



Predicting Food-Web Structure With Metacommunity Models

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1 **Research Paper:**

2 **Predicting Food-Web Structure with Metacommunity Models**

3

4 **Benjamin Baiser^{1*}, Hannah L. Buckley^{2§}, Nicholas J. Gotelli^{3†}, Aaron M. Ellison^{1‡}**

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6 ¹*Harvard University, Harvard Forest, 324 N. Main St., Petersham, MA 01366, USA*

7 ²*Department of Ecology, P.O. Box 84, Lincoln University, Canterbury, New Zealand*

8 ³*Department of Biology, University of Vermont, Burlington, VT 05405, USA*

9

10 *Correspondance: B. Baiser, *Harvard University, Harvard Forest, 324 N. Main St., Petersham, MA*

11 *01366, USA, E-Mail: bbaiser@fas.harvard.edu, Phone: 1-978-756-6155, Fax: 1-978-724-3595*

12 §*Hannah.Buckley@lincoln.ac.nz*

13 †*ngotelli@uvm.edu*

14 ‡*aellison@fas.harvard.edu*

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17 *species sorting*

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23 **Abstract**

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

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46 **Introduction**

47 Food-web structure and dynamics play important roles in maintaining species diversity and
48 functioning of ecosystems (Lawler and Morin 1993, Dunne et al. 2002, Duffy et al. 2007).
49 Variation in food-web structure has been linked to habitat size (Post et al. 2000, Gotelli and
50 Ellison 2006, Baiser et al. 2011), productivity (Winemiller 1990, Kaunzinger and Morin 1998),
51 disturbance (McHugh et al. 2010), species interactions (Paine 1969), assembly history (Piechnick
52 et al. 2008), and dynamical constraints such as the instability of longer food chains (Pimm 1982).
53 Although individual drivers such as ecosystem size are highly correlated with certain measures
54 of food-web structure (e.g., Post et al. 2000), variation in food-web structure results from
55 context-dependent interactions among these (and other) drivers operating at both local and
56 regional scales (Holt 2002, Post 2002, McHugh et al. 2010).

57 Ecologists have studied food webs at local scales to understand how biotic and abiotic
58 factors in a particular location influence food-web structure and composition (e.g., Winemiller
59 1990, Martinez 1999, Polis 1991). For example, competitive exclusion and resource exploitation
60 can result in local species losses, whereas keystone predation can facilitate co-existence of
61 species at lower trophic levels (e.g., Paine 1969, Cochran-Stafira and von Ende 1998). Habitat
62 size and productivity influence species richness, composition, and trophic position through
63 species-area and productivity-diversity relationships (Holt et al. 1999, Mittlebach et al. 2001)
64 and species richness is strongly correlated with food-web structure across a variety of well-
65 studied food webs (Riede et al. 2010).

66 Increasingly, regional-scale factors that drive spatial dynamics are being recognized as
67 important determinants of local food-web structure (Holt 2002, Amarasekare 2008, Pillai et al.
68 2010). Dispersal among patches intersects with, for example, heterogeneity in ecosystem size,

69 productivity, and disturbance regimes to influence food-web structure and dynamics (Holt 2002,
70 Holt and Hoopes 2005, Amarasekare 2008, Gouhier et al. 2010). Dispersal can influence food-
71 web structure by stabilizing or destabilizing predator-prey dynamics through spatial subsidies
72 (Holt 2002, Gouhier et al. 2010), determining the number of suitable patches that consumers can
73 colonize (Calcagno 2011, Gravel 2011), providing rescue effects for species that are over-
74 exploited by predators (Holyoke 2000), and providing refuges that allow over-exploited prey
75 species to persist on a regional scale (Huffaker 1958). Moreover, the spatial scale of dispersal
76 can influence food-web structure (Pillai et al. 2011) and habitat heterogeneity can directly affect
77 colonization and extinction dynamics, altering food-web structure across the landscape (Holt
78 2002).

79 Metacommunity theory posits that spatially distinct assemblages are linked through the
80 dispersal of multiple interacting species; it provides a framework for assessing simultaneously
81 the roles that local and regional-scale dynamics play in generating diversity patterns across the
82 landscape (Leibold et al. 2004, Holyoke et al. 2005). So far, metacommunity models and
83 empirical studies have largely focused on assemblages of competing organisms within a single
84 trophic level (Louge et al. 2011). Studies focusing on multi-trophic metacommunities are
85 predominantly restricted to models of simplified webs and trophic motifs (Holt and Hoopes
86 2005, Amarasekare 2008, Gouhier et al. 2010, Pillai et al. 2010; Calcagno et al. 2011, Gravel et al.
87 2011, Massol et al. 2011), but some recently have been extended to complex species-rich webs
88 (Calcagno et al. 2011, Gravel et al. 2011, Pillai et al. 2011). The study of entire food webs in a
89 metacommunity context represents a large gap in our understanding of metacommunities (Louge
90 et al. 2011).

91 Here, we begin to fill this gap by testing the ability of metacommunity models to
92 reproduce empirical patterns of species richness, composition, and network structure of aquatic
93 food webs inhabiting the water-filled leaves of the northern pitcher plant, *Sarracenia purpurea*
94 L. We built metacommunity models based on *patch dynamics*, *species sorting*, *mass effects*, and
95 *neutral dynamics*, each of which makes different assumptions about the relative importance of
96 dispersal, habitat heterogeneity, and species interactions in structuring communities (Table 1;
97 Liebold et al. 2004, Holyoke et al. 2005, Louge et al. 2011). We used these models to explore
98 whether the incorporation of regional-scale processes in a metacommunity framework yielded
99 better predictions of *Sarracenia* food-web structure than do correlations of food-web structure
100 with geographic and climatic variables, which explain at most 40% of the variation in food-web
101 structure (Buckley et al. 2003; 2010, Baiser et al. 2012).

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

109

110 **Study system and empirical data**

111 *The Sarracenia food web*

112 *Sarracenia purpurea* is a long-lived, perennial, carnivorous plant that inhabits nutrient-poor bogs
113 and seepage swamps along the coastal plain of eastern North America, and in bogs and poor fens

114 across the upper Midwestern states and across Canada (Buckley et al. 2010). The plant possesses
115 tubular leaves that open during the growing season, fill with rainwater, and subsequently capture
116 invertebrate prey that serves as the resource base of a food web (Fig. 2) that includes bacteria,
117 protozoa, the bdelloid rotifer *Habrotrocha rosa* Donner, and a suite of obligate arthropods: the
118 mite *Sarraceniopus gibsoni* (Nesbitt), and aquatic larvae of the pitcher-plant mosquito *Wyeomyia*
119 *smithii* (Coq.), the midge *Metriocnemus knabi* Coq. and the sarcophagid fly *Fletcherimyia*
120 *fletcheri* (Aldrich) (Addicott 1974, Heard 1994, Bledzki and Ellison 2003). Less common
121 members of this food web include loricate rotifers, cladocerans, copepods, amphipods,
122 nematodes, and multicellular algae (Addicott 1974, Harvey and Miller 1996, Bledzki and Ellison
123 2003). Feeding interactions in the *Sarracenia* food web center on a detritus “processing chain”
124 (Heard 1994). Prey items that are captured by the plant are shredded by the midge and the
125 sarcophagid fly into particulate organic matter (POM). Bacteria directly decompose prey items
126 and also consume POM. Bacteria are preyed upon by a suite of intraguild predators including
127 protozoa, rotifers, *W. smithii*, and *F. fletcheri*. *Wyeomyia smithii*, and late-instar *F. fletcheri* also
128 consume protozoa, rotifers, and each other, and are the top predators in this five-level food web
129 (Fig. 2).

130 *Sarracenia* food webs are an ideal system with which to test metacommunity theory in a
131 food-web context (Miller and Kneitel 2005). Replicate pitchers provide spatially distinct habitat
132 patches that undergo an assembly process consisting of both active and passive dispersal (Ellison
133 et al. 2003, Kneitel and Miller 2003). The resulting food webs vary at both local and regional
134 spatial scales in species richness, composition, and food-web structure (Buckley et al. 2003;
135 2004; 2010, Baiser et al. 2012). Dispersal rates (Kneitel and Miller 2003), pitcher size and age
136 (Buckley et al. 2010, Baiser et al. 2012), trophic interactions (Goteli and Ellison 2006, Cochran-

137 Stafira et al. 1998), and latitude (Buckley et al. 2003) all are correlated with species richness,
138 composition, and food-web structure.

139

140 *Empirical food web and regional pool data*

141 We collected presence/absence data from 20 pitcher-plant food webs at each of two sites and 19
142 food webs at a third site across the range of *Sarracenia purpurea*. The three sites spanned the
143 range of *S. purpurea*, with one site in the southern part of its range in Georgia (GEO: 32.10 N, -
144 81.60 W), one in the northeast, Québec City (QUS: 46.71 N,-71.27 W), and one in the northwest
145 corner of its range in eastern British Columbia (FTN: 58.49 N, -122.54 W). Data from these
146 three sites were collected as part of a larger effort in which we sampled pitchers at each of 39
147 sites across the range of *S. purpurea* (see Buckley et al. 2003, 2010 for details on site selection,
148 leaf selection, sampling protocol, and a complete list of species found in all food webs).

149 At each site, we sampled first-year pitchers, each on a different plant, that were 3-6
150 weeks old. Our sampling protocol adjusted for the influence of leaf age (i.e., we were not
151 comparing a newly opened leaf with a 2nd year leaf), seasonal differences in dispersal (i.e., each
152 leaf was sampled on the same day at a given site) and explicit spatial structure (i.e., leaves on the
153 same plant have more similar communities than leaves on different plants, but spatial location of
154 plants does not explain variation in pitcher plant communities, Buckley et al. 2004). For
155 modeling purposes, therefore, we defined each metacommunity as the 20 (19 in the case of
156 GEO) pitchers that opened on the same day. As a result, we viewed dispersal as a lottery, in
157 which species colonize from a regional pool (Miller and Kneitel 2005). Each site's regional pool
158 consisted of all species found at that site. Within each regional species pool, we quantified the
159 dispersal probability, G_i (i.e. probability of a species i being drawn from the regional pool and

160 introduced into a pitcher), as the maximum likelihood estimate of a multinomial distribution
161 based on all species presence across all pitchers. The observed measures of food-web species
162 richness, composition, and network structure from metacommunities at each site were quantified
163 for comparison with food webs generated by our metacommunity models. The three sites in this
164 study contained a total of 25 taxa with bacteria aggregated into a single tropho-species (All data
165 are available from the Harvard Forest Data Archive, data set HF-193
166 <http://harvardforest.fas.harvard.edu/data-archive>).

