability’ below). Recent evidence suggests that the distribution of interaction strengths within a food web is positively skewed, with relatively few strong interactions and many weak ones (Wooten and Emmerson 2005). Therefore,  $a_{ij}$ , the effect of a predator  $X_i$  on the growth rate of prey species  $X_j$  was sampled randomly from a gamma distribution ( $k = 1$ ,  $\theta = 0.1$ ) and multiplied by  $-1$ ;  $a_{ji}$ , the effect on the predator, was also sampled randomly from a gamma distribution ( $k = 1$ ,  $\theta = 0.1$ ). For interspecific competition,  $a_{ij}$  and  $a_{ji}$  were randomly chosen values from a gamma distribution ( $k = 1$ ,  $\theta = 0.1$ ) and multiplied by  $-1$ ; intraspecific competition,  $a_{ii}$ , was set to  $-1$  for all species. The structure of the interaction matrix (i.e. who eats whom and who competes with whom) was based on our observations and published accounts of trophic and competitive interactions in the *Sarracenia* food web (Addicott 1974, Heard 1994, Cochran-Stafira and von Ende 1998, Miller et al. 2002). Species were seeded into each pitcher at an (arbitrary) biomass of 0.02 and populations went locally extinct if their biomasses dropped below 0.01. The pitcher-plant mosquito *Wyeomyia smithii* and midge *Metriocnemus knabi* pupated and eclosed from a pitcher once their biomass reached 0.1. The pitcher plant system is a non-equilibrium system (Ellison et al. 2003) and our goal was to compare food webs after approximately the same amount of species interaction time. Therefore, we simulated local dynamics for 40 days (= pitcher leaf age) to approximate the amount of time during which species interacted before we sampled the *Sarracenia* webs (~3–6 weeks). Each day in the model consisted of ten iterations of Lotka–Volterra dynamics, which is the estimated number of generations that the organism with the fastest turnover (bacteria) experiences, yielding 400 model iterations. Food-web structural characteristics were determined for the web resulting from these 400 iterations.

### Dynamics of resource availability

The basal resource of the *Sarracenia* food web is detritus, which consists of carcasses of insects that are captured by the plant. Empirical studies have shown that prey capture is a function of pitcher size and age (Cresswell 1993, Heard 1998), rainfall and subsequent evaporation of rain (Kingsolver 1979), and morphological characteristics of pitchers (Cresswell 1993, Bennett and Ellison 2009). We modeled prey capture using a set of coupled equations that included functions of pitcher age ( $L$ ), amount of water in the pitcher ( $W$ ), and air temperature ( $T$ ) (see Supplementary Material Appendix A1 for example prey capture curves),

which affects not only evaporation of water but also activity of insect prey. Total prey capture, for which daily biomass was normalized to scale between 0 and 1, was set equal to the product of  $L$ ,  $W$ , and  $T$ :

$$\text{capture} = LWT \quad (2)$$

The relationship between prey capture rate and leaf age  $L$  was modeled with a gamma function:

$$f(d, k, \theta) = \frac{d^{k-1} e^{-d/\theta}}{(k-1)! \theta^k} \quad (3)$$

where  $d$  (days) ranges from 1 to  $n$  (the maximum lifespan of the pitcher in the model;  $n = 40$ ). The other parameters of this distribution are  $\theta$ , the scale parameter, which in this case sets the age of the leaf (in days) at which prey capture reaches its maximum, and  $k$ , the shape parameter for the gamma distribution. Both  $\theta$  and  $k$  were selected to approximate empirical prey capture curves (Heard 1998).

The amount of water in the pitcher,  $W$ , was modeled as a function of accumulating rain, evaporation, and loss that occurs when leaves were damaged:

$$R_v = R_f A_p \quad (4)$$

$$W = R_v - (E + M) \quad (5)$$

In these two equations, rain accumulation ( $R_v$  in  $\text{cm}^3$ ) is the product of rainfall ( $R_f$ , in  $\text{cm day}^{-1}$ ) and area of the pitcher opening ( $A_p$ , in  $\text{cm}^2$ );  $W$  equals  $R_v$  minus loss of water due to evaporation ( $E$ ) and mining ( $M$ ) by larvae of the noctuid moth *Exyra fax* Grt., both in  $\text{cm}^3 \text{ day}^{-1}$ . Over time, leaf mining by *E. fax* can completely drain leaves, leaving them without a food web. Daily  $R_f$  values were taken from the weather station nearest to each site (< 100 km) in 2001, and  $A_p$  was the mean area of the pitcher opening at each site (Ellison et al. 2004). Loss of water due to evaporation,  $E$ , was set to  $0.04 \text{ cm}^3 \text{ day}^{-1}$ . The probability that moth herbivory would occur in a given plant was set equal to 0.5 (Atwater et al. 2006) and the loss of water due to moth herbivory ( $M$ ) was held constant at  $0.01 \text{ cm}^3 \text{ day}^{-1}$ . Finally, temperature ( $T$ ) was assumed to have a linear relationship with prey capture, because insect activity and mobility increased with temperature across the range of temperatures observed at our three sites (Lynch et al. 1980).

### Metacommunity dynamics

We modeled the assembly of pitcher plant metacommunities containing 19 or 20 local food webs depending on the site (Fig. 1). The assumptions of each metacommunity model (Table 1) were incorporated by altering specific aspects of local dynamics. For patch similarity, we altered resource availability such that similar patches had the same amount of resources while different patches varied in resource availability. Species differences related to dispersal differences (patch dynamics) and patch differences (species sorting and mass effects) were generated by adjusting the Lotka–Volterra competition coefficients,  $a_{ij}$  and  $a_{ji}$ . Finally,

we altered the relative time scale of local and regional dynamics by changing the number of Lotka–Volterra iterations between dispersal events. In addition to the four basic metacommunity models, we also examined three hybrid models that combined assumptions of the single-factor models. Model code and input files are available from the Harvard Forest Data Archive, dataset HF-193.

