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# **Modeling Foundation Species in Food Webs**

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10 **Abstract.** Foundation species are basal species that play an important role in determining  
11 community composition by physically structuring ecosystems and modulating ecosystem  
12 processes. Foundation species largely operate via non-trophic interactions, presenting a challenge  
13 to incorporating them into food-web models. Here, we used non-linear, bioenergetic predator-  
14 prey models to explore the role of foundation species and their non-trophic effects. We explored  
15 four types of models in which the foundation species reduced the metabolic rates of species in a  
16 specific trophic position. We examined the outcomes of each of these models for six metabolic  
17 rate “treatments” in which the foundation species altered the metabolic rates of associated  
18 species by one-tenth to ten times their allometric baseline metabolic rates. For each model  
19 simulation, we looked at how foundation species influenced food-web structure during  
20 community assembly and the subsequent change in food-web structure when the foundation  
21 species was removed. When a foundation species lowered the metabolic rate of only basal  
22 species, the resultant webs were complex, species-rich, and robust to foundation species  
23 removals. On the other hand, when a foundation species lowered the metabolic rate of only  
24 consumer species, all species, or no species, the resultant webs were species-poor and the  
25 subsequent removal of the foundation species resulted in the further loss of species and  
26 complexity. This suggests that in nature we should look for foundation species to predominantly  
27 facilitate basal species.

28  
29 Key words: foundation species, food-web modeling, metabolic rate, network, non-linear  
30 dynamics

31

32 INTRODUCTION

33 Foundation species (sensu Dayton 1972) are basal species that structure ecological  
34 communities by creating physical structure and modulating ecosystem processes (Ellison et al.  
35 2005). Recent declines (e.g., *Tsuga canadensis*) and extirpations (e.g., *Castanea dentata*) of  
36 foundation species in terrestrial ecosystems have called attention to the need for new methods for  
37 identifying and quantifying the role of foundation species in ecological communities (reviewed  
38 by Ellison et al. 2005; 2010, Van der Putten 2012). Numerous field studies have shown that  
39 foundation species can alter trajectories of the assembly of ecological communities (e.g., Gibson  
40 et al. 2012, Schoeb et al. 2012, Butterfield et al. 2013, Martin and Charles 2013, Orwig et al.  
41 2013). However, general models of how foundation species affect ecological systems are scarce  
42 and generally qualitative (Ellison and Baiser, *in press*).

43 Foundation species can interact trophically within a community, but they exert their  
44 influence primarily through non-trophic effects (Ellison and Baiser, *in press*). Some examples of  
45 non-trophic actions of foundation species include; altering local climates and microclimates (e.g.,  
46 Schoeb et al. 2012, Butterfield et al. 2013); changing soil temperature, moisture, and acidity  
47 (e.g., Prevey et al. 2010, Lustenhouwer et al. 2012, Martin and Charles 2013); providing refuge  
48 for prey species and perches for predators (e.g., Yakovis et al. 2008, Tovar-Sanchez et al. 2013);  
49 and stabilizing stream banks and shorelines against erosion (reviewed by Ellison et al. 2005).  
50 Because foundation species exert system-wide effects on biodiversity and ecosystem functioning  
51 primarily through these (and other) non-trophic interactions, it has proven difficult to link effects  
52 of foundation species into theories of the structure and function of food webs. Food-web theory  
53 aims to elucidate the persistence of the types of complex, species-rich webs that we see in nature  
54 (e.g., May 1972, Allesina and Tang 2012). Measures of network properties, such as connectance,

55 compartmentalization, and species richness, as well as the strength of species interactions, all can  
56 influence the stability and persistence of food webs (e.g., May 1972, Dunne et al. 2002, Gravel et  
57 al. 2011, Stouffer and Bascompte 2011). Adding non-trophic interactions, such as those  
58 exhibited by foundation species or mutualists in general, provides an additional step towards  
59 understanding persistence and stability of ecological networks (Thébault and Fontaine 2010,  
60 Allesina and Tang 2012, Kéfi et al. 2012)

61         Here, we adapt non-linear, bioenergetic predator-prey models to explore non-trophic  
62 roles of foundation species in food webs. To make explicit linkages between trophic and non-  
63 trophic interactions, we model the metabolic rate of individual “species” as a function of  
64 foundation species biomass. Metabolic rate is good proxy for a wide variety of positive non-  
65 trophic species interactions (sensu Kéfi et al. 2012), because “stressful conditions” may be  
66 reduced when foundation species ameliorate temperature extremes, provide associated species  
67 with habitat resources or shelters, or enhance their growth rate (Schiel 2006, Shelton 2010,  
68 Gedan et al. 2011, Angelini and Silliman 2012, Dijkstra et al. 2012, Noumi et al. 2012,  
69 Butterfield et al. 2013).