167

168 **Models**

169 *Local population dynamics*

170 We simulated local population dynamics within each pitcher using generalized Lotka–Volterra
171 equations, similar to those used to model local dynamics of competitive (Levin 1974, Wilson
172 1992) and predator-prey metacommunities (Massol et al. 2011). The equations have the
173 following form:

$$174 \quad dX_i / dt = X_i (b_i + \sum a_{ij} X_j) \quad (1)$$

175 where dX_i / dt is the rate of change in biomass X for species i , b_i is the intrinsic growth rate of
176 species i , and a_{ij} is the per capita effect of species j on the per capita growth rate of species i . In
177 this model, consumers cannot establish in a food web in the absence of a prey population, thus
178 $-0.03 < b_i < 0$. The dynamics of the basal resource, prey captured by the pitcher plant, is
179 modeled by a prey-capture function (see *Dynamics of resource availability* below). Recent
180 evidence suggests that the distribution of interaction strengths within a food web is positively
181 skewed, with relatively few strong interactions and many weak ones (Wooten and Emmerson
182 2005). Therefore, a_{ij} , the effect of a predator X_i on the growth rate of prey species X_j was

183 sampled randomly from a gamma distribution ($k=1, \theta=0.1$) and multiplied by -1 ; a_{ji} , the effect
184 on the predator, was also sampled randomly from a gamma distribution ($k=1, \theta=0.1$). For
185 interspecific competition, a_{ij} and a_{ji} were randomly chosen values from a gamma distribution (k
186 $=1, \theta=0.1$) and multiplied by -1 ; intraspecific competition, a_{ii} , was set to -1 for all species. The
187 structure of the interaction matrix (i.e. who eats whom and who competes with whom) was based
188 on our observations and published accounts of trophic and competitive interactions in the
189 *Sarracenia* food web (Addicott 1974, Heard 1994, Cochran-Stafira & von Ende 1998, Miller et
190 al. 2002). Species were seeded into each pitcher at an (arbitrary) biomass of 0.02 and populations
191 went locally extinct if their biomasses dropped below 0.01. The pitcher-plant mosquito
192 (*Wyeomyia smithii*) and midge (*Metriocnemus knabi*) pupated and eclosed from a pitcher once
193 their biomass reached 0.1. The pitcher plant system is a non-equilibrium system (Ellison et al.
194 2003) and our goal was to compare food webs after approximately the same amount of species
195 interaction time. Therefore, we simulated local dynamics for 40 days (= pitcher leaf age) to
196 approximate the amount of time during which species interacted before we sampled the
197 *Sarracenia* webs (~3-6 weeks). Each day in the model consisted of ten iterations of Lotka–
198 Volterra dynamics, which is the estimated number of generations that the organism with the
199 fastest turnover (bacteria) experiences, yielding 400 model iterations. Food-web structural
200 characteristics were determined for the web resulting from these 400 iterations.

201

202 *Dynamics of resource availability*

203 The basal resource of the *Sarracenia* food web is detritus, which consists of carcasses of insects
204 that are captured by the plant. Empirical studies have shown that prey capture is a function of
205 pitcher size and age (Cresswell 1993, Heard 1998), rainfall and subsequent evaporation of rain

206 (Kingsolver 1979), and morphological characteristics of pitchers (Cresswell 1993; Bennett and
 207 Ellison 2009). We modeled prey capture using a set of coupled equations that included functions
 208 of pitcher age (L), amount of water in the pitcher (W), and air temperature (T) (see Supplemental
 209 Materials Appendix 1 for example prey-capture curves), which affects not only evaporation of
 210 water but also activity of insect prey. Total prey capture, for which daily biomass was
 211 normalized to scale between 0 and 1, was set equal to the product of L , W , and T :

$$212 \text{ capture} = LWT \quad (2)$$

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

$$214 f(d, k, \theta) = \frac{d^{k-1} e^{-d/\theta}}{(k-1)! \theta^k} \quad (3)$$

215 where d (days) ranges from 1 to n (the maximum lifespan of the pitcher in the model; $n = 40$).

216 The other parameters of this distribution are θ , the scale parameter, which in this case sets the
 217 age of the leaf (in days) at which prey capture reaches its maximum, and k , the shape parameter
 218 for the gamma distribution. Both θ and k were selected to approximate empirical prey capture
 219 curves (Heard 1998).

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

$$222 R_v = R_f A_p \quad (4)$$

$$223 W = R_v - (E + M) \quad (5)$$

224 In these two equations, rain accumulation (R_v , in cm^3) is the product of rainfall (R_f , in cm/day)
 225 and area of the pitcher opening (A_p , in cm^2); W equals R_v minus loss of water due to evaporation
 226 (E) and mining (M) by larvae of the noctuid moth *Exyra fax* Grt., both in cm^3/day . Over time,
 227 leaf mining by *E. fax* can completely drain leaves, leaving them without a food web. Daily R_f

228 values were taken from the weather station nearest to each site (<100 km) in 2001, and A_p was
229 the mean area of the pitcher opening at each site (Ellison et al. 2004). Loss of water due to
230 evaporation, E , was set to $0.04 \text{ cm}^3/\text{day}$. The probability that moth herbivory would occur in a
231 given plant was set equal to 0.5 (Atwater et al. 2006) and the loss of water due to moth herbivory
232 (M) was held constant at $0.01 \text{ cm}^3/\text{day}$. Finally, temperature (T) was assumed to have a linear
233 relationship with prey capture, because insect activity and mobility increased with temperature
234 across the range of temperatures observed at our three sites (Lynch et al. 1980).

235

236 *Metacommunity dynamics*

237 We modeled the assembly of pitcher plant metacommunities containing 19 or 20 local food webs
238 depending on the site (Fig. 1). The assumptions of each metacommunity model (Table 1) were
239 incorporated by altering specific aspects of local dynamics. For patch similarity, we altered
240 resource availability such that similar patches had the same amount of resources while different
241 patches varied in resource availability. Species differences related to dispersal differences (patch
242 dynamics) and patch differences (species sorting and mass effects) were generated by adjusting
243 the Lotka-Volterra competition coefficients, a_{ij} and a_{ji} . Finally, we altered the relative time scale
244 of local and regional dynamics by changing the number of Lotka-Volterra iterations between
245 dispersal events. In addition to the four basic metacommunity models, we also examined three
246 hybrid models that combined assumptions of the single-factor models. Model code and input
247 files are available from the Harvard Forest Data Archive, dataset HF-193.

248

249 *Patch-dynamic model*

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

$$257 \quad a_{ij} = -\alpha \quad (6)$$

$$258 \quad a_{ji} = -\alpha(1 - p_{ij}) \quad (7)$$

259
260 Here, α is a base-line competition coefficient shared by any two competing species and was
261 randomly drawn from a gamma distribution ($k=1, \theta=0.1$). Parameter p_{ij} is the dispersal
262 difference calculated by subtracting the dispersal rate of the inferior disperser (species j) from
263 that of the superior disperser (species i); because dispersal rates are frequencies; $0 < p < 1$. For
264 species j , a_{ij} is equal to α (Eqn. 6). For species i , the competition coefficient, a_{ji} , increased
265 linearly (i.e. became less negative, resulting in a weaker competitor) with the complement of p_{ij}
266 (Eqn. 7). The dispersal-based competition coefficients (a_{ij}, a_{ji}) are state variables in the Lotka-
267 Volterra equations that describe local dynamics (see *Local population dynamics* above). We met
268 the final assumption of patch-dynamics models—that local population dynamics occur at a
269 greater rate than species dispersal events—by introducing species at a rate of 1 every 2.5 days for
270 a total of 16 introductions. Twenty-five iterations of local population dynamics were simulated
271 between each introduction.

272

273 *Species-sorting model*

274 The species-sorting approach assumes that 1) patches are different; 2) different species do well in
275 different types of patches; and 3) local population dynamics occur on a shorter time-scale than
276 assembly dynamics (Table 1; Leibold et al. 2004, Holyoak et al. 2005). We altered patches by
277 allowing resource dynamics to vary along a continuous gradient from pitchers with low prey
278 capture (maximum daily prey capture ~0.006 g/day) to pitchers with high (maximum daily prey
279 capture ~0.6 g/day; see Supplementary Materials Appendix 1). Species were randomly assigned
280 to either increase (Eqn. 8, below) or decrease (Eqn. 9, below) their competitive ability as a
281 function of resource levels. N_{\max} is the maximum amount of resources caught by a pitcher in one
282 day and, as in the patch-dynamic model, α is a competition coefficient randomly drawn from a
283 gamma distribution ($k = 1, \theta = 0.1$). For species whose competitive abilities increase with
284 resource availability;

285
$$a_{ij} = -\alpha N_{\max} \tag{8}$$

286 For species whose competitive abilities decrease with resource availability;

287
$$a_{ij} = -\alpha(1 - N_{\max}) \tag{9}$$

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

289

290 *Mass-effects model*

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

296

297 *Neutral model*

298 The neutral model assumes no differences among dispersal abilities or among patch suitabilities
299 for any species (Holyoak et al. 2005). As a result, for this model, we did not simulate local
300 population dynamics, and species dispersal probabilities were set to be uniformly equal.

301 Although the “neutral model of biodiversity” works at the level of the individual, not at the level
302 of a species, we are using “neutral model” here in the sense of a null model with no differences
303 among species to contrast with species-specific differences in the other metacommunity models.

304 However, in a true neutral model, differences among species in dispersal abilities would appear
305 as a consequence of different abundances of each species in local communities. These

306 differences do not arise here, because our “neutral model” does not have abundances (no local
307 population dynamics and uniformly equal dispersal probabilities); these assumptions are relaxed
308 our hybrid neutral model with empirical dispersal (see below). To assemble pitcher-plant food
309 webs in this neutral model, we randomly selected a value from the range of species richness in
310 the empirical data set and randomly selected that number of species from the species pool.

311 Bacteria and detritus were present in every neutral web because they were present in every
312 empirical web and to avoid the unrealistic scenario of a consumer being present without a prey
313 item (i.e. every species in the regional pool preys upon detritus, bacteria, or both).

314

315 *Hybrid Models*

316 Each of the four metacommunity models described above include specific mechanisms that can
317 drive variation in metacommunity structure and dynamics (Leibold et al. 2004, Holyoak et al
318 2005). Empirical metacommunities are unlikely to be perfectly described by any single model

319 (Louge et al. 2011), so we also created three hybrid models that combine assumptions from the
320 different metacommunity perspectives.

321

322 *Species sorting/mass effects (SS/ME)*

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

330

331 *Neutral model with empirical dispersal (NMED)*

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

338

339 *Species sorting/neutral model (SS/NM)*

340 The SS/NM model is the alternative to the NMED model, and tests whether competitive and
341 trophic interactions that are structured by patch differences maintain metacommunity structure in

342 the absence of species-specific dispersal patterns. To test this, we ran the species-sorting model
343 with uniform dispersal probabilities to create the SS/NM model.

344

345 *Entire model simulations*

346 A metacommunity simulation consisted of local dynamics for 20 food webs (19 for GEO), where
347 parameters were drawn from statistical distributions (Supplemental Material Appendix 2).

348 Designation of species as superior competitors at either high or low resources levels (for the
349 species-sorting and mass-effects models) and empirically based parameters (dispersal

350 probabilities, interaction matrix) were held constant across all webs *within* a simulation. We ran
351 each of the seven metacommunity models for each of the three sites, yielding a total of 21

352 models, each of which was then simulated 1,000 times. To maintain generality *across*

353 simulations, parameters drawn from statistical distributions (Supplemental Material Appendix 2)

354 and species designation as superior competitors in either high or low resources levels (for the

355 species-sorting and mass effects models) were resampled for each simulation. Regional species

356 pools and dispersal probabilities were held constant across all 1,000 simulations for a given

357 model at a given site. We conducted all simulations using Mathematica 8.0.