### Patch-dynamic model

The three main assumptions of the patch-dynamic model are that; 1) all patches (here, pitchers) are equal and are capable of containing populations of any species in the species pool; 2) there is a tradeoff between dispersal and competitive abilities; and 3) local population dynamics occur at a faster time-scale than assembly dynamics (Table 1; Leibold et al. 2004, Holyoak et al. 2005). We met the assumption of patch similarity by using the same prey capture dynamics for all pitchers within each metacommunity simulation. To meet the second assumption, we modeled a tradeoff among species between dispersal and competitive abilities:

$$a_{ij} = -\alpha \quad (6)$$

$$a_{ji} = -\alpha(1 - p_{ij}) \quad (7)$$

Here,  $\alpha$  is a base-line competition coefficient shared by any two competing species and was randomly drawn from a gamma distribution ( $k = 1$ ,  $\theta = 0.1$ ). Parameter  $p_{ij}$  is the dispersal difference calculated by subtracting the dispersal rate of the inferior disperser (species  $j$ ) from that of the superior disperser (species  $i$ ); because dispersal rates are frequencies;  $0 < p < 1$ . For species  $j$ ,  $a_{ij}$  is equal to  $-\alpha$  (Eq. 6). For species  $i$ , the competition coefficient,  $a_{ji}$ , increased linearly (i.e. became less negative, resulting in a weaker competitor) with the complement of  $p_{ij}$  (Eq. 7). The dispersal-based competition coefficients ( $a_{ij}$ ,  $a_{ji}$ ) are state variables in the Lotka–Volterra equations that describe local dynamics (see ‘Local population dynamics’ above). We met the final assumption of patch-dynamics models – that local population dynamics occur at a greater rate than species dispersal events – by introducing species at a rate of 1 every 2.5 days for a total of 16 introductions. Twenty-five iterations of local population dynamics were simulated between each introduction.

### Species-sorting model

The species-sorting approach assumes that 1) patches are different; 2) different species do well in different types of patches; and 3) local population dynamics occur on a shorter time-scale than assembly dynamics (Table 1; Leibold et al. 2004, Holyoak et al. 2005). We altered patches by allowing resource dynamics to vary along a continuous gradient from pitchers with low prey capture (maximum daily prey capture  $\sim 0.006$  g day<sup>-1</sup>) to pitchers with high (maximum daily prey capture  $\sim 0.6$  g day<sup>-1</sup>; Supplementary material Appendix A1). Species were randomly assigned to either increase (Eq. 8, below) or decrease (Eq. 9, below) their competitive ability as a function of resource levels.  $N_{\max}$  is the maximum amount of resources caught by a pitcher in one day and, as in the patch-dynamic model,  $\alpha$  is a

competition coefficient randomly drawn from a gamma distribution ( $k = 1$ ,  $\theta = 0.1$ ). For species whose competitive abilities increase with resource availability;

$$a_{ij} = -\alpha N_{\max} \quad (8)$$

For species whose competitive abilities decrease with resource availability;

$$a_{ij} = -\alpha(1 - N_{\max}) \quad (9)$$

We introduced species at a rate of 1 every 2.5 days (as in the patch-dynamics model).

### Mass-effects model

The first two assumptions of mass-effects models are the same as species-sorting models. The mass-effects model differs from the species-sorting model in that local population dynamics and assembly dynamics occur at the same time scale. For the mass-effects simulations, we simply took the species-sorting model and introduced ten species per day (i.e. one species for each iteration of local population dynamics; see ‘Local population dynamics’ above).

### Neutral model

The neutral model assumes no differences among dispersal abilities or among patch suitabilities for any species (Holyoak et al. 2005). As a result, for this model, we did not simulate local population dynamics, and species dispersal probabilities were set to be uniformly equal. Although the ‘neutral model of biodiversity’ works at the level of the individual, not at the level of a species, we are using ‘neutral model’ here in the sense of a null model with no differences among species to contrast with species-specific differences in the other metacommunity models. However, in a true neutral model, differences among species in dispersal abilities would appear as a consequence of different abundances of each species in local communities. These differences do not arise here, because our ‘neutral model’ does not have abundances (no local population dynamics and uniformly equal dispersal probabilities); these assumptions are relaxed in our hybrid neutral model with empirical dispersal. To assemble pitcher-plant food webs in this neutral model, we randomly selected a value from the range of species richness in the empirical data set and randomly selected that number of species from the species pool. Bacteria and detritus were present in every neutral web because they were present in every empirical web and to avoid the unrealistic scenario of a consumer being present without a prey item (i.e. every species in the regional pool preys upon detritus, bacteria, or both).

### Hybrid models

Each of the four metacommunity models described above include specific mechanisms that can drive variation in metacommunity structure and dynamics (Leibold et al. 2004, Holyoak et al. 2005). Empirical metacommunities are unlikely to be perfectly described by any single model (Louge et al. 2011), so we also created three hybrid models

that combine assumptions from the different metacommunity perspectives.

### Species sorting/mass effects (SS/ME)

This first hybrid model links species-sorting and mass-effect models. These two models assume patch differences in resource availability and that different species are better competitors in different patches, but they fall on opposite ends of a continuum in terms of the time scales of regional and local dynamics. Species-sorting models introduce one species for every 25 iterations of local dynamics, while mass-effects models introduce one species every iteration. We explored an intermediate parameter value by introducing one species every 10 iterations in the SS/ME model.

### Neutral model with empirical dispersal (NMED)

Neutral models assume that niche characteristics of species do not determine their dynamics (Hubbell 2001). This hybrid model asks if empirical species-specific dispersal patterns can maintain metacommunity structure in the absence of trophic and competitive dynamics. Our NMED model excluded trophic and competitive dynamics, but included empirical variation in dispersal probabilities. We achieved this by running the neutral model with empirical dispersal probabilities instead of uniform dispersal probabilities.

### Species sorting/neutral model (SS/NM)

The SS/NM model is the alternative to the NMED model, and tests whether competitive and trophic interactions that are structured by patch differences maintain metacommunity structure in the absence of species-specific dispersal patterns. To test this, we ran the species-sorting model with uniform dispersal probabilities to create the SS/NM model.

### Entire model simulations

A metacommunity simulation consisted of local dynamics for 20 food webs (19 for GEO), where parameters were drawn from statistical distributions (Supplementary material Appendix A2). Designation of species as superior competitors at either high or low resources levels (for the species-sorting and mass-effects models) and empirically based parameters (dispersal probabilities, interaction matrix) were held constant across all webs 'within' a simulation. We ran each of the seven metacommunity models for each of the three sites, yielding a total of 21 models, each of which was then simulated 1000 times. To maintain generality 'across' simulations, parameters drawn from statistical distributions (Supplementary material Appendix A2) and species designation as superior competitors in either high or low resources levels (for the species-sorting and mass effects models) were resampled for each simulation. Regional species pools and dispersal probabilities were held constant across all 1000 simulations for a given model at a given site. We conducted all simulations using Mathematica 8.0.