70         We developed four different foundation species models to explore non-trophic effects of  
71 foundation species in food webs. In each, the foundation species influences target species at  
72 different trophic positions in the food web: 1) a *basal model*, in which the foundation species  
73 reduces the metabolic rates of only other, albeit non-foundation, basal species, 2) a *consumer*  
74 *model*, in which the foundation species reduces the metabolic rates of only consumers, 3) a *total*  
75 *model*, in which the foundation species reduces the metabolic rates of all species, and 4) a  
76 *control model*, in which the foundation species is only consumed and has no effect on the  
77 metabolic rates of any associated species. We examined the outcomes of each of these models

78 for six metabolic rate “treatments” in which the foundation species alters the metabolic rates of  
79 associated species by one-tenth to ten times their allometric baseline metabolic rates. For each  
80 model simulation, we looked at how foundation species influence different measures of food-  
81 web structure during community assembly and the subsequent change of food-web structure  
82 when the foundation species was removed.

83

## 84 METHODS

85 We modeled dynamic ecological networks using a four-step process (Brose et al. 2006,  
86 Berlow et al. 2009, Kéfi et al. 2012): 1) model initial network structure; 2) calculate body mass  
87 for each species based on trophic level; 3) simulate population dynamics using an allometric  
88 predator-prey model; and 4) add non-trophic interactions into the allometric predator-prey  
89 model.

90

### 91 *Network structure*

92 We used the niche model of Williams and Martinez (2000) to designate trophic links in  
93 our model food webs. The niche model is an algorithm with two parameter inputs: species  
94 richness ( $S$ ) and connectance ( $C = L/S^2$ , where  $L$  = the number of trophic links). Each species in  
95 the web has a niche value uniformly drawn from  $[0,1]$  and a niche range that is placed on a one-  
96 dimensional axis. Any one species whose niche value falls within the niche range of another is  
97 defined to be the latter’s prey (for specific details on the niche model see Williams and Martinez  
98 2000). The niche model has been shown to reproduce accurately a wide range of food-web  
99 network properties for many empirical webs (Williams and Martinez 2000, Dunne et al. 2004,  
100 Williams and Martinez 2008).

101

102 *Body mass*

103 We calculated body mass,  $M_i$ , for species  $i$  as:

104

105 
$$M_i = Z^{T-1} \quad (1)$$

106

107 In eq. (1),  $Z$  is the predator-prey biomass ratio and  $T$  is the average trophic level of species  $i$   
108 calculated using the prey-averaged method (Williams and Martinez 2004). We set basal species  
109  $M$  to unity and used a predator-prey biomass ratio of  $Z = 10^2$ . We used body mass to  
110 allometrically scale biological parameters in the predator-prey model.

111

112 *Allometric predator-prey model*

113 We simulated food-web population dynamics using an allometric predator-prey model  
114 (Yodzis and Innes 1992, Williams and Martinez 2004, Brose et al. 2006). Following Brose et al.  
115 (2006):

116 
$$\frac{dB_i}{dt} = r_i(M_i)G_iB_i - x_i(M_i)B_i - \sum_{j=consumers} \frac{x_j(M_j)y_jB_jF_{ji}(B)}{e_{ji}f_{ji}} \quad (2a)$$

117 
$$\frac{dB_i}{dt} = -x_i(M_i)B_i + \sum_{j=resources} x_i(M_i)y_iB_iF_{ij}(B) - \sum_{j=consumers} \frac{x_j(M_j)y_jB_jF_{ji}(B)}{e_{ji}f_{ji}} \quad (2b)$$

118

119 Equation 2a describes change in biomass,  $B$ , of primary producer species  $i$ , and equation 2b  
120 describes changes in  $B$  of consumer  $i$ . All model variables are listed and defined in Table 1.