358

359 *Metrics of food-web structure and statistical analysis of model fit*

360 For each simulated metacommunity, we calculated the mean and standard deviation of species

361 richness, connectance ($C = L/S^2$; where L is the number of links and S is the number of species),

362 linkage density ($LD = L/S$), and TD , a trophic based measure of functional diversity (Petchey et

363 al. 2008). We also calculated the multi-site Sørensen index, $\beta_{sør}$, (Baselga 2010) to quantify β -

364 diversity. We compared the observed value of each statistic for the empirical data with model

365 distributions from the 1,000 simulations to calculate a p-value for each metacommunity model at
366 each site. If $0.025 \geq p\text{-value} \leq 0.975$, we concluded that the model predictions fit the observed
367 data. When $p < 0.025$, the observed statistic was significantly less than expected from the
368 metacommunity model and when $p > 0.975$, the observed statistic was significantly greater than
369 expected from the metacommunity model.

370

371 *Model Sensitivity*

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

383 We explored how varying the initial dispersal and interaction coefficient distributions
384 influenced within-model sensitivity for the three single-factor metacommunity models that
385 contained these parameters (species sorting, patch dynamics, mass effects). We modified the
386 multinomial dispersal distribution, by increasing dispersal probabilities for species found in less

387 than 25% of pitchers by 20% and decreasing species found in greater than 25% of pitchers by
388 20%. The new dispersal distribution is called *Emod* (empirical modified). We also drew a_{ij} from
389 a uniform distribution and a gamma distribution ($k=6, \theta=0.05$) that is roughly normal. We ran
390 simulations that crossed our two dispersal distributions with our three a_{ij} distributions for species
391 sorting, patch dynamics, mass effects models at each site. This yielded 45 new models, in
392 addition to the 15 models from the original set of simulations. Each model was simulated 1000
393 times.

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

396

$$397 \quad z = \frac{\text{observed estimate} - \text{mean of model distribution}}{\text{standard deviation of model distribution}} \quad (10)$$

398

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

407

408 **Results**

409 *Single-factor metacommunity models*

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

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

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

430

431 *Hybrid models*

432 The species-sorting/mass-effects (SS/ME) model was the best hybrid model and fit the observed
433 data nearly as well as the species-sorting and patch-dynamic models (Fig. 3e). The SS/ME model
434 correctly estimated mean S for two of the three sites and TD for all sites (Fig. 3e). Similar to the
435 species-sorting and patch-dynamic models, the SS/ME model accurately fit the observed values
436 for the mean and variation of LD and C , with the exception of mean C for the site in British
437 Columbia (Fig. 3e). However, the SS/ME model could not reproduce $\beta_{s\text{or}}$ or variation in S for
438 any site and observed values for variation in TD did not fall within model distribution for two of
439 the three sites (Fig. 3e). Community metrics that did not fall within SS/ME distributions
440 consistently exceeded the model distributions, except for mean S at the FTN site (Fig. 3e).

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

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

452 Overall, the patch-dynamic, species-sorting, and SS/ME effects models were generally
453 successful in reproducing mean S , LD , variation in C and LD , and TD of the empirical food
454 webs. However, these models, along with the other four models, did a poor job in reproducing

455 the observed variation in S and TD of the real *Sarracenia* food webs. In addition, the NMED was
456 the only model to accurately reproduce $\beta_{s\sigma r}$ for all sites (Fig. 3f).

457

458 *Model sensitivity*

459 Analysis of variance revealed that altering the shape of the distributions of dispersal and species-
460 interaction coefficient a_{ij} significantly changed the estimates of food-web structure, but only for
461 the mass-effects model. Overall, *model type* \times a_{ij} explained 11% (SD = 7%) and *model type* \times
462 *dispersal* explained 3% (SD = 2%) of the variation in model fit, respectively. The *model type* \times
463 a_{ij} term was significant ($p < 0.05$) for every food web metric except $\beta_{s\sigma r}$ and LD (Fig 4;
464 Supplemental Material Appendix 3). Tukey's HSD showed that only comparisons within the
465 mass-effects models were significantly different ($p < 0.05$) across all metrics when the *model type*
466 \times a_{ij} term was significant (Fig 4; Supplemental Material Appendix 4). The *model type* \times
467 *dispersal* term was significant ($p < 0.05$) for the food web metrics variance in C , S , variance in S ,
468 and $\beta_{s\sigma r}$ (Supplemental Material Appendix 3). Tukey's HSD showed that only comparisons
469 within the mass-effects models were significantly different ($p < 0.05$) for variance in C and S ,
470 while within model pairwise comparisons were not significant for variance in S , and $\beta_{s\sigma r}$ (Fig 4;
471 Supplemental Material Appendix 5). Overall, mass effects models were sensitive to changes in
472 a_{ij} distribution for seven of nine metrics and sensitive to changes in dispersal distribution for two
473 metrics. Species-sorting and patch-dynamics models were not sensitive to changes in dispersal or
474 a_{ij} distributions (Fig 4).

475 Partitioning the variance in the ANOVA's showed that the average proportion of
476 explained variance across all metrics was highest for *model type* (mean = 40%, SD = 27%). The

477 *model type* × a_{ij} interaction term was the only other factor explaining > 5% of the variance
478 (Supplemental Material Appendix 6).

479

480 **Discussion**

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

487

488 *The role of local interactions*

489 The best models (species-sorting, patch-dynamic, SS/ME) all include the assumption that local-
490 scale interactions (e.g., competition and predation, here within an individual pitcher) are
491 important in structuring metacommunities. Trophic interactions are known to affect species
492 establishment, composition, richness, and ecosystem functioning within the *Sarracenia* food web
493 (Addicott 1974, Cochran-Stafira et al. 1998, Miller et al. 2002, Baiser et al. 2012). The classic
494 example from this well-studied food web is the influence of keystone predation (Paine 1969). In
495 pitcher plants, the mosquito, *Wyeomyia smithii*, is a keystone predator that exerts strong top
496 down control of species richness and composition of the pitcher-plant food web (Cochran-Stafira
497 and von Ende 1998, Kneitel and Miller 2002, Gotelli and Ellison 2006). Furthermore,
498 competition between a suite of bacterivorous protozoa alters competitor abundances and growth
499 rates (terHorst 2010).

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

513

514 *The role of regional scale processes*

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

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

527 The second way that regional scale processes shape food webs is through species-specific
528 dispersal probabilities. This is evident from the poor performance of the SS/NM model (Fig. 3g)
529 in which we replaced empirical dispersal probabilities from the species-sorting model (Fig. 3b)
530 with uniform dispersal probabilities. On the other hand, when we employed empirical dispersal
531 probabilities in the absence of local dynamics in the NMED model (Fig. 3f), this model also
532 performed poorly, suggesting that empirical dispersal probabilities in the absence of trophic and
533 competitive interactions did not structure food webs in pitcher plant metacommunities.

534

535 *Model Sensitivity*

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

545 more important than variation in the distribution of dispersal probabilities and interaction
546 coefficients.

547

548 *Model failures*

549 All of the metacommunity models, even the best-fit ones, were unable to reproduce variation in
550 species richness and *TD*. This, coupled with the consistent underestimation of β_{SOR} by all but the
551 NMED model, suggests that simulated food webs are more similar in species richness and
552 composition than observed food webs in real metacommunities. The lack of variation in *TD* is a
553 logical extension of having similar richness and composition across food webs.

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

565 However, model failures point to the type of approach necessary for future studies of
566 food webs in a metacommunity context. We combined metacommunity models in an attempt
567 increase realism, (Louge et al. 2011), but it is unnecessary for all species in a food web to obey

568 the same metacommunity “rules” (Driscoll and Lindenmayer 2009). This is especially important
569 in food webs because constituent species are more likely to diverge taxonomically and differ in
570 life history traits (e.g. dispersal ability, range) than they would in communities consisting only of
571 competing species or guilds of functionally similar species. In addition, by randomly sampling
572 interaction and growth rates from statistical distributions, we may have lost the competitive
573 hierarchy among species that can play a non-trivial role in the establishment of rare species, and
574 also missed priority effects that can lead to greater variation in composition and richness lacking
575 in our model metacommunities. Finally, the strength of ecological interactions in the *Sarracenia*
576 web, as well as in other systems, can be altered by evolution in ecological time (terHorst 2010).
577 Such eco-evolutionary interactions can also increase the persistence of rare species and variation
578 in composition and species richness.

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

584

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590 **Literature Cited**

591 Addicott, J. F. 1974. Predation and prey community structure: an experimental study of the effect of
592 mosquito larvae on the protozoan communities of pitcher plants. – Ecology 55: 475–492.

593 Amarasekare, P. 2008. Spatial dynamics of food webs. – Annu. Rev. Ecol. Evol. Syst. 39: 479–500.

594 Atwater, D. Z. et al. 2006. Spatial distribution and impacts of moth larvae on northern pitcher plants. – N.
595 Nat. 13: 43–56.

596 Baiser, B., et al. 2012. Geographic variation in network structure of a Nearctic aquatic food web. – Global
597 Ecol. Biogeogr. 21: 579–591.

598 Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. – Global Ecol.
599 Biogeogr. 19: 134–14.

600 Bennett, K. F. and Ellison, A. M. 2009. Nectar, not colour, may lure insects to their death. – Biol. Lett. 5:
601 469–472.

602 Bledzki, L. A. and Ellison, A. M. 2003. Diversity of rotifers from northeastern USA bogs with new species
603 records for North America and New England. – Hydrobiol. 497: 53–62.

604 Buckley, H. L. et al. 2003. Reverse latitudinal trends in species richness of pitcher-plant food webs. –
605 Ecol. Lett. 6: 825–829.

606 Buckley, H. L. et al. 2004. Small-scale patterns in community structure of *Sarracenia purpurea* inquiline
607 communities. – Comm. Ecol. 5: 181–188.

608 Buckley, H. L. et al. 2010. Local- to continental-scale variation in the richness and composition of an
609 aquatic food web. – Global Ecol. Biogeogr. 19: 711–723.

610 Calcagno V., et al. 2011. Constraints on food chain length arising from regional metacommunity
611 dynamics. – Proc. R. Soc. B doi:10.1098/rspb.2011.0112.

612 Cochran-Stafira, D. L. et al. 1998. Integrating bacteria into food webs: studies with *Sarracenia purpurea*
613 inquilines. – Ecology 79: 880–898.

614 Cresswell, J. E. 1993. The morphological correlates of prey capture and resource parasitism in pitchers of
615 the carnivorous plant *Sarracenia purpurea*. – Am. Mid. Nat. 129: 35–41.

616 Driscoll, D. A., and D. B. Lindenmayer. 2009. Empirical tests of metacommunity theory using an
617 isolation gradient. – *Ecol. Mon.* 79: 485–501.

618 Duffy J. E., et al. 2007. The functional role of biodiversity in ecosystems: incorporating trophic
619 complexity. – *Ecol. Lett.* 10: 522–38.

620 Dunne, J. A., et al. 2002. Network structure and biodiversity loss in food webs: robustness increases with
621 connectance. – *Ecol. Lett.* 5: 558–567.

622 Ellison, A. M., et al. 2003. The evolutionary ecology of carnivorous plants. – *Adv. Ecol. Res.* 33: 1–74.

623 Ellison, A. M. et al. 2004. Morphological variation in *Sarracenia purpurea* (Sarraceniaceae): geographic,
624 environmental, and taxonomic correlates. – *Am. J. Bot.* 91: 1930–1935.