### Metrics of food-web structure and statistical analysis of model fit

For each simulated metacommunity, we calculated the mean and standard deviation of species richness, connectance ( $C = L/S^2$ ; where  $L$  is the number of links and  $S$  is the number of species), linkage density ( $LD = L/S$ ), and  $TD$ , a trophic based measure of functional diversity (Petchey et al. 2008). We also calculated the multi-site Sørensen index,  $\beta_{\text{sor}}$  (Baselga 2010) to quantify  $\beta$ -diversity. We compared the observed value of each statistic for the empirical data with model distributions from the 1000 simulations to calculate a p-value for each metacommunity model at each site. If  $0.025 \geq \text{p-value} \leq 0.975$ , we concluded that the model predictions fit the observed data. When  $\text{p} < 0.025$ , the observed statistic was significantly less than expected from the metacommunity model and when  $\text{p} > 0.975$ , the observed statistic was significantly greater than expected from the metacommunity model.

### Model sensitivity

The seven metacommunity models explore how varying dispersal rate, heterogeneity in pitcher conditions, and dispersal probabilities influence food web structure. However, two assumptions about initial model inputs may influence variation in food web metrics 'within' models. First, for models with varying dispersal probabilities among species (e.g. patch dynamics, species sorting, mass effects), we used a multinomial distribution for species dispersal probabilities based on empirical presence/absence data across sites. Although this is an informed assumption, it is not a true quantification of the frequency that a given species will reach a pitcher, but implicitly reflects competitive and trophic interactions (e.g. a poor competitor may not be present in many pitchers due to its competitive ability, not infrequent dispersal). Second, the distribution of interaction coefficients,  $a_{ij}$ , was assumed to be skewed with few strong interactions and many weak ones (i.e. gamma ( $k = 1, \theta = 0.1$ )).

We explored how varying the initial dispersal and interaction coefficient distributions influenced within-model sensitivity for the three single-factor metacommunity models that contained these parameters (species sorting, patch dynamics, mass effects). We modified the multinomial dispersal distribution, by increasing dispersal probabilities for species found in less than 25% of pitchers by 20% and decreasing dispersal probabilities for species found in greater than 25% of pitchers by 20%. The new dispersal distribution is called *Emod* (empirical modified). We also drew  $a_{ij}$  from a uniform distribution and a gamma distribution ( $k = 6, \theta = 0.05$ ) that is roughly normal. We ran simulations that crossed our two dispersal distributions with our three  $a_{ij}$  distributions for species sorting, patch dynamics, mass effects models at each site. This yielded 45 new models, in addition to the 15 models from the original set of simulations. Each model was simulated 1000 times.

To test model sensitivity to initial distributions of dispersal and  $a_{ij}$ , we calculated a Z-score for each empirical estimate relative to the model distributions:

$$Z = \frac{\text{observed estimate} - \text{mean of model distribution}}{\text{standard deviation of model distribution}} \quad (10)$$

We used a three-way ANOVA to test the effects of model type, shape of dispersal distribution, and shape of the distribution of the interaction coefficient  $a_{ij}$  on the  $Z$ -score for each food web metric. In this ANOVA, site entered as a blocking variable, and the other factors were treated as fixed effects. The main focus of this analysis was to determine whether the species-sorting, patch-dynamics, or mass-effects models were more or less sensitive to changes in dispersal or  $a_{ij}$ . In the ANOVA, the interaction terms model type  $\times$  dispersal and model type  $\times$   $a_{ij}$  identify this sensitivity, and we estimated the amount of variation explained by these interaction terms through partitioning the variance in the ANOVA (Gotelli and Ellison 2004).

## Results

### Single-factor metacommunity models

In terms of their ability to reproduce observed food web patterns, the patch-dynamics and species-sorting models were the most accurate single-factor metacommunity models. These models correctly predicted mean  $S$ , mean and variance of  $C$ , and mean  $LD$  at all sites. Mean  $TD$  at all three sites by the patch-dynamics model and at two of the three sites by the species-sorting model was not significantly different from that observed (Fig. 3a–b). Variation in  $LD$  fell within model distributions at all three sites for the species-sorting model and at two of the three sites for the patch-dynamics model.  $\beta_{\text{sor}}$  was not significantly different from observed estimates at two sites for the species-sorting model and at one site for the patch-dynamics model. When these models were inaccurate (e.g. variation in species richness and  $TD$  at all sites), they significantly underestimated the observed food-web metric (Fig. 3a–b).

The neutral model fit the observed data more poorly than either the patch-dynamics model or the species-sorting model (Fig. 3c). The neutral model reproduced mean  $TD$  and variance in  $C$  at all sites, and variation in  $LD$  and  $\beta_{\text{sor}}$  at two of the three sites (Fig. 3c). The neutral model significantly overestimated the observed mean  $S$  and variation in  $S$  and  $TD$  at all sites (Fig. 3c). The neutral model significantly underestimated  $C$  at all sites and  $\beta_{\text{sor}}$  at the GEO site (Fig. 3c).

The mass-effects model was the least successful at reproducing community characteristics of the observed sites; it correctly predicted variation in  $LD$  only for two sites and variation in  $S$  at one site (Fig. 3d). Otherwise, the mass-effects model significantly overestimated  $LD$ ,  $S$  and  $TD$ , and significantly underestimated all other food-web metrics (Fig. 3d).

### Hybrid models

The species-sorting/mass-effects (SS/ME) model was the best hybrid model and fit the observed data nearly as well as the species-sorting and patch-dynamic models (Fig. 3e). The SS/ME model correctly estimated mean  $S$  for two of the three

sites and  $TD$  for all sites (Fig. 3e). Similar to the species-sorting and patch-dynamic models, the SS/ME model accurately fit the observed values for the mean and variation of  $LD$  and  $C$ , with the exception of mean  $C$  for the site in British Columbia (Fig. 3e). However, the SS/ME model could not reproduce  $\beta_{\text{sor}}$  or variation in  $S$  for any site and observed values for variation in  $TD$  did not fall within model distributions for two of the three sites (Fig. 3e). Community metrics that did not fall within SS/ME distributions consistently exceeded the model distributions, except for mean  $S$  at the FTN site (Fig. 3e).