121 For primary producer species  $i$ ,  $r_i$  is its mass-specific maximum growth rate;  $M_i$  is its  
 122 individual body mass; and  $G_i$  is its logistic growth rate:  $G_i = 1 - (B_i/K)$  and  $K$  is the carrying  
 123 capacity (in our model,  $K = 1$ ). Both for primary producers and consumers, the mass-specific  
 124 metabolic rate for species  $i$  is  $x_i$ . For consumers,  $y_i$  is the maximum consumption rate of species  $i$   
 125 relative to its metabolic rate;  $e_{ji}$  is the assimilation efficiency for species  $i$  when consuming  
 126 species  $j$ ; and  $f_{ij}$  is the fraction of biomass removed from the resource biomass that is actually  
 127 ingested. The functional response,  $F_{ij}$ , describes how consumption rate varies as a function of  
 128 prey biomass. We used a type II functional response:

$$129 \quad F_{ij} = \frac{w_{ij}B_j}{B_0 + \sum_{k=\text{resources}} w_{ik}B_k} \quad (3)$$

130 In eq. (3),  $\omega_{ij}$  is the uniform relative consumption rate of consumer  $i$  preying on resource  $j$  (i.e.,  
 131 the preference of consumer  $i$  for resource  $j$ ) when the consumer has  $n$  total resources ( $\omega_{ij} = 1/n$ )  
 132 and  $B_0$  is the half-saturation constant (i.e., resource biomass at which consumer reaches half of  
 133 its maximum consumption rate). In all of our models,  $B_0$  was set equal to 0.5.

134 Body size is an important component of both predator-prey interactions (Warren and  
 135 Lawton 1987, Woodward and Hildrew 2002, Brose et al. 2006) and metabolic functioning of  
 136 organisms (Brown et al. 2004). As a result, body size is an important factor for energy flow  
 137 throughout food webs (Woodward et al. 2005). Predator-prey body-size ratios found in empirical  
 138 food webs have been shown to stabilize dynamics in complex networks (Brose et al. 2006).  
 139 Thus, we allometrically scaled the biological parameters  $r_i$ ,  $x_i$ , and  $y_i$  in eqns (2a) and (2b) to  
 140 body size (Brose et al 2006). We modeled the biological rates of production,  $R$ , metabolism,  $X$ ,  
 141 and maximum consumption rate,  $Y$ , using a negative-quarter power-law dependence on body size  
 142 (Brown et al. 2004):



143 
$$R_P = a_r M_P^{-0.25} \quad (4a)$$

144

145 
$$X_C = a_x M_C^{-0.25} \quad (4b)$$

146

147 
$$Y_C = a_y M_C^{-0.25} \quad (4c)$$

148 In eqns (4a-4c), subscripts  $P$  and  $C$  correspond to producers and consumers respectively;  $a_r$ ,  $a_x$ ,  
 149 and  $a_y$  are allometric constants; and  $M$  is the body mass of an individual (Yodzis and Innes  
 150 1992). The time scale of the system is specified by fixing the mass-specific growth rate,  $r_i$ , to  
 151 unity. Following this, we normalized the mass-specific metabolic rate,  $x_i$ , for all species in the  
 152 model by time scale and in turn, we normalized the maximum consumption rate,  $y_i$ , by the  
 153 metabolic rates:

154 
$$r_i = 1 \quad (5a)$$

155 
$$x_i = \frac{X_C}{R_P} = \frac{ax}{ar} \left( \frac{M_C}{M_P} \right)^{-0.25} \quad (5b)$$

156 
$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x} \quad (5c)$$

157 We then entered the allometrically scaled parameters for  $r_i$ ,  $x_i$ , and  $y_i$  into equations 2a and 2b,  
 158 yielding an allometrically scaled, dynamic predator-prey model. We set the allometric constants  
 159 to be  $y_i = 8$ ,  $e_{ij} = 0.85$  for carnivores and  $e_{ij} = 0.45$  for herbivores,  $a_r = 1$ , and  $a_x = 0.314$  (Yodzis  
 160 and Innes 1992, Brown et al. 2004, Brose et al. 2006).

161

162 *Foundation species and non-trophic interactions*

163 For each food web, we randomly designated one basal species as a foundation species.  
164 Each foundation species engaged in a non-trophic interaction with a given number of target  
165 species in a food web, depending on the model described in the next section. The foundation  
166 species alters the metabolic rate ( $x$ ) of a target species with which it interacts following a general  
167 saturating function (after Otto and Day 2007):

$$168 \quad \frac{dx_i}{dB} = \frac{x_{fsp}B + x_a B_a}{B + B_a} \quad (6)$$

169 In eq. (6),  $x_{fsp}$  is the metabolic rate of the target species in the presence of the foundation species;  
170  $x_a$  is the metabolic rate of the target species in the absence of the foundation species (i.e.,  
171 baseline metabolic rate, eqn 5b);  $B$  is the biomass density of the foundation species; and  $B_a$  is the  
172 “typical” (i.e., ~average across trial runs) biomass density for the foundation species. The  
173 metabolic rate of species  $i$ ,  $x_i$ , decreases from  $x_a$  when  $B = 0$  to an asymptote at  $x_{fsp}$  when  $B$  is  
174 large (we assume that  $x_{fsp} < x_a$  because the foundation species reduces the metabolic rates of its  
175 associated species).