625 Gotelli, N. J., and Ellison, A. M. 2004. *A Primer of Ecological Statistics*. Sinauer Associates.

626 Gotelli, N. J., and Ellison, A. M. 2006. Food-web models predict species abundance in response to habitat
627 change. – *PLoS Biol.* 44: e324.

628 Gravel, D., E. et al. 2011. Persistence increases with diversity and connectance in trophic
629 metacommunities. – *PLoS ONE* 6: e1937.

630 Gouhier, T. C. et al. 2010. Synchrony and stability of food webs in metacommunities. – *Am. Nat.* 175:
631 E16–E34.

632 Harvey, E. and Miller, T. E. 1996. Variance in composition of inquiline communities in leaves of
633 *Sarracenia purpurea* L. on multiple spatial scales. – *Oecologia* 108: 562–566.

634 Heard, S. B. 1994. Pitcher plant midges and mosquitoes: a processing chain commensalism. – *Ecology*
635 75: 1647–1660.

636 Heard, S. B. 1998. Capture rates of invertebrate prey by the pitcher plant, *Sarracenia purpurea* L. – *Am.*
637 *Mid. Nat.* 139: 79–89.

638 Holt, R. D. et al. 1999. Trophic rank and the species-area relationship. – *Ecology* 80: 1495–1505.

639 Holt, R. D. 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. –
640 *Ecol. Res.* 17: 261-273.

641 Holt, R. D. and Hoopes, M. F. 2005. Food web dynamics in a metacommunity context. - In Holyoak,
642 M.et al. (eds.) Metacommunities: Spatial Dynamics and Ecological Communities. University of
643 Chicago Press, pp 68–93.

644 Holyoak, M. 2000. Habitat subdivision causes changes in food web structure. – Ecol. Lett. 3: 509–515.

645 Holyoak, M. et al. 2005. Metacommunities: a framework for large-scale community ecology. - In
646 Holyoak, M.et al. (eds.) Metacommunities: Spatial Dynamics and Ecological Communities.
647 University of Chicago Press, pp 1–31.

648 Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University
649 Press, Princeton, N.J.

650 Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey
651 oscillations. – Hilgardia 27: 343–383.

652 Kaunzinger, C. M. K. and Morin, P. J. 1998. Productivity controls food-chain properties in microbial
653 communities. – Nature 395: 495–497.

654 Kingsolver, J. G. 1979. Thermal and hydric aspects of environmental heterogeneity in the pitcher
655 plant mosquito. – Ecol. Mon. 49: 357-376.

656 Kneitel, J. M. and Miller, T. E. 2002. Resource and top predator regulation in the pitcher plant
657 (*Sarracenia purpurea*) inquiline community. – Ecology 83: 680–688.

658 Kneitel, J. M. and Miller, T. E. 2003. Dispersal rates affect species composition in metacommunities of
659 *Sarracenia purpurea* inquilines. – Am. Nat. 162: 165–171.

660 Lawler, S. P. and Morin, P. J. 1993. Food web architecture and population dynamics in laboratory
661 microcosms of protists. – Am. Nat. 141: 675–686.

662 Leibold, M. A.et al. 2004. The metacommunity concept: a framework for multi-scale community ecology.
663 – Ecol. Lett. 7: 601–613.

664 Levin, S. A. 1974. Dispersion and population interactions. – Am. Nat. 108:207–228.

665 Lynch, J. et al. 1980. Foraging patterns in three sympatric forest ant species, *Prenolepis imparis*,
666 *Paratrecha melanderi* and *Aphaenogaster rudis* (Hymenoptera: Formicidae). – *Ecol. Ent.* 5: 353-
667 37.

668 Logue, J. B. et al. 2011. Empirical approaches to metacommunities: a review and comparison with theory.
669 – *Trends Ecol. Evol.* 26: 482–491.

670 Massol, F. et al. 2011. Linking community and ecosystem dynamics through spatial ecology. – *Ecol. Lett.*
671 14: 313–323.

672 Martinez N. D. 1991. Artifacts or attributes - effects of resolution on the Little-Rock Lake food web. –
673 *Ecol. Mon.* 61: 367–392.

674 McHugh, P. A. et al. 2010. Dual influences of ecosystem size and disturbance on food chain length in
675 streams. – *Ecol. Lett.* 13: 881–890.

676 Miller, T. E., L. Horth, and R. H. Reeves. 2002. Trophic interactions in the phytotelmata communities of
677 the pitcher plant, *Sarracenia purpurea*. – *Comm. Ecol.* 109–116.

678 Miller, T. E., and Kneitel, J. M. 2005. Inquiline communities in pitcher plants as prototypical
679 metacommunities. - In Holyoak, M. et al. (eds.) *Metacommunities: Spatial Dynamics and*
680 *Ecological Communities*. University of Chicago Press, pp 122–145.

681 Mittelbach, G. G. et al. 2001. What is the observed relationship between species richness and
682 productivity? – *Ecology* 82: 2381–2396.

683 Paine, R. T. 1969. A note on trophic complexity and community stability. – *Am. Nat.* 103: 91–93.

684 Piechnik, D.A. et al. 2008. Food-web assembly during a classic biogeographic study: species “trophic
685 breadth” corresponds to colonization order. – *Oikos* 117: 665–67.

686 Petchey O. L. et al. 2008. Trophically unique species are vulnerable to cascading extinction. – *Am. Nat.*
687 171: 568–579.

688 Pillai P. et al. 2010. A patch-dynamic framework for food web metacommunities. – *Theor. Ecol.* 3: 223–
689 237.

690 Pillai P. et al. 2011. Metacommunity theory explains the emergence of food web complexity. – *Proc. Natl*

691 Acad. Sci. USA 108: 19293–19298.

692 Pimm, S. L. 1982. Food Webs. Chapman and Hall, London.

693 Polis, G. A. 1991. Complex Desert food webs: an empirical critique of food web theory. – Am. Nat. 138:
694 123–155.

695 Post, D. M. et al. 2000. Ecosystem size determines food-chain length in lakes. – Nature 405: 1047–1049.

696 Post, D. M. 2002. The long and short of food-chain length. – Trends Ecol. Evol. 17: 269–277.

697 Riede, J. O. et al. 2010. Scaling of food web properties with diversity and complexity across ecosystems.
698 – Adv. Ecol. Res. 42: 139–170.

699 terHorst, C. P. 2010. Evolution in response to direct and indirect ecological effects in pitcher plant
700 inquiline communities. – Am. Nat. 176: 675–685.

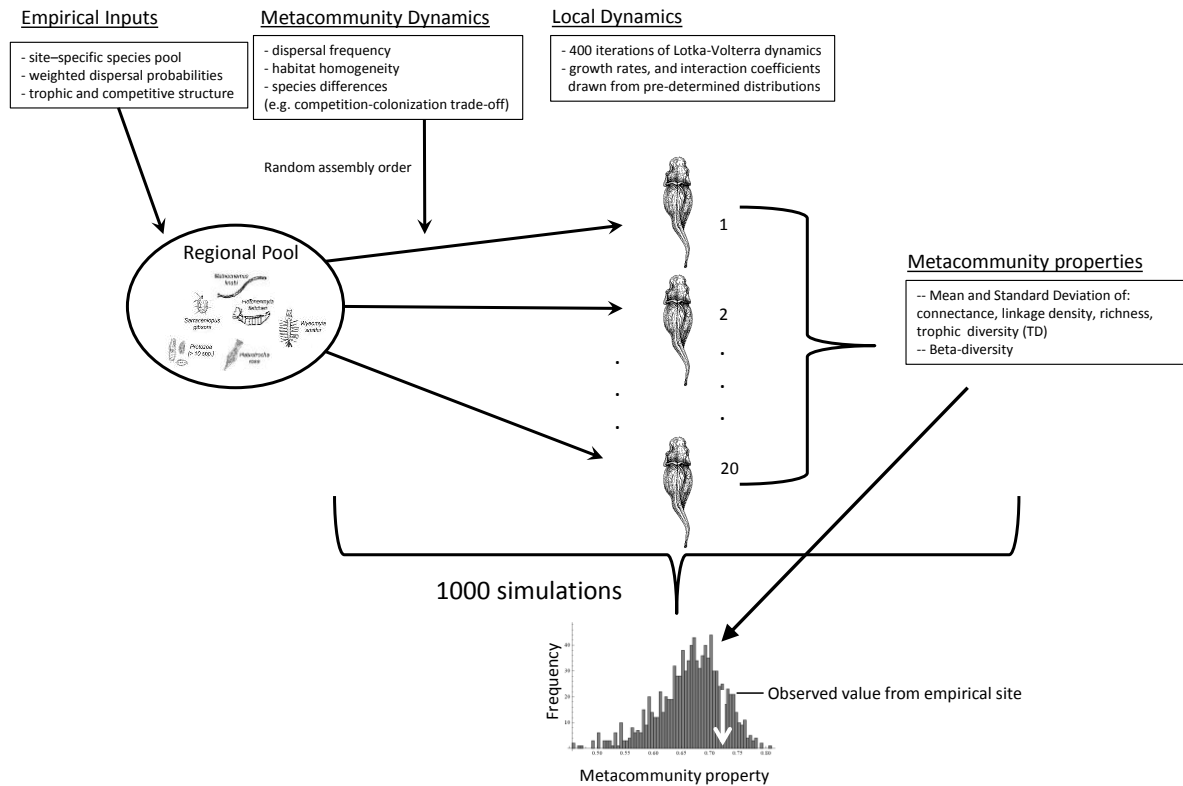
701 Wilson, D. S. 1992. Complex interactions in metacommunities, with implications for biodiversity and
702 higher levels of selection. – Ecology 73: 1984–2000.

703 Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. – Ecol. Mon.
704 60: 331–367.

705 Wootton, J. T. and Emmerson, M. C. 2005. Measurement of interaction strength in nature. – Annu. Rev.
706 Ecol. Evol. Syst. 36: 419–44.

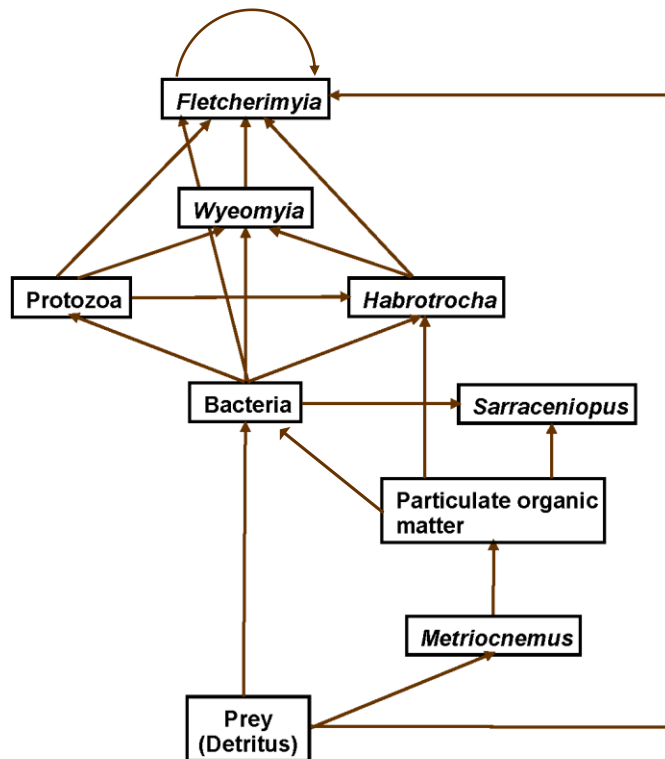
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709

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



719

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

727

728

729 **Figure 3.** Metacommunity model distributions for pitcher plant food web characteristics. Each
730 distribution consists of 1000 simulated values from a specific metacommunity model and site.
731 Diamonds indicate the location of the empirically observed value within the model distribution.
732 A white diamond (\diamond) indicates that the observed value fell within 95% of the model estimates, a
733 $0.025 \geq p\text{-value} \leq 0.975$. A black diamond (\blacklozenge) indicates that the observed value was greater or
734 less than 95% of the model estimates, a $0.025 < p\text{-value} > 0.975$. Partial black diamonds indicate
735 that the observed value fell completely outside the model distribution. A: Patch-dynamic models;
736 B: Species-sorting models; C: Neutral model; D: Mass-effects model; E: Species-sorting/mass-
737 effects hybrid model; F: Neutral model with empirical dispersal; G: Species-sorting/neutral
738 hybrid model. For each panel, the rows represent the three sites (top to bottom: FTN, QUS,
739 GEO), and the columns are the nine different measures of food-web structure (left to right: Mean
740 and SD connectance (C), mean and SD linkage density (LD), mean and SD species richness (S), β
741 diversity, SD and mean trophic diversity (TD)).