The distributions from the neutral model with empirical dispersal (NMED) fit 10 observed parameter estimates. Observed values for  $LD$ ,  $\beta_{\text{sor}}$ , and variation in  $C$  fell within model distributions for all sites. In addition, the observed value for  $TD$  at the GEO site fell within model distributions (Fig. 3f). The NMED model significantly underestimated  $C$  and significantly overestimated all other parameters that did not fall within model distributions including mean  $S$  (Fig. 3f).

The species-sorting/neutral model (SS/NM) performed poorly, accurately fitting distributions to only five observed values (Fig. 3g). These included variation in  $C$  at two sites and variation in  $LD$ ,  $S$  and  $TD$  at one site (Fig. 3g). The SS/NM model significantly underestimated values of  $C$ ,  $\beta_{\text{sor}}$ , and variation in  $C$ ,  $S$  and  $TD$  for food-web metrics that fell outside the model distribution. The remaining metrics were significantly overestimated by this model (Fig. 3g).

Overall, the patch-dynamic, species-sorting, and SS/ME effects models were generally successful in reproducing mean  $S$ ,  $LD$ , variation in  $C$  and  $LD$  and  $TD$  of the empirical food webs. However, these models, along with the other four models, did a poor job in reproducing the observed variation in  $S$  and  $TD$  of the real *Sarracenia* food webs. In addition, the NMED was the only model to accurately reproduce  $\beta_{\text{sor}}$  for all sites (Fig. 3f).

### Model sensitivity

Analysis of variance revealed that altering the shape of the distributions of dispersal and species-interaction coefficient  $a_{ij}$  significantly changed the estimates of food-web structure, but only for the mass-effects model. Overall, model type  $\times$   $a_{ij}$  explained 11% (SD = 7%) and model type  $\times$  dispersal explained 3% (SD = 2%) of the variation in model fit, respectively. The model type  $\times$   $a_{ij}$  term was significant ( $p < 0.05$ ) for every food web metric except  $\beta_{\text{sor}}$  and  $LD$  (Fig. 4; Supplementary material Appendix A3). Tukey's HSD showed that only comparisons within the mass-effects models were significantly different ( $p < 0.05$ ) across all metrics when the model type  $\times$   $a_{ij}$  term was significant (Fig. 4; Supplementary material Appendix A4). The model type  $\times$  dispersal term was significant ( $p < 0.05$ ) for the food web metrics variance in  $C$ ,  $S$ , variance in  $S$  and  $\beta_{\text{sor}}$  (Supplementary Material Appendix A3). Tukey's HSD showed that only comparisons within the mass-effects models were significantly different ( $p < 0.05$ ) for variance in  $C$  and  $S$ , while within model pairwise comparisons were not significant for variance in  $S$  and  $\beta_{\text{sor}}$  (Fig. 4; Supplementary material Appendix A5). Overall, mass effects models were