176

#### 177 *Four foundation species models*

178 We varied the number and position of non-trophic interactions in four different ways  
179 (Fig. 1). In the *control* model, there are no non-trophic interactions (i.e., the species designated  
180 as the foundation species has only trophic interactions). In the *basal model*, the foundation  
181 species influences the metabolic rate of all basal species. In the *consumer model*, the foundation  
182 species influences the metabolic rate of all consumers (i.e., non-basal species). Finally, in the  
183 *total model*, the foundation species influences the metabolic rate of all species in the food web.

184

#### 185 *Simulations and analysis*

186 We created 100 niche-model webs, in all of which we set  $S = 30$  and  $C = 0.15$ . We  
187 parameterized allometric predator-prey models with an initial biomass ( $B_i$ ) vector drawn  
188 randomly from a uniform distribution:  $B_i \sim \text{Uniform}[0.5, 1]$ . The initial value of  $B_i$  was the same  
189 for any given food web in all four of the foundation species models. We solved equations 2a and  
190 2b using the standard 4<sup>th</sup> order Runge-Kutta method with a time step of 0.001. For each model  
191 run, we ran the initial “food-web assembly” simulations for 2,000 time steps. A species was  
192 considered extinct and removed from model simulations (i.e.,  $B_i = 0$ ) when  $B_i < 10^{-30}$  (Brose et al.  
193 2006, Berlow et al. 2009). At the end of this “assembly” period we calculated the number of  
194 species present and nine additional measures of food-web structure (Table 2) and then removed  
195 food webs with unconnected species or chains from further simulation. We next “removed” the  
196 foundation species from the remaining webs and ran the “foundation species removal”  
197 simulation for an additional 2,000 time-steps. At  $t = 4,000$ , we again calculated the number of  
198 species present and the nine additional measures of food web structure (Table 2).

199 Food-web metrics (Table 2) were calculated using Network 3D (Williams 2010). For the  
200 *food web assembly analysis* (i.e., the first 2,000 time steps of each model run), we tested the  
201 effect of each model (foundation species effects) using analysis of covariance (ANCOVA). In  
202 the ANCOVA, foundation species model was the factor, and  $\log(\text{metabolic rate} + 1)$  was the  
203 covariate. Because measures of food-web structure are often correlated (Vermaat et al. 2009), we  
204 used principle components analysis (prcomp in R version 2.13.1) to reduce the food-web metrics  
205 into two orthogonal principle components that were used as response variables in the ANCOVA.  
206 In this analysis, we did not include food webs that collapsed (i.e., had zero species). ANCOVA  
207 was implemented using glm in R; a Poisson link function was used when species richness was

208 the response variable, and a Gaussian link function was used for the analysis of food-web metrics  
209 (principal axis scores).

210 For the *foundation species removal analyses* (i.e., time steps 2,001 – 4,000), we  
211 calculated standardized change ( $\Delta z = z_{t=2001} - z_{t=4000} / z_{t=2001}$ ) in species richness and food-web  
212 metrics (principal axis scores) between the end of food-web assembly ( $t = 2,001$ ) and the end of  
213 the foundation species removal ( $t = 4,000$ ) because webs had different species richness at the  
214 time the foundation species was removed ( $t = 2,000$ ). As described above, we then used  
215 ANCOVA to test the effects of each model.

216

### 217 *Exploring the parameter space*

218 An important assumption in our models is that species have higher metabolic rates in the  
219 absence of the foundation species. However, it was not clear how to set the baseline metabolic  
220 rate,  $x_a$ , (i.e., how poorly should any particular species perform in the absence of the foundation  
221 species) and how much the foundation species should improve [= reduce] the metabolic rate  
222 ( $x_{fsp}$ ). To explore a range of reasonable possibilities, we ran one set of simulations in which  $x_a$   
223 was set equal to the allometrically scaled metabolic rate in eqn. (5b) and  $x_{fsp}$  was set equal to one  
224 of 0.5, 0.2 or, 0.1 of  $x_a$  (Fig. 2A; referred to henceforth as  $0.5\times$ ,  $0.2\times$ , and  $0.1\times$  treatments). In  
225 this first set of simulations, species start at the (allometric) baseline and the presence of the  
226 foundation species further reduces the metabolic rates of species associated with it. In the second  
227 set of simulations,  $x_{fsp}$  was set equal to the allometrically scaled metabolic rate in eqn. (5b) and  $x_a$   
228 was set equal to one of 2, 5, or 10 times  $x_{fsp}$  (Fig. 2B; referred to henceforth as  $2\times$ ,  $5\times$ , and  $10\times$   
229 treatments). Our metabolic rates encompass the variation observed between basal metabolic rates  
230 and maximum metabolic rates in empirical studies (Nagy 1987, Gillooly et al. 2001).