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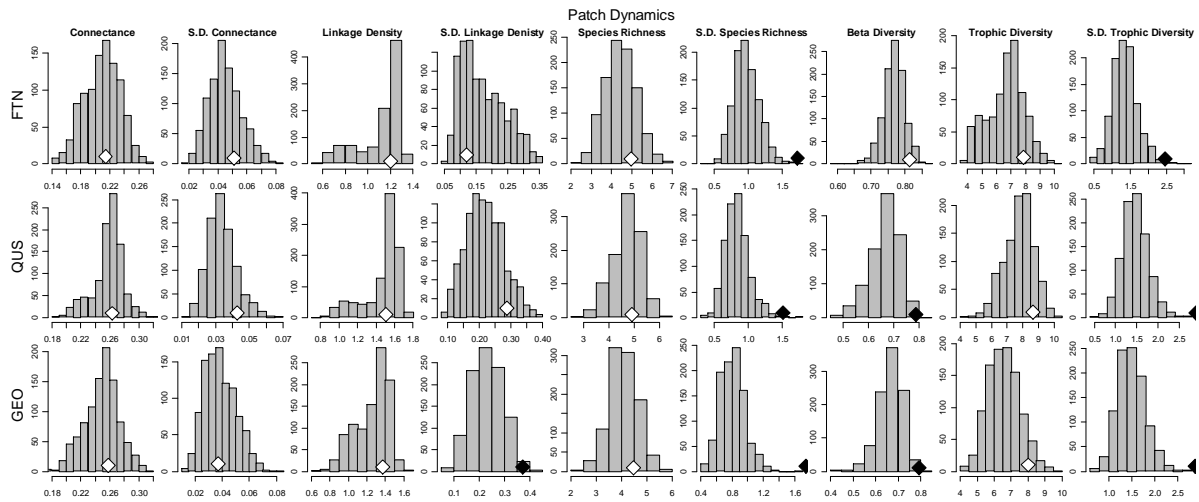
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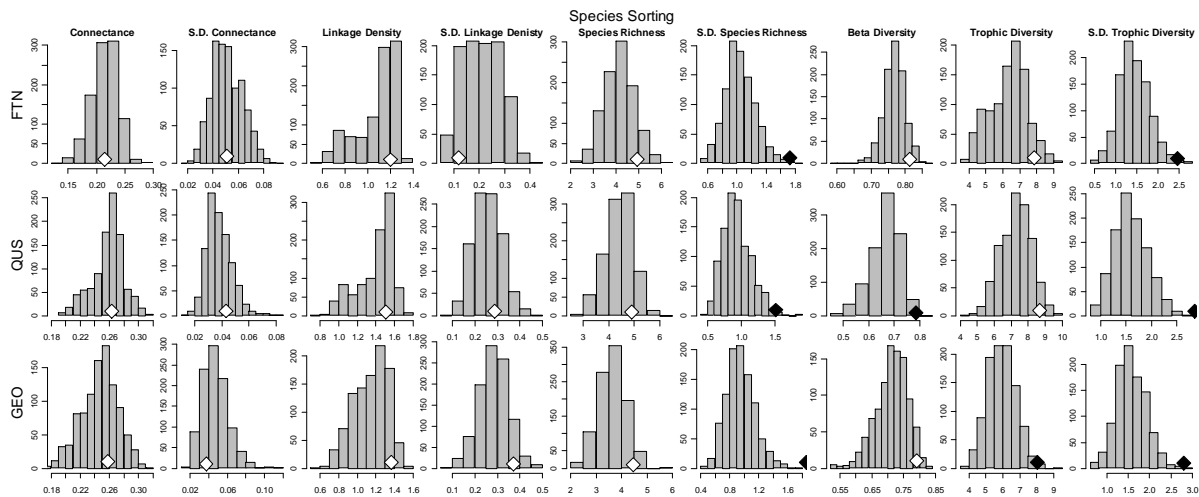
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755 B)



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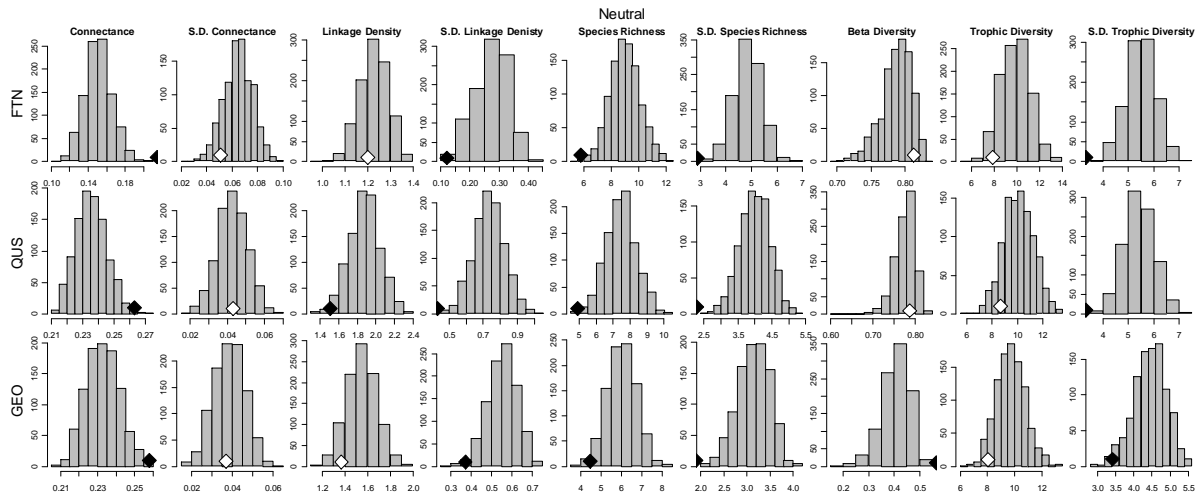
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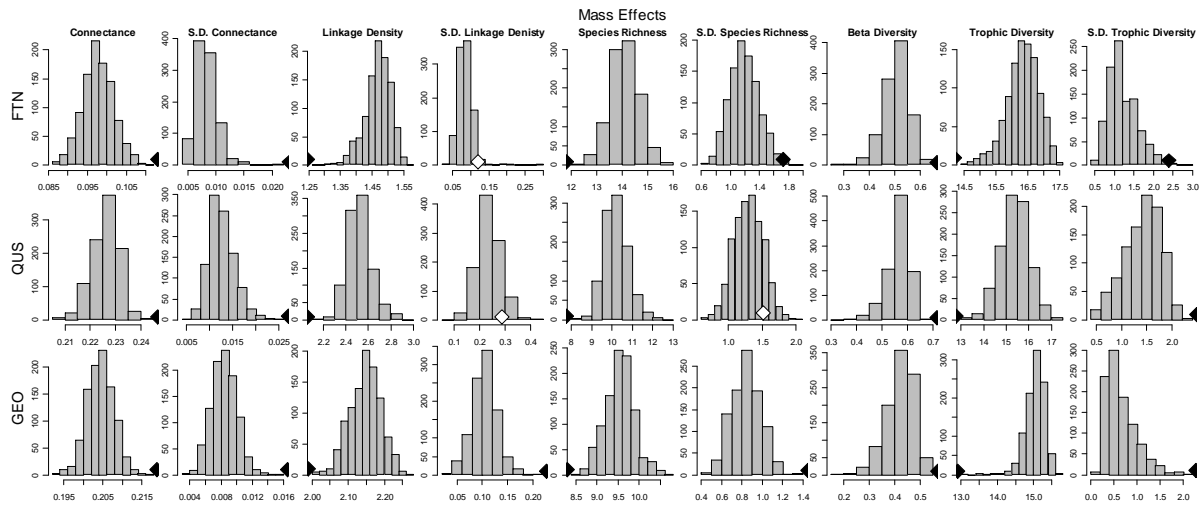
763 C)



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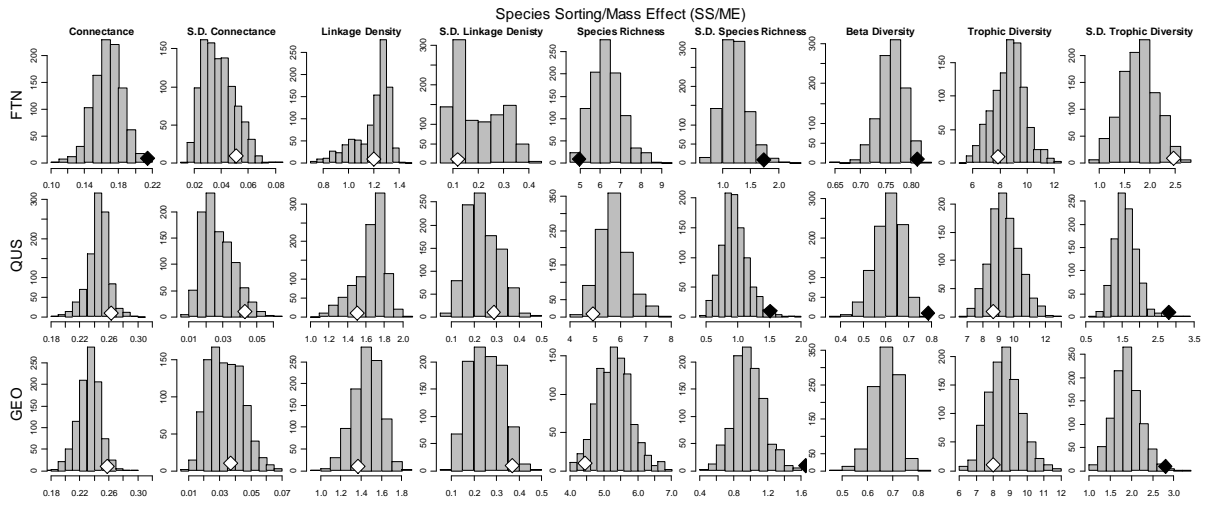
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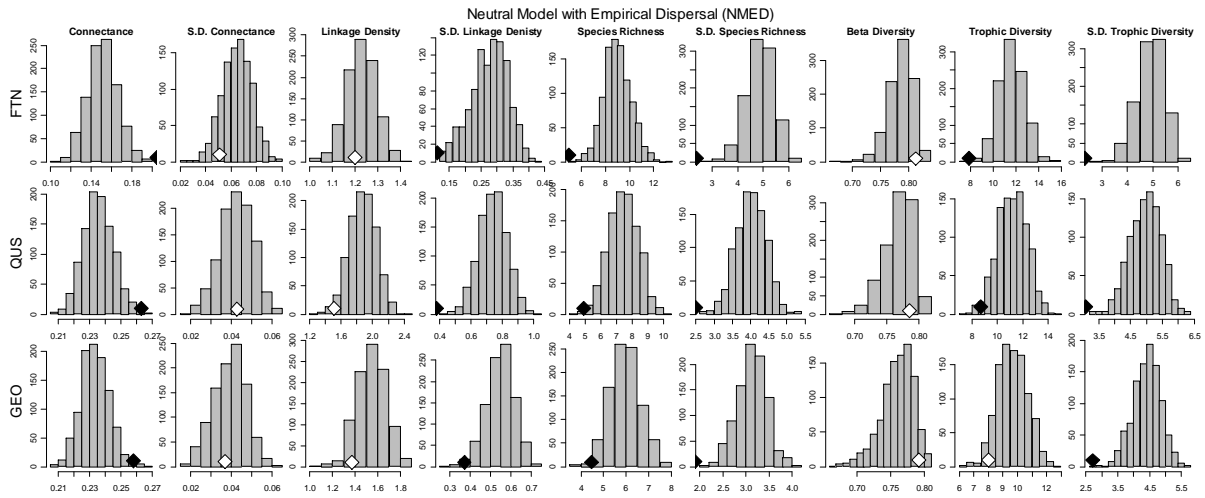
774 E)