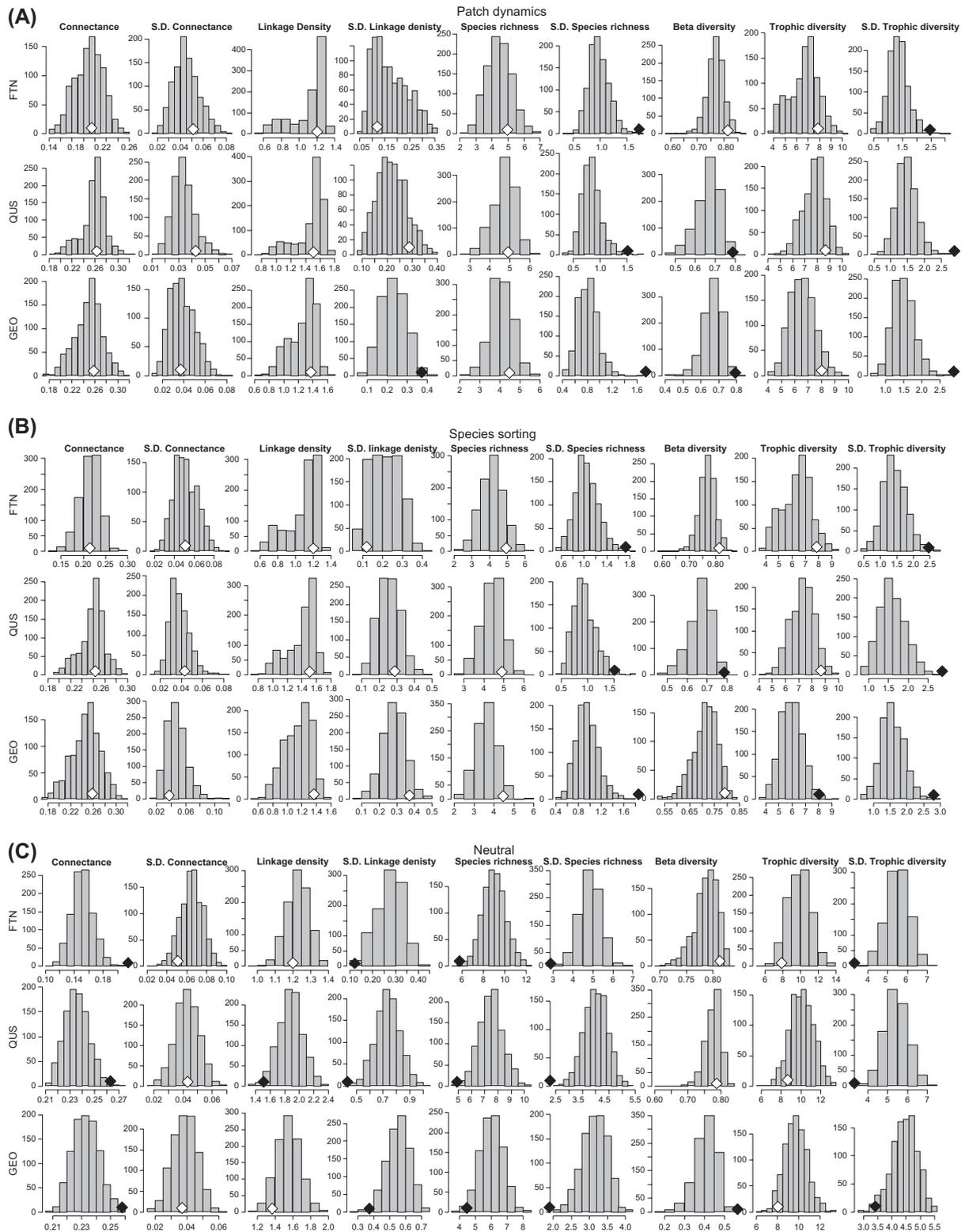


Figure 3. Metacommunity model distributions for pitcher plant food web characteristics. Each distribution consists of 1000 simulated values from a specific metacommunity model and site. Diamonds indicate the location of the empirically observed value within the model distribution. A white diamond ( $\diamond$ ) indicates that the observed value fell within 95% of the model estimates, a  $0.025 \leq p\text{-value} \leq 0.975$ . A black diamond ( $\blacklozenge$ ) indicates that the observed value was greater or less than 95% of the model estimates, a  $0.025 < p\text{-value} > 0.975$ . Partial black diamonds indicate that the observed value fell completely outside the model distribution. (A) patch-dynamic models; (B) species-sorting models; (C) neutral model; (D) mass-effects model; (E) species-sorting/mass-effects hybrid model; (F) neutral model with empirical dispersal; (G) species-sorting/neutral hybrid model. For each panel, the rows represent the three sites (top to bottom: FTN, QUS, GEO), and the columns are the nine different measures of food-web structure (left to right: Mean and  $SD$  connectance ( $C$ ), mean and  $SD$  linkage density ( $LD$ ), mean and  $SD$  species richness ( $S$ ),  $\beta$  diversity,  $SD$  and mean trophic diversity ( $TD$ )).

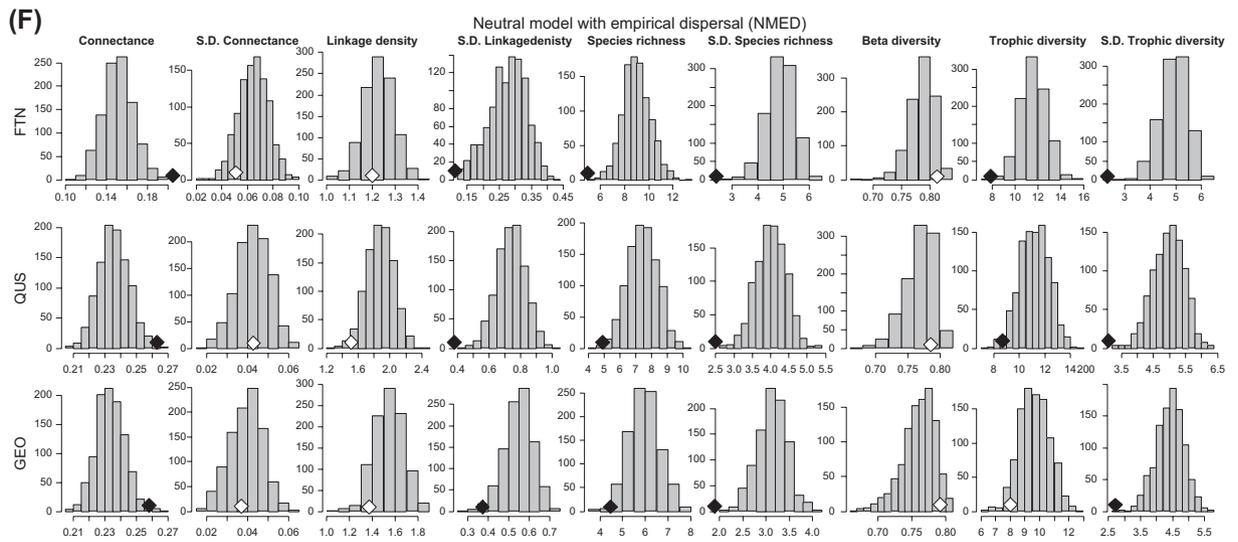
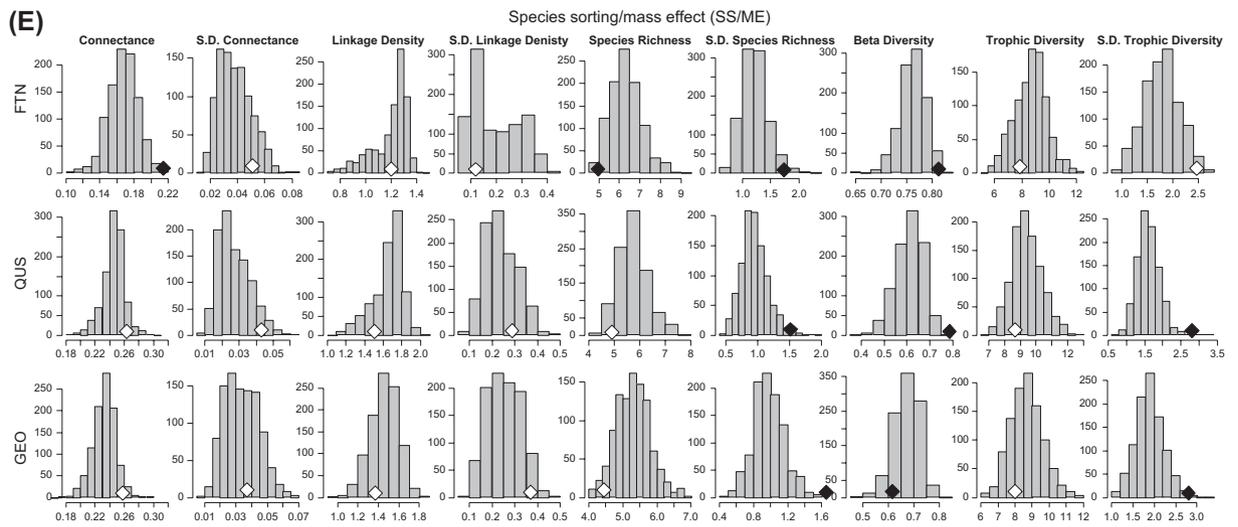
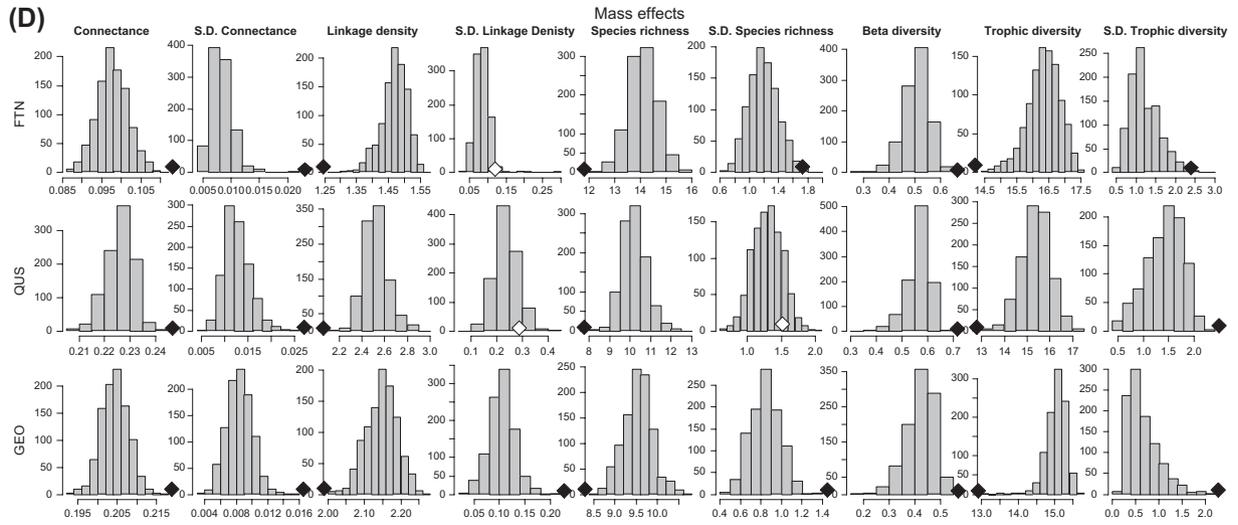