231 In total, we simulated 100 webs for each combination of the four foundation species  
232 models and the six metabolic treatments:  $100 \times 4 \times 6 = 2,400$  food-web simulations. Model code  
233 is available from the Harvard Forest Data Archive ([http://harvardforest.fas.harvard.edu/data-](http://harvardforest.fas.harvard.edu/data-archive)  
234 [archive](http://harvardforest.fas.harvard.edu/data-archive)), dataset HF-211.

235

## 236 RESULTS

### 237 *Assembly*

#### 238 SPECIES RICHNESS

239 Species richness varied with metabolic rate ( $F_{1, 1300} = 224.05$ ,  $P < 0.001$ ) and foundation  
240 species model ( $F_{3, 1300} = 13.33$ ,  $P < 0.001$ ), and there was a significant interaction between the  
241 model type and metabolic rate ( $F_{3, 1300} = 49.37$ ,  $P < 0.001$ ) (Fig. 3A). Species richness increased  
242 with increasing metabolic rate in the *basal* model webs (slope = 0.082,  $t = 2.39$ ,  $P < 0.02$ ),  
243 whereas it decreased with increasing metabolic rate in webs derived from the other three models  
244 (*total*: slope =  $-0.51$ ,  $t = -11.83$ ,  $P < 0.001$ ; *consumer*: slope =  $-0.77$ ,  $t = -16.41$ ,  $P < 0.001$ ;  
245 *control*: slope =  $-0.29$ ,  $t = -7.43$ ,  $P < 0.001$ ). Webs collapsed entirely (i.e., species richness = 0 at  
246  $t = 2,000$  model time steps) only in the  $10\times$  treatment; these collapses occurred in the *total*  
247 (33%), *control* (42%), and *consumer* (2%), but not in the *basal* foundation species models.

248

#### 249 FOOD-WEB STRUCTURE

250 The first two principal components of food-web structure (Fig. 4) accounted for 67% of  
251 the variation across model food webs (Table 3). Model webs with low PC-1 scores were  
252 relatively species-rich with high  $C$ ,  $LS$ , and cluster coefficients, and also had a high fraction of  
253 intermediate species and omnivores. Conversely, webs with high PC-1 scores were species-poor

254 with low  $C$  and  $LS$ ; these webs also had long path lengths and large fractions of top, basal, and  
255 herbivore species. Webs with high PC-2 scores were species-rich with low  $C$ , and had large  
256 proportions of top species, low proportions of basal species, and low cluster coefficients. Webs  
257 with low PC-2 scores were species-poor with high  $C$  and cluster coefficients, and had a large  
258 fraction of basal species.

259 PC-1 scores of food-web structure were significantly associated with model type ( $F_{3, 1224}$   
260 = 10.78,  $P < 0.001$ ) and the interaction between model type and metabolic rate ( $F_{3, 1224} = 15.27$ ,  $P$   
261  $< 0.001$ ), but not with metabolic rate alone ( $F_{1, 1224} = 1.86$ ,  $P = 0.17$ ) (Fig. 3B). PC-1 scores  
262 decreased with metabolic rate in *basal* model webs (slope =  $-1.40$ ,  $t = -3.99$ ,  $P < 0.01$ ), and *total*  
263 and *control* webs were not significantly different from the *basal* model webs (*total*: slope =  $-$   
264  $0.47$ ,  $t = 1.72$ ,  $P = 0.08$ , *control*: slope =  $-1.28$ ,  $t = 0.2$ ,  $P = 0.84$ ). In contrast, PC-1 scores  
265 increased with metabolic rate in the *consumer* model (slope =  $1.55$ ,  $t = 6.09$ ,  $P < 0.001$ ).

266 Both metabolic rate ( $F_{1, 1224} = 23.42$ ,  $P < 0.001$ ) and model type ( $F_{3, 1224} = 6.24$ ,  $P < 0.001$ )  
267 had significant effects on PC-2 scores, and the interaction term was also significant ( $F_{3, 1224} =$   
268  $7.71$ ,  $P < 0.001$ ) (Fig. 3C). PC-2 scores significantly decreased with metabolic rate in the  
269 *control* model webs (slope =  $-1.45$ ,  $t = -4.72$ ,  $P < 0.001$ ), whereas the PC-2 scores of the webs  
270 generated by the other three foundation species models did not change across metabolic rates  
271 (*basal*: slope =  $-0.02$ ,  $t = -0.13$ ,  $P = 0.90$ , *total*: slope =  $-0.44$ ,  $t = -1.43$ ,  $P = 0.15$ , *consumer*:  
272 slope =  $-0.38$ ,  $t = -1.35$ ,  $P = 0.18$ ).