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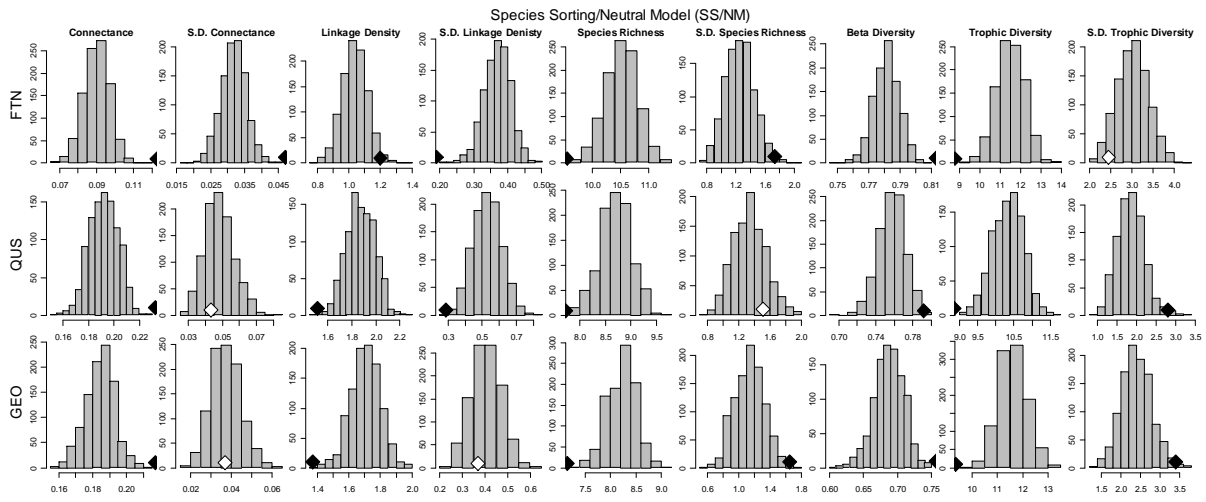
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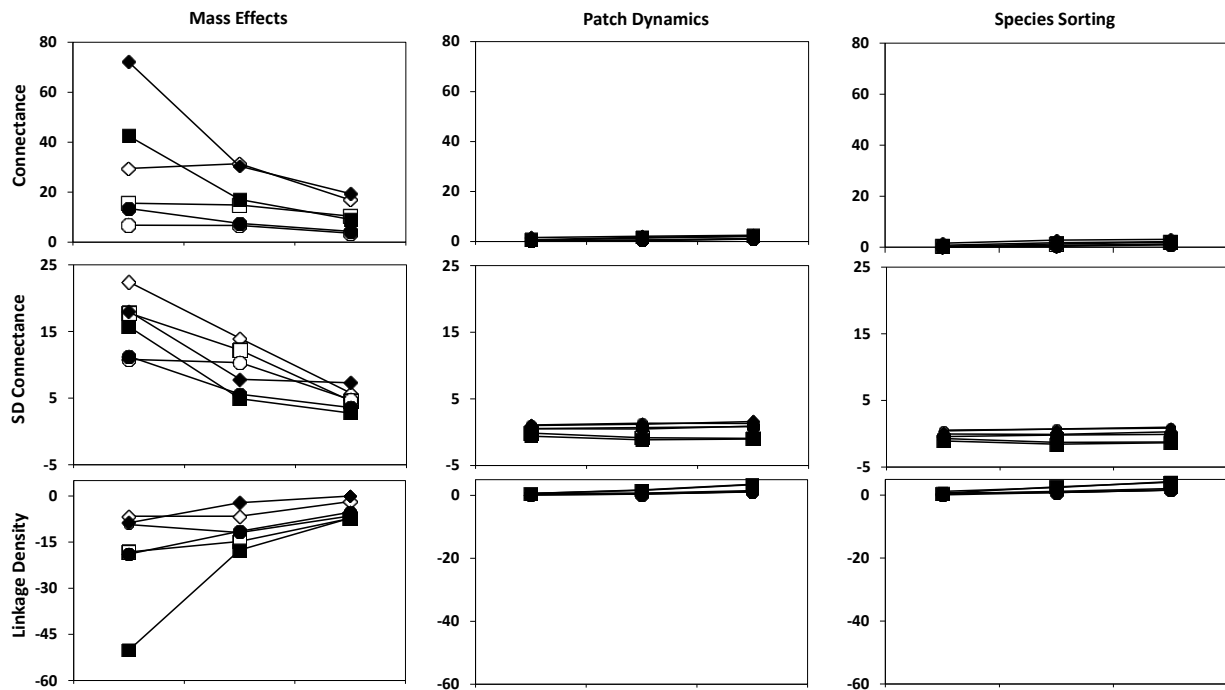
785 G)



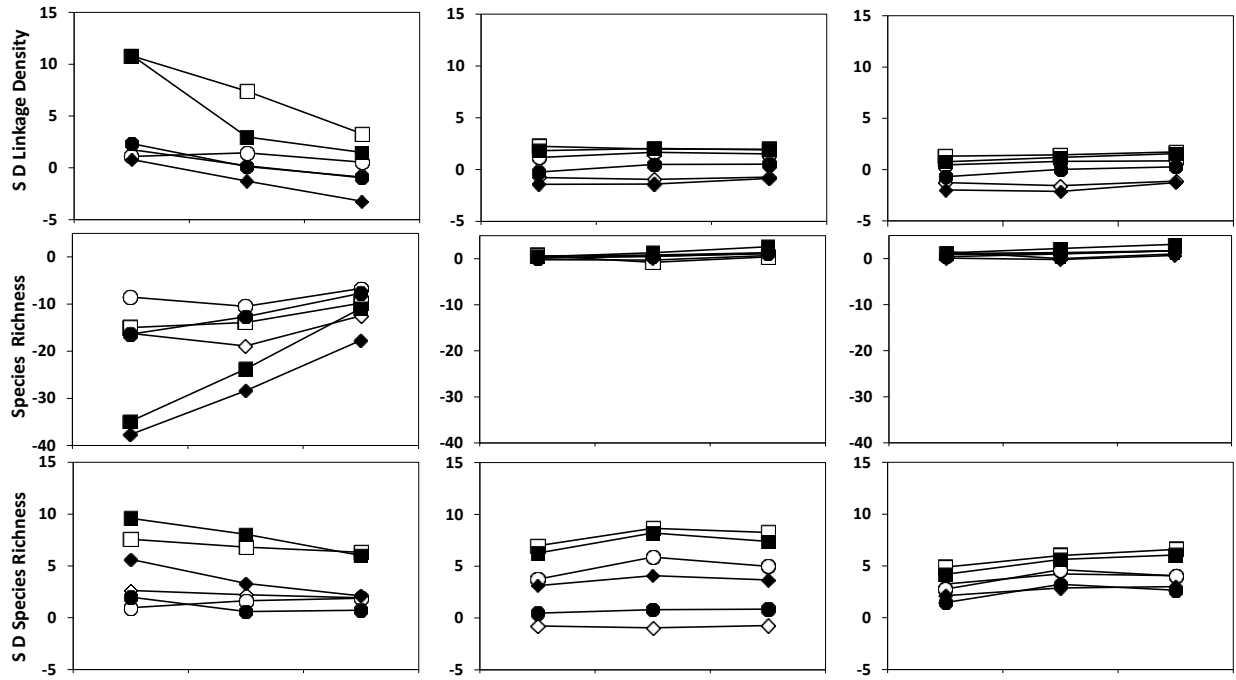
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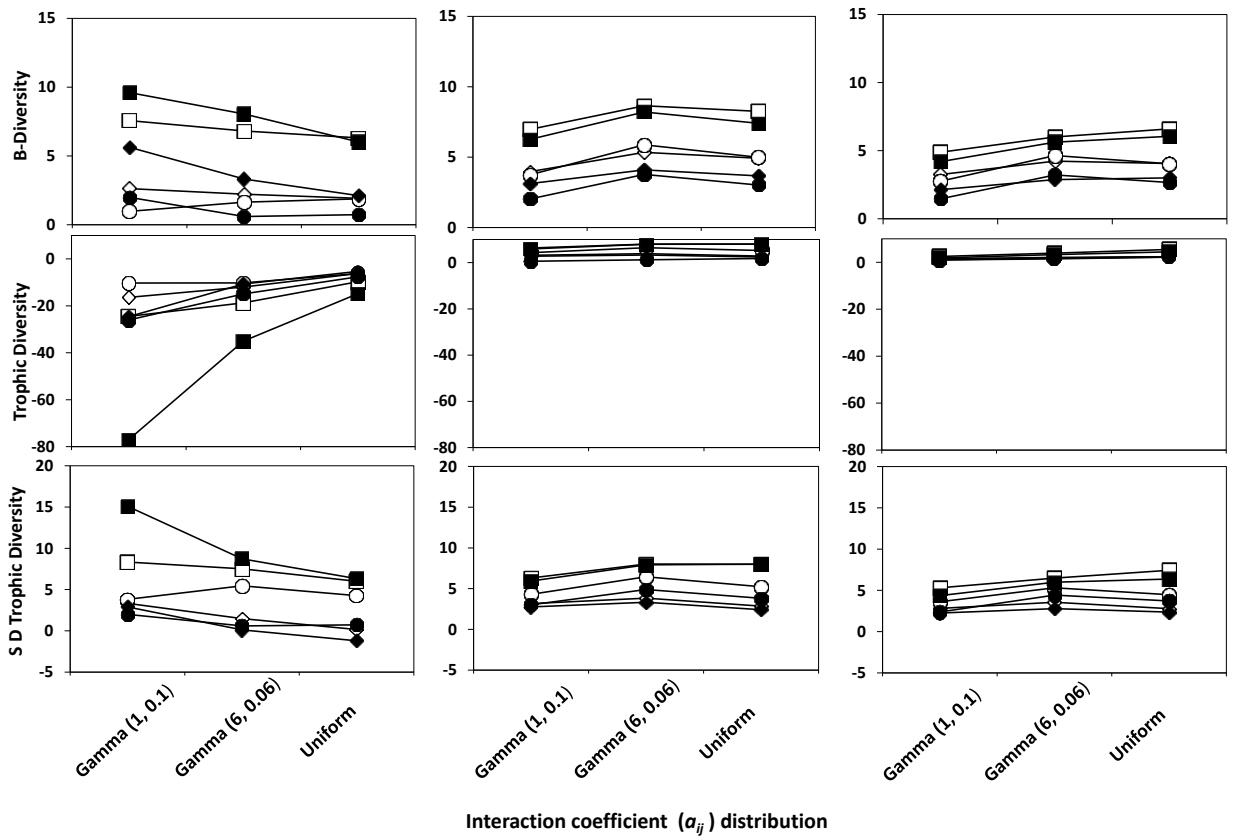
788 **Figure 4.** Interaction plots comparing standardized z -scores of the nine measures of food-web
 789 structure as a function of different distribution functions for dispersal (open symbols: empirical;
 790 solid symbols: modified empirical [E_{mod}] and species' interaction coefficient (a_{ij}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