Figure 3. (Continued).

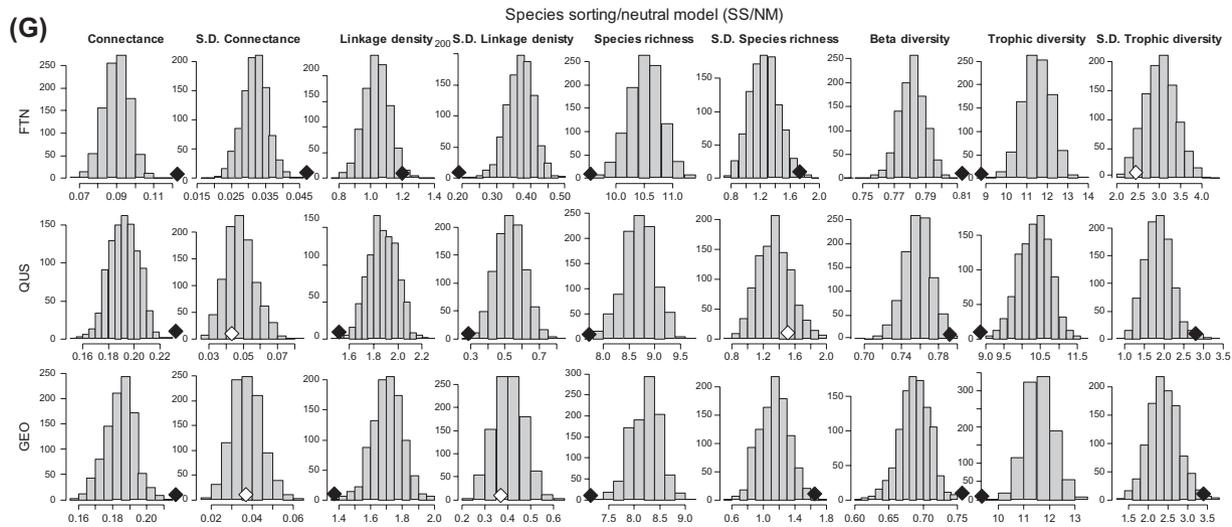


Figure 3. (Continued).

sensitive to changes in  $a_{ij}$  distribution for seven of nine metrics and sensitive to changes in dispersal distribution for two metrics. Species-sorting and patch-dynamics models were not sensitive to changes in dispersal or  $a_{ij}$  distributions (Fig. 4).

Partitioning the variance in the ANOVA's showed that the average proportion of explained variance across all metrics was highest for model type (mean = 40%, SD = 27%). The model type  $\times$   $a_{ij}$  interaction term was the only other factor explaining  $> 5\%$  of the variance (Supplementary material Appendix A6).

## Discussion

Our models represent a new approach to predicting food-web structure using metacommunity theory. We integrated local food-web dynamics and regional-scale processes in a metacommunity framework to develop new insights into potential controls on food-web structure. Although we developed and tested our models using pitcher-plant food webs, our approach can be applied to any well resolved food web for which data are available at multiple locations.

### The role of local interactions

The best models (species-sorting, patch-dynamic, SS/ME) all include the assumption that local-scale interactions (e.g. competition and predation, here within an individual pitcher) are important in structuring metacommunities. Trophic interactions are known to affect species establishment, composition, richness, and ecosystem functioning within the *Sarracenia* food web (Addicott 1974, Cochran-Stafira and von Ende 1998, Miller et al. 2002, Baiser et al. 2012). The classic example from this well-studied food web is the influence of keystone predation (Paine 1969). In pitcher plants, the mosquito *Wyeomyia smithii* is a keystone predator that exerts strong top-down control of species richness and composition of the pitcher-plant food web (Cochran-Stafira and von Ende 1998, Kneitel and Miller 2002, Gotelli and

Ellison 2006). Furthermore, competition between a suite of bacterivorous protozoa alters competitor abundances and growth rates (terHorst 2010).

The species-sorting and patch-dynamic models both assume that local interactions occur more rapidly than dispersal, allowing deterministic outcomes to structure food webs (Liebold et al. 2004, Holyoke et al. 2005). Interestingly, our models could not distinguish whether species differences due to the competition-colonization tradeoff in the patch-dynamics model or a tradeoff between competitive ability and patch quality in the species-sorting model drive food-web structure. This may be the result of focusing largely on food-web properties as opposed to individual species, proportion of patches occupied, or species-abundance distributions. Although the number of patches occupied by a given species or interacting pairs of species may show different responses to patch-dynamics and species-sorting models, this difference does not necessarily extend to food-web structure, in which trophically redundant species can replace one another but network structure of the food web is conserved. How closely variation in species composition and food-web structure are correlated is highly dependent on trophic redundancy in the regional species pool (Baiser et al. 2012).