273

274 *Foundation species removal*

275 SPECIES RICHNESS

276 Species loss varied across metabolic rate ( $F_{1, 1004} = 116.54, P < 0.001$ ) and foundation  
277 species model ( $F_{3, 1004} = 22.41, P < 0.001$ ) (Fig. 5A). The interaction term (*metabolic rate*  
278 *treatment*  $\times$  *type of foundation species model*) also was significant (ANCOVA:  $F_{3,1004} = 22.27, P$   
279  $< 0.001$ ). Species loss in the *total* (slope = 0.35,  $t = 8.03, P < 0.001$ ), *control*, (slope = 0.11,  $t =$   
280 1.97,  $P < 0.05$ ), and *consumer* models (slope = 0.15,  $t = 3.34, P < 0.001$ ) increased with  
281 metabolic rate. The species loss for *basal* model webs was not influenced by metabolic rate  
282 (slope = 0.03,  $t = 1.11, P = 0.28$ ). The  $10\times$  treatment was the only treatment in which webs  
283 completely collapsed (i.e., had a final species richness of zero) after the removal of the  
284 foundation species. Web collapse occurred in the 92 % of the *total* and 40% of the *control* webs.  
285

#### 286 FOOD-WEB STRUCTURE

287 The first two principal components accounted for 60% of the variation in food-web  
288 structure after the removal of the foundation species (Table 3). Model webs with high PC-1  
289 scores lost a greater proportion of species, and showed relatively larger decreases in *LS* and  
290 cluster coefficients (Fig. 6). These structural changes were due primarily to a decrease in the  
291 proportion of intermediate and omnivore species and an increase in the proportion of basal  
292 species after foundation species removal. Webs with low PC-1 scores lost fewer species and  
293 experienced smaller declines or increases in *LS* and cluster coefficients. These webs also had  
294 larger proportions of intermediate and omnivore species. Webs with high PC-2 scores lost a  
295 greater proportion of species, showed an increase in *C*, and decreased path lengths. Webs with  
296 low PC-2 scores lost fewer species, experienced a decrease in *C*, and increased in path length.

297 Metabolic rate ( $F_{1, 974} = 14.36, P < 0.001$ ), foundation species model type ( $F_{3, 974} = 21.36,$   
298  $P < 0.001$ ) and their interaction ( $F_{3, 974} = 6.61, P < 0.001$ ) significantly influenced PC-1 scores

299 (Fig. 5B). PC-1 scores increased with metabolic rate in webs generated using the *total* (slope =  
300 1.35,  $t = 3.20$ ,  $P < 0.01$ ), *control*, (slope = 1.31,  $t = 3.31$ ,  $P < 0.001$ ), and *consumer* models  
301 (slope = 1.35,  $t = 3.88$ ,  $P < 0.001$ ). However, PC-1 scores for *basal* model webs were not  
302 influenced by metabolic rate (slope =  $-0.59$ ,  $t = -1.63$ ,  $P = 0.10$ ). PC-2 scores varied with  
303 metabolic rate ( $F_{1,974} = 26.79$ ,  $P < 0.001$ ), foundation species model ( $F_{3,974} = 5.44$ ,  $P < 0.01$ ), and  
304 their interaction ( $F_{3,974} = 8.59$ ,  $P < 0.001$ ) (Fig. 5C). PC-2 scores increased with metabolic rate  
305 in *basal* (slope = 0.7,  $t = 2.84$ ,  $P < 0.01$ ) and *consumer* (slope = 1.57,  $t = 2.55$ ,  $P < 0.05$ ) model  
306 webs, but decreased with metabolic rate in *total* model webs (slope =  $-0.14$ ,  $t = -2.03$ ,  $P < 0.05$ )  
307 and showed no change in *control* webs (slope =  $-0.03$ ,  $t = -1.87$ ,  $P = 0.06$ ).