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

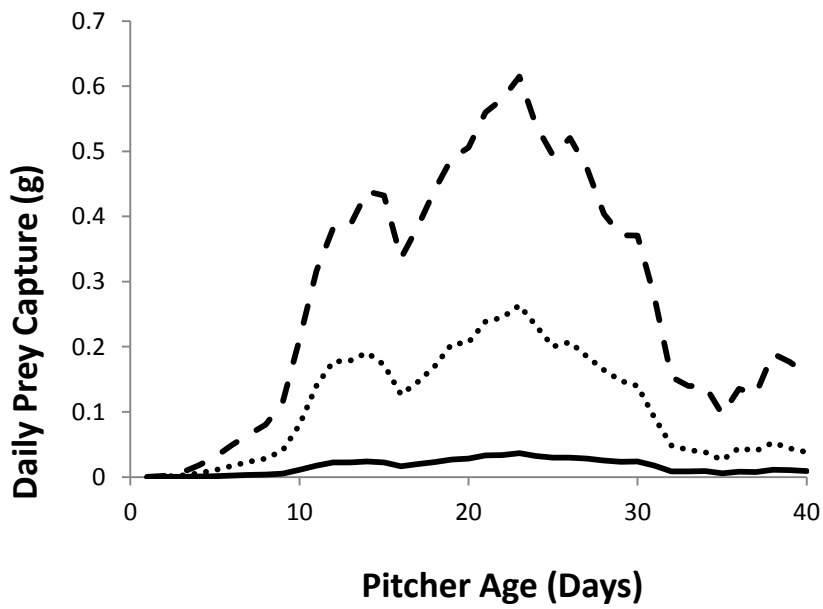
	Characteristic		
Model	Patch similarity	Species interactions	Time-scale of regional and local dynamics
Patch Dynamics	Similar <i>-Pitchers share identical resource levels (i.e. have the same prey capture function)</i>	Competition-colonization trade-off <i>-Better dispersers have higher (less negative) competition coefficients (a_{ij}) (Eqn. 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 (Eqn. 8) or decrease (Eqn. 9) their competitive ability (a_{ij}) 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 (Eqn. 8) or decrease (Eqn. 9) their competitive ability (a_{ij}) 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>

799 *Table adapted from Holyoak et al. 2005.

800 Supplementary Material

801 **Appendix 1**

802 **Fig. A1.** Example prey capture curves for model pitcher plants. The three lines represent pitchers
803 with high (dashed), medium (dotted), and low (solid) prey capture rates. For models where
804 pitchers have the same resource levels (e.g., patch dynamics), the same exact prey curve was
805 used for all 20 pitchers the simulation. Prey capture in grams is standardized between 0-1 per
806 day.



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816 **Appendix 2**

817 **Table A2.** Table of model parameters. Parameters re-drawn each simulation are shaded.

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Parameter	Description	Value	Source
G_i	Probability of species i dispersing into a pitcher	Normalized frequency of species i presence	Empirical site data
b_i	Intrinsic growth rate for species i	$-0.03 < b_i < 0$	Statistical distribution
a_{ij}	per capita effect of species j on the per capita growth rate of species i	Gamma distribution ($k = 1, \theta = 0.1$)	Statistical distribution
a_{ii}	Per capita effect of intraspecific competition	-1	Constant
R_v	Daily rainfall in cm^3	Empirical distribution	Empirical site data
A_p	Area of pitcher opening in cm^2	FTN= 4.15, QUS= 5.31, GEO=3.14	Empirical site data
E	Daily evaporation in cm^3	0.04	Constant
M	Daily water loss due to <i>E. fax</i> in cm^3	0.01	Constant
N_{max}	Maximum prey capture per pitcher	Prey capture function	Model derived
p_{ij}	Dispersal difference between species i and j	$G_i - G_j$	Empirical data

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820 **Appendix 3**

821 **Tables A3.** ANOVA tables for each food web metric. Significant terms ($p < 0.05$) are italicized.

Metric: Connectance					
	Df	Sum Sq	Mean Sq	F	p
<i>Site (Block)</i>	2	762	381.01	5.95	0.006
<i>Model Type</i>	2	4054.3	2027.17	31.65	< 0.001
Dispersal	1	159.9	159.89	2.50	0.122
Coefficient (a_{ij})	2	298.6	149.31	2.33	0.111
Model Type × Dispersal	2	201.9	100.93	1.58	0.220
<i>Model Type × Coefficient</i>	4	858.2	214.55	3.35	0.019
Dispersal × Coefficient	2	203	101.52	1.58	0.218
Residuals	38	2434.2	64.06		

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Metric: SD Connectance					
	Df	Sum Sq	Mean Sq	F	p
<i>Site (Block)</i>	2	44.72	22.36	7.54	0.002
<i>Model Type</i>	2	1183.54	591.77	199.70	< 0.001
<i>Dispersal</i>	1	16.3	16.3	5.50	0.024
<i>Coefficient (a_{ij})</i>	2	125.73	62.86	21.21	< 0.001
<i>Model Type × Dispersal</i>	2	20.63	10.32	3.48	0.041
<i>Model Type × Coefficient</i>	4	258.35	64.59	21.80	< 0.001
Dispersal × Coefficient	2	8.48	4.24	1.43	0.252
Residuals	38	112.61	2.96		

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Metric: Linkage Density					
	Df	Sum Sq	Mean Sq	F	p
Site (Block)	2	153.85	76.93	2.38	0.106
<i>Model Type</i>	2	1943.51	971.76	30.10	< 0.001
Dispersal	1	24.83	24.83	0.77	0.386
<i>Coefficient (a_{ij})</i>	2	296.36	148.18	4.59	0.016
Model Type × Dispersal	2	57.24	28.62	0.89	0.420
Model Type × Coefficient	4	306.28	76.57	2.37	0.069
Dispersal × Coefficient	2	81.26	40.63	1.26	0.296
Residuals	38	1226.74	32.28		

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Metric: SD Linkage Density					
	Df	Sum Sq	Mean Sq	F	p
<i>Site (Block)</i>	2	157.815	78.908	38.14	< 0.001
<i>Model Type</i>	2	43.597	21.799	10.54	<0.001
<i>Dispersal</i>	1	9.455	9.455	4.57	0.039
<i>Coefficient (a_{ij})</i>	2	14.487	7.244	3.50	0.040
Model Type × Dispersal	2	2.015	1.008	0.49	0.618
Model Type × Coefficient	4	50.393	12.598	6.09	< 0.001
Dispersal × Coefficient	2	0.931	0.465	0.23	0.800
Residuals	38	78.612	2.069		

829

Metric: Species Richness					
	Df	Sum Sq	Mean Sq	F	p
<i>Site (Block)</i>	2	144.2	72.12	5.54	0.008
<i>Model Type</i>	2	3746	1873.01	143.88	< 0.001
<i>Dispersal</i>	1	109.7	109.65	8.42	0.006
<i>Coefficient (a_{ij})</i>	2	160	80.01	6.15	0.005
Model Type × Dispersal	2	228.9	114.45	8.79	< 0.001
Model Type × Coefficient	4	194.6	48.64	3.74	0.012
Dispersal × Coefficient	2	66.9	33.47	2.57	0.090
Residuals	38	494.7	13.02		

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Metric: SD Species Richness					
	Df	Sum Sq	Mean Sq	F	p
<i>Site (Block)</i>	2	171.627	85.813	97.68	< 0.001
<i>Model Type</i>	2	20.392	10.196	11.61	< 0.001
<i>Dispersal</i>	1	3.77	3.77	4.29	0.045
<i>Coefficient (a_{ij})</i>	2	4.109	2.054	2.34	0.110
Model Type × Dispersal	2	9.942	4.971	5.66	0.007
Model Type × Coefficient	4	18.47	4.618	5.26	0.002
Dispersal × Coefficient	2	1.849	0.925	1.05	0.359
Residuals	38	33.384	0.879		

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Metric: β -Diversity					
	Df	Sum Sq	Mean Sq	F	p
Site (Block)	2	0.116	0.058	0.09	0.918
<i>Model Type</i>	2	306.121	153.061	226.82	< 0.001
<i>Dispersal</i>	1	2.983	2.983	4.42	0.042
<i>Coefficient (a_{ij})</i>	2	9.824	4.912	7.28	0.002
<i>Model Type</i> \times <i>Dispersal</i>	2	8.434	4.217	6.25	0.005
<i>Model Type</i> \times <i>Coefficient</i>	4	3.468	0.867	1.28	0.293
<i>Dispersal</i> \times <i>Coefficient</i>	2	0.291	0.145	0.22	0.807
Residuals	38	25.643	0.675		

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Metric: Trophic Diversity					
	Df	Sum Sq	Mean Sq	F	p
Site (Block)	2	270.7	135.35	2.20	0.124
<i>Model Type</i>	2	4999.3	2499.63	40.70	< 0.001
<i>Dispersal</i>	1	211.5	211.51	3.44	0.071
<i>Coefficient (a_{ij})</i>	2	552.7	276.37	4.50	0.018
<i>Model Type</i> \times <i>Dispersal</i>	2	336.8	168.4	2.74	0.077
<i>Model Type</i> \times <i>Coefficient</i>	4	884.8	221.19	3.60	0.014
<i>Dispersal</i> \times <i>Coefficient</i>	2	214.8	107.38	1.75	0.188
Residuals	38	2333.7	61.41		

838

839

Metric: SD Trophic Diversity					
	Df	Sum Sq	Mean Sq	F	p
<i>Site (Block)</i>	2	228.436	114.218	60.22	< 0.001
<i>Model Type</i>	2	6.148	3.074	1.62	0.211
<i>Dispersal</i>	1	0.63	0.63	0.33	0.568
<i>Coefficient (a_{ij})</i>	2	6.025	3.012	1.59	0.218
<i>Model Type</i> \times <i>Dispersal</i>	2	7.371	3.685	1.94	0.157
<i>Model Type</i> \times <i>Coefficient</i>	4	45.725	11.431	6.03	< 0.001
<i>Dispersal</i> \times <i>Coefficient</i>	2	4.101	2.05	1.08	0.349
Residuals	38	72.072	1.897		

840

841 **Appendix 4**

842 **Table A4**

843 Tukey’s HSD test for within model comparisons for the *model type* × *a_{ij} distribution* term. ME
 844 corresponds to mass effects, SS to species sorting, and Patch to patch dynamics. Tables are only
 845 shown for food web metrics for which *model type* × *a_{ij} distribution* was significant in the
 846 ANOVA and within model pairwise comparisons were significant (p <0.05). Column head “diff”
 847 is the difference in means between factor levels and “lwr”, “upr” are the 95% confidence
 848 intervals. Significant differences in means are italicized.