### The role of regional scale processes

Local interactions clearly play a role in structuring food webs within pitcher plant metacommunities, but our models show that regional-scale processes can influence food-web structure in two ways. First, the frequency of dispersal alters the impact of local interactions. Although the SS/ME model predicted metacommunity structure with similar accuracy to the patch-dynamics and species-sorting models, when we implemented a full mass-effects model, in which species dispersal occurs at the same time-scale as local population dynamics, the resultant metacommunities did not resemble the empirical ones. Rather, the mass effects model metacommunities maintained higher species richness than observed metacommunities due to

the increase in dispersal frequency. Rescue effects due to the increase in dispersal are able to override competitive exclusion and resource over-exploitation, potentially stabilizing predator–prey interactions (Holt 2002). Consequently, food-web structure and composition created by local deterministic processes is altered.

The second way that regional scale processes shape food webs is through species-specific dispersal probabilities.

This is evident from the poor performance of the SS/NM model (Fig. 3g) in which we replaced empirical dispersal probabilities from the species-sorting model (Fig. 3b) with uniform dispersal probabilities. On the other hand, when we employed empirical dispersal probabilities in the absence of local dynamics in the NMED model (Fig. 3f), this model also performed poorly, suggesting that empirical dispersal probabilities in the absence of trophic and

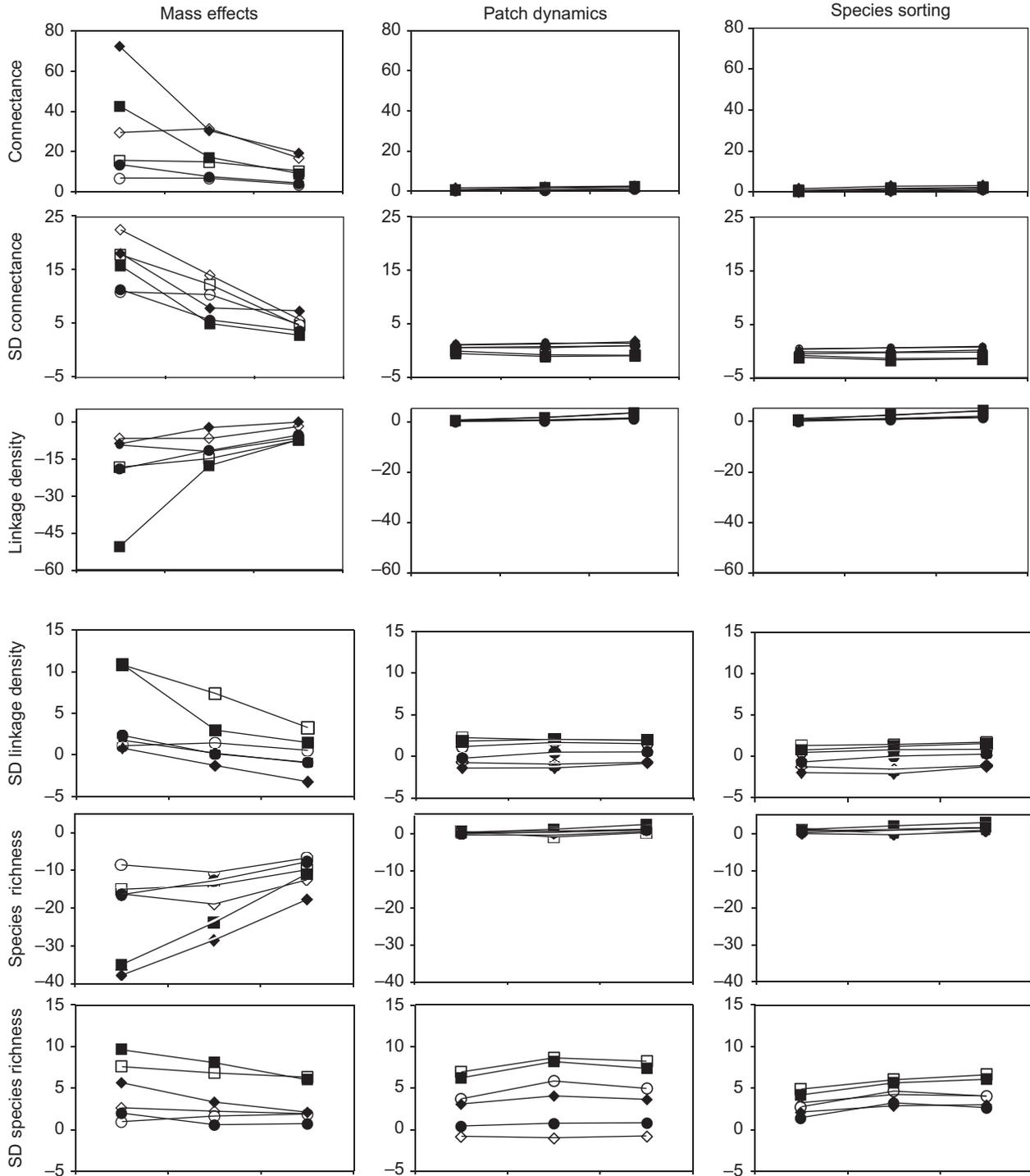


Figure 4. Interaction plots comparing standardized Z-scores of the nine measures of food-web structure as a function of different distribution functions for dispersal (open symbols: empirical; solid symbols: modified empirical [ $E_{mod}$ ] and species' interaction coefficient ( $a_{ij}$ ; along x-axis). Each of the nine metrics is compared across three sites (diamonds: FTN; squares: GEO; circles: QUS) and three metacommunity models (mass effects, patch dynamics, and species sorting).