308

## 309 DISCUSSION

310 Our simulations have illustrated that foundation species can play an important role in the  
311 assembly and collapse of food webs. By definition, foundation species influence community  
312 composition and functioning largely through non-trophic interactions (Ellison et al. 2005). Here,  
313 we have shown that the trophic position of the species that receive benefits (in this case a  
314 decrease in metabolic rate) from the presence of a foundation species can influence the food web  
315 assembly process and the response of a food web to the loss of a foundation species. When a  
316 foundation species lowered the metabolic rate of only basal species the resultant webs were  
317 complex and species-rich. In general, *basal* model webs also were robust to foundation species  
318 removals, retaining high species richness and complexity. On the other hand, when a foundation  
319 species lowered the metabolic rate of only consumer species (our *consumer* model), all species  
320 (*total* model), or no species (*control* model) the resultant webs were species-poor and the  
321 consumer webs had low complexity (i.e. low  $C$ ,  $LS$ , clustering coefficient). Furthermore, the



322 subsequent removal of the foundation species from the *consumer*, *total*, and *control* model webs  
323 resulted in a greater loss of species and complexity than in the *basal* model webs.

324         One potential explanation for the species-rich complex food webs produced by *basal*  
325 models and the species-poor simplified webs produced by the *consumer* and *total* models may be  
326 found in the population dynamics of the system. When a foundation species lowers the metabolic  
327 rate of the consumers (top predators and intermediate consumers in both the *consumer* and *total*  
328 models), consumer populations reach higher abundances, which in turn can lead to stronger  
329 predator-prey interactions (Holling 1965, Abrams and Ginzberg 2000). Strong interactions can  
330 lead to unstable predator-prey dynamics and result in the extinction of both the predator and the  
331 prey species (May 1972, McCann et al. 1998). In the *basal* model, lower metabolic rates  
332 increased energy for growth and reproduction, allowing basal species to withstand transient  
333 dynamics of early assembly or low initial population abundances. Once gaining a foothold, even  
334 non-foundational basal species can provide multiple energy pathways to species at higher trophic  
335 levels. And once the foundation species was removed, the other basal species were already  
336 established and maintained energy pathways to higher trophic levels, limiting further extinctions.  
337 This mechanism is also consistent with the standard facilitation model of succession (Connell  
338 and Slatyer 1977), where later-successional (facilitated) species can maintain high abundances  
339 even after early-successional species have disappeared. Two important differences, however, are  
340 that in the field, foundation species persist in the system much longer than early-successional  
341 species, and associated species composition changes dramatically following foundation species  
342 removal (e.g., Orwig et al. 2013).

343         In addition to the trophic position of the target species that a foundation species  
344 influences, the magnitude of the metabolic rates of the associated species in the absence of the

345 foundation species (or more generally, the cost of not having the foundation species) was also  
346 important in determining food-web structure and the response of food webs to foundation species  
347 removal. When metabolic rates were highest in the absences of foundation species (the  $10\times$   
348 treatment), webs lost the most species both during assembly and after removal of the foundation  
349 species. The  $10\times$  treatment also was the only one for which webs collapsed entirely (to zero  
350 species). This collapse was observed most frequently in the *control* webs, in which the  
351 foundation species did not have any non-trophic interactions with other species. Interestingly,  
352 *basal* model webs in the  $10\times$  metabolic rate group maintained species richness at levels similar  
353 to those seen in the lower metabolic rate treatments. This result is consistent with that seen in the  
354 *food-web assembly* dynamics, and implies that facilitation of basal species by foundation species  
355 can overcome even the highest metabolic rates (costs). Overall, our results suggest that  
356 foundation species that influence other basal species will result in robust food webs, whereas  
357 those that influence consumers lead to the loss of species and complexity both during the  
358 assembly process and after foundation species removal. Additionally, these effects are magnified  
359 when metabolic costs to other species increase in the absence of the foundation species.

360 In our models, foundation species exerted influence by lowering metabolic rates for  
361 certain species. This is only one type of non-trophic interaction that can occur in a food web, and  
362 it is likely that foundations species have many other non-trophic interactions and effects (e.g.,  
363 providing refuge from predators, facilitating establishment; Kéfi et al. 2012) that deserve further  
364 exploration. In addition, in all of our models, foundation species had a positive influence on all  
365 species at similar trophic positions. In real food webs, however, this generalization is unlikely to  
366 hold, as foundation species can have different effects on species that share the same trophic  
367 position and may also have negative effects on some species in the food web (e.g., Ellison et al.