849

Metric: Connectance				
	diff	lwr	upr	p
ME×Gamma (6,0.05)–ME×Gamma (1,0.1)	-12.01	-27.19	3.18	0.221
<i>ME×Uniform–ME×Gamma (1,0.1)</i>	<i>-19.39</i>	<i>-34.57</i>	<i>-4.20</i>	<i>0.004</i>
ME×Uniform–ME×Gamma (6,0.05)	-7.38	-22.56	7.81	0.801
Patch×Gamma (6,0.05)–Patch×Gamma (1,0.1)	0.51	-14.68	15.70	1.000
Patch×Uniform–Patch×Gamma (1,0.1)	1.08	-14.10	16.27	1.000
Patch×Uniform–Patch×Gamma (6,0.05)	0.57	-14.61	15.76	1.000
SS×Gamma (6,0.05)–SS×Gamma (1,0.1)	0.72	-14.46	15.91	1.000
SS×Uniform–SS×Gamma (1,0.1)	1.21	-13.97	16.40	1.000
SS×Uniform–SS×Gamma (6,0.05)	0.49	-14.70	15.68	1.000

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851

Metric: SD Connectance				
	diff	lwr	upr	p
<i>ME×Gamma (6,0.05)–ME×Gamma (1,0.1)</i>	<i>-6.86</i>	<i>-10.13</i>	<i>-3.59</i>	<i><0.001</i>
<i>ME×Uniform–ME×Gamma (1,0.1)</i>	<i>-11.22</i>	<i>-14.49</i>	<i>-7.95</i>	<i><0.001</i>
<i>ME×Uniform–ME×Gamma (6,0.05)</i>	<i>-4.36</i>	<i>-7.63</i>	<i>-1.09</i>	<i>0.003</i>
Patch×Gamma (6,0.05)–Patch×Gamma (1,0.1)	-0.12	-3.39	3.15	1.000
Patch×Uniform–Patch×Gamma (1,0.1)	0.03	-3.24	3.29	1.000
Patch×Uniform–Patch×Gamma (6,0.05)	0.15	-3.12	3.41	1.000
SS×Gamma (6,0.05)–SS×Gamma (1,0.1)	-0.07	-3.34	3.19	1.000
SS×Uniform–SS×Gamma (1,0.1)	0.12	-3.15	3.39	1.000
SS×Uniform–SS×Gamma (6,0.05)	0.19	-3.07	3.46	1.000

852

Metric: Linkage Density				
	diff	lwr	upr	p
ME×Gamma (6,0.05)–ME×Gamma (1,0.1)	7.86	-2.92	18.64	0.315
ME×Uniform–ME×Gamma (1,0.1)	13.94	3.16	24.72	0.004
ME×Uniform–ME×Gamma (6,0.05)	6.08	-4.70	16.86	0.648
Patch×Gamma (6,0.05)–Patch×Gamma (1,0.1)	0.49	-10.29	11.27	1.000
Patch×Uniform–Patch×Gamma (1,0.1)	1.58	-9.20	12.36	1.000
Patch×Uniform–Patch×Gamma (6,0.05)	1.09	-9.69	11.87	1.000
SS×Gamma (6,0.05)–SS×Gamma (1,0.1)	0.64	-10.14	11.42	1.000
SS×Uniform–SS×Gamma (1,0.1)	1.69	-9.09	12.48	1.000
SS×Uniform–SS×Gamma (6,0.05)	1.05	-9.73	11.83	1.000

853

854

Metric: SD Linkage Density				
	diff	lwr	upr	p
ME×Gamma (6,0.05)–ME×Gamma (1,0.1)	-2.80	-5.53	-0.07	0.041
ME×Uniform–ME×Gamma (1,0.1)	-4.57	-7.30	-1.84	<0.001
ME×Uniform–ME×Gamma (6,0.05)	-1.77	-4.50	0.96	0.470
Patch×Gamma (6,0.05)–Patch×Gamma (1,0.1)	0.17	-2.56	2.90	1.000
Patch×Uniform–Patch×Gamma (1,0.1)	0.25	-2.48	2.98	1.000
Patch×Uniform–Patch×Gamma (6,0.05)	0.08	-2.65	2.81	1.000
SS×Gamma (6,0.05)–SS×Gamma (1,0.1)	0.19	-2.54	2.92	1.000
SS×Uniform–SS×Gamma (1,0.1)	0.57	-2.16	3.30	0.999
SS×Uniform–SS×Gamma (6,0.05)	0.38	-2.35	3.11	1.000

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856

Metric: Species Richness				
	diff	lwr	upr	p
ME×Gamma (6,0.05)–ME×Gamma (1,0.1)	3.40	-3.44	10.25	0.780
ME×Uniform–ME×Gamma (1,0.1)	10.56	3.72	17.41	< 0.001
ME×Uniform–ME×Gamma (6,0.05)	7.16	0.31	14.01	0.034
Patch×Gamma (6,0.05)–Patch×Gamma (1,0.1)	0.02	-6.82	6.87	1.000
Patch×Uniform–Patch×Gamma (1,0.1)	0.90	-5.94	7.75	1.000
Patch×Uniform–Patch×Gamma (6,0.05)	0.88	-5.97	7.73	1.000
SS×Gamma (6,0.05)–SS×Gamma (1,0.1)	0.02	-6.82	6.87	1.000
SS×Uniform–SS×Gamma (1,0.1)	0.80	-6.05	7.64	1.000
SS×Uniform–SS×Gamma (6,0.05)	0.78	-6.07	7.62	1.000

857

Metric: Trophic Diversity				
	diff	lwr	upr	p
ME×Gamma (6,0.05)–ME×Gamma (1,0.1)	-0.96	-2.74	0.82	0.701
<i>ME×Uniform–ME×Gamma (1,0.1)</i>	-1.57	-3.35	0.21	0.121
ME×Uniform–ME×Gamma (6,0.05)	-0.61	-2.39	1.17	0.966
Patch×Gamma (6,0.05)–Patch×Gamma (1,0.1)	1.64	-0.14	3.42	0.090
Patch×Uniform–Patch×Gamma (1,0.1)	1.03	-0.75	2.80	0.621
Patch×Uniform–Patch×Gamma (6,0.05)	-0.62	-2.39	1.16	0.964
SS×Gamma (6,0.05)–SS×Gamma (1,0.1)	1.32	-0.46	3.10	0.292
SS×Uniform–SS×Gamma (1,0.1)	1.29	-0.49	3.07	0.322
SS×Uniform–SS×Gamma (6,0.05)	-0.03	-1.81	1.75	1.000

858

859

Metric: SD Trophic Diversity				
	diff	lwr	upr	p
ME×Gamma (6,0.05)–ME×Gamma (1,0.1)	-2.14	-4.75	0.47	0.184
<i>ME×Uniform–ME×Gamma (1,0.1)</i>	-3.60	-6.21	-0.98	0.002
ME×Uniform–ME×Gamma (6,0.05)	-1.45	-4.07	1.16	0.663
Patch×Gamma (6,0.05)–Patch×Gamma (1,0.1)	1.49	-1.12	4.11	0.632
Patch×Uniform–Patch×Gamma (1,0.1)	0.81	-1.81	3.42	0.982
Patch×Uniform–Patch×Gamma (6,0.05)	-0.69	-3.30	1.93	0.994
SS×Gamma (6,0.05)–SS×Gamma (1,0.1)	1.30	-1.31	3.91	0.780
SS×Uniform–SS×Gamma (1,0.1)	1.07	-1.55	3.68	0.912
SS×Uniform–SS×Gamma (6,0.05)	-0.23	-2.85	2.38	1.000

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861

862 **Appendix 5**

863 **Table A5**

864 Tukey's HSD test for within model comparisons for the *model type* × *dispersal distribution*
 865 term. ME corresponds to mass effects, SS to species sorting, and Patch to patch dynamics.
 866 Tables are only shown for food web metrics for which *model type* × *dispersal distribution* was
 867 significant in the ANOVA and within model pairwise comparisons were significant (p
 868 <0.05). Significant differences in means are italicized.

869

Metric: SD Connectance				
	diff	lwr	upr	p
<i>ME×Emod–ME×Empirical</i>	-2.85	-5.28	-0.41	0.014
Patch×Emod-Patch×Empirical	-0.27	-2.70	2.16	0.999
SS×Emod-SS×Empirical	-0.18	-2.61	2.25	1.000

870

871

Metric: Species Richness				
	diff	lwr	upr	p
<i>ME×Emod–ME×Empirical</i>	-8.67	-13.78	-3.57	<0.001
Patch×Emod-Patch×Empirical	0.14	-4.96	5.25	1.000
SS×Emod-SS×Empirical	-0.02	-5.12	5.08	1.000

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873

874 **Appendix 6**

875 **Table A6.** Variance partitioning for ANOVA's for 9 food web metrics. Terms that are
 876 significant in the ANOVA are italicized. The final two columns are the mean and standard
 877 deviation of variance explained across all food web metrics for a given factor.

	Con	SD Con	LD	SD LD	S	SD S	β	TD	SD TD	Mean	SD
Site (Block)	<i>0.07</i>	<i>0.02</i>	0.02	<i>0.40</i>	<i>0.02</i>	<i>0.60</i>	0.00	0.01	<i>0.55</i>	0.19	0.24
Model Type	<i>0.41</i>	<i>0.59</i>	<i>0.44</i>	<i>0.10</i>	<i>0.67</i>	<i>0.07</i>	<i>0.84</i>	0.46	0.01	0.40	0.27
Dispersal	0.01	<i>0.01</i>	0.00	<i>0.02</i>	<i>0.02</i>	<i>0.01</i>	<i>0.01</i>	0.01	0.00	0.01	0.01
Coefficient (a_{ij})	0.02	<i>0.06</i>	<i>0.05</i>	<i>0.03</i>	<i>0.02</i>	0.01	<i>0.02</i>	0.04	0.01	0.03	0.02
Model Type \times Dispersal	0.02	<i>0.01</i>	0.00	0.00	<i>0.07</i>	<i>0.06</i>	<i>0.04</i>	0.04	0.02	0.03	0.02
Model Type \times Coefficient	<i>0.11</i>	<i>0.22</i>	0.07	<i>0.20</i>	<i>0.05</i>	<i>0.09</i>	0.00	0.11	<i>0.17</i>	0.11	0.07
Dispersal \times Coefficient	0.02	0.00	0.01	0.00	0.01	0.00	0.00	0.02	0.00	0.01	0.01
Residuals	0.36	0.08	0.41	0.29	0.13	0.17	0.10	0.31	0.25	0.23	0.11

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