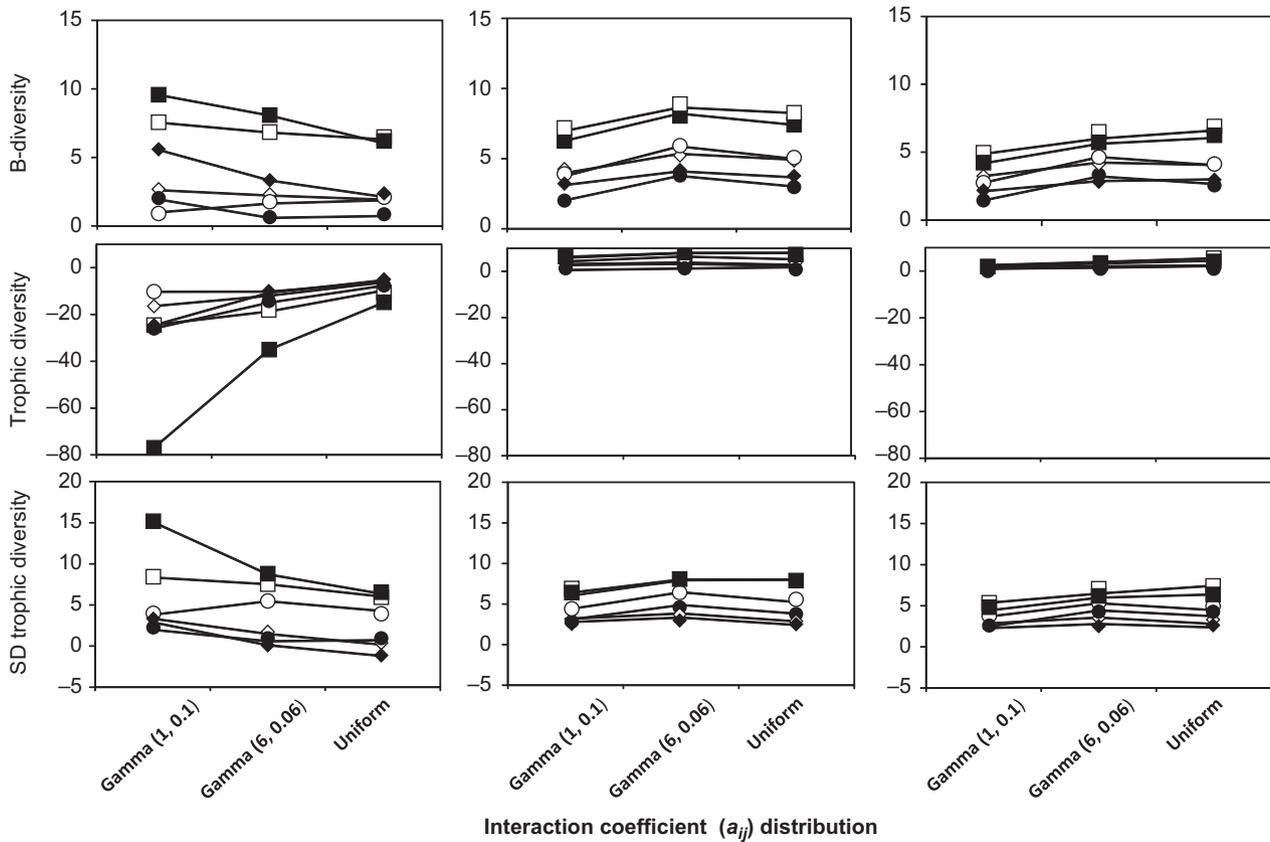


Figure 4. (Continued).

competitive interactions did not structure food webs in pitcher plant metacommunities.

### Model sensitivity

The mass-effects model differed from both the patch-dynamics and species-sorting models in its ability to reproduce empirical estimates of food web structure (Fig. 3). The sensitivity analysis showed that this difference was not due to the specific shape of the dispersal or  $a_{ij}$  distributions. Although the mass-effects model was extremely sensitive to changes in the  $a_{ij}$  distribution, and to a lesser extent the dispersal distribution, the patch-dynamics and species-sorting models were robust to changes in these distributions and reproduced empirical estimates regardless of their shapes. The fact that the two models that more accurately estimated empirical observations are also robust to changes in dispersal and  $a_{ij}$  distributions suggests that the rate of dispersal (frequent in mass effects, infrequent in patch dynamics and species sorting) may be more important than variation in the distribution of dispersal probabilities and interaction coefficients.

### Model failures

All of the metacommunity models, even the best-fit ones, were unable to reproduce variation in species richness and  $TD$ . This, coupled with the consistent underestimation of  $\beta_{sor}$  by all but the NMED model, suggests that simulated

food webs are more similar in species richness and composition than observed food webs in real metacommunities. The lack of variation in  $TD$  is a logical extension of having similar richness and composition across food webs.

An important point that may have influenced our model food webs, and one that we tested with the model sensitivity analysis, was that our empirical dispersal probabilities were based on the observed frequency of establishment for each species across our empirical webs. Thus, they are not a true quantification of the frequency that a given species will reach a pitcher, but implicitly reflect competitive and trophic interactions (e.g. a poor competitor may not be present in many pitchers due to its competitive ability, not infrequent dispersal). As a result, our models that include trophic and competitive dynamics (all but the neutral and NMED) may have implicitly double-counted trophic interactions for certain species. Such double-counting may have resulted in increased rarity for species that are either poor competitors or highly susceptible to predation and increased presence for species that are competitively dominant or efficient predators.

However, model failures point to the type of approach necessary for future studies of food webs in a metacommunity context. We combined metacommunity models in an attempt increase realism, (Louge et al. 2011), but it is unnecessary for all species in a food web to obey the same metacommunity 'rules' (Driscoll and Lindenmayer 2009). This is especially important in food webs because constituent species are more likely to diverge taxonomically

and differ in life history traits (e.g. dispersal ability, range) than they would in communities consisting only of competing species or guilds of functionally similar species. In addition, by randomly sampling interaction and growth rates from statistical distributions, we may have lost the competitive hierarchy among species that can play a non-trivial role in the establishment of rare species, and also missed priority effects that can lead to greater variation in composition and richness lacking in our model metacommunities. Finally, the strength of ecological interactions in the *Sarracenia* web, as well as in other systems, can be altered by evolution in ecological time (terHorst 2010). Such eco–evolutionary interactions can also increase the persistence of rare species and drive variation in composition and species richness.

Our study highlights the challenges of elucidating food-web structure for complex naturally occurring metacommunities. However, fairly simple models were able to accurately reproduce several properties of pitcher plant food webs including connectance, linkage density, trophic diversity, and species richness and provide insight into the relative impacts of local and regional-scale processes.

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Supplementary material (available online as Appendix oik-00005 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix A1–A6.