368 2005b, Sackett et al. 2010, Prevey et al. 2010, Kane et al. 2011). Furthermore, the effects of  
369 foundation species in our simulations are strongest when associated species do really poorly  
370 without the foundation species present (i.e., the  $5\times$  and  $10\times$  metabolic treatments). This result  
371 implies that the role of a foundation species largely depends on the magnitude of its influence,  
372 but weak trophic (McKann et al. 1998, Neutel et al. 2002, Rooney and McCann 2012) and  
373 facilitative links (Allesina and Tang 2012) are also import in maintaining network structure and  
374 dynamics. Thus, measuring the influence of foundation species on other species in the food web  
375 through experimental removal studies (e.g., Ellison et al. 2010, Sackett et al. 2010) will continue  
376 to be an important component of understanding foundation species roles in the assembly and  
377 collapse of food webs.

378         Future exploration of foundation species in both modeled and real food webs should  
379 consider how foundations species differentially influence species in similar trophic positions, the  
380 threshold of metabolic rates (or other factors that foundations species influence) at which food  
381 webs respond, and non-trophic interactions that influence model parameters other than metabolic  
382 rate. Nonetheless, this first theoretical exploration of foundation species in a food-web context  
383 shows that we should look for foundation species to strongly influence basal species, leading to  
384 robust species-rich food webs that are the least susceptible to cascading extinctions when  
385 foundation species are lost.

386

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515 Table 1. Model Variables

Parameter	Description	Value or Equation
$M_i$	Body mass of species $i$	eq.1
$Z$	Predator-prey biomass ratio	$10^2$
$T$	Trophic level	Calculated using the prey-averaged method
$B_i$	Biomass of species $i$	Initial draw from Uniform[0.5,1]
$r_i$	Mass specific growth rate of species $i$	1
$K$	Carrying capacity	1
$G_i$	Logistic growth rate of species $i$	$1-(B_i/K)$
$x_i$	Mass specific metabolic rate of species $i$	0.01
$y_i$	Maximum consumption rate of species $i$	8
$e_{ji}$	Assimilation efficiency for species $i$ when consuming species $j$	0.85 for carnivores 0.45 for herbivores
$f_{ij}$	The fraction of species $j$ that is ingested by species $i$	1
$F_{ij}$	Functional response for species $i$ feeding on species $j$	eq. 3
$w_{ij}$	the uniform relative consumption rate of consumer $i$ preying on resource	1/number of prey items
$B_0$	Half-saturation constant	0.5
$R$	Production	eq. 4a
$X$	Metabolism	eq. 4b
$Y$	Maximum consumption rate	eq. 4c
$a_r$	Allometric constant	1

$a_x$	Allometric constant	0.314
$x_a$	Metabolic rate in the absence of the foundation species	Depends on model run; see <i>exploring parameter space</i>
$x_{fsp}$	Metabolic rate of target species in the presence of the foundation species	Depends on model run; see <i>exploring parameter space</i>
$B_a$	Typical biomass for the foundation species	1

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517

518 Table 2. Metrics of food-web structure

<b>Metric</b>	<b>Definition*</b>
C	connectance, or the proportion of possible links realized. $C = L/S^2$ , where L is number of links and S is the number of species
S	species richness
LS	linkage density = $L/S$ , number of links per species
ClustCoef	clustering coefficient, probability that two taxa linked to the same taxon are also linked
PathLen	characteristic path length, the mean shortest set of links (where links are treated as undirected) between species pairs
Top	percentage of top species in a web (taxa have no predators)
Int	percentage of intermediate species in a web (taxa with both predators and prey)
Omniv	percentage of omnivores in a web (taxa that feed on more than one trophic level)
Herbiv	percentage of herbivores in a web (taxa that only prey on basal species)
Basal	percentage of primary producers in a web (taxa that have no prey)

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520

521 Table 3. Principal component loadings for food-web structure after food-web assembly ( $t =$   
 522 2,000 modeled time steps) and after foundation species removal ( $t = 4,000$  time steps).

523

Metric	After assembly ( $t = 2,000$ )		After foundation species removal ( $t = 4,000$ )	
	PC1	PC2	PC1	PC2
	(52%)	(15%)	(41%)	(19%)
S	-0.34	0.40	0.36	0.39
LS	-0.40	0.17	0.45	-0.02
C	-0.22	-0.46	0.16	-0.66
Top	0.26	0.32	-0.23	-0.06
Int	-0.40	0.11	0.41	0.15
Basal	0.32	-0.38	-0.39	-0.15
Herbiv	0.28	0.20	-0.17	0.06
Omniv	-0.36	0.19	0.34	0.00
PathLen	0.26	0.31	-0.18	0.59
ClusterCoeff	-0.27	-0.41	0.30	-0.14

524

525

526 Figure Legends

527 Fig. 1. Schematic diagrams of the four foundation species models; A) *control*, B) *basal*,  
528 C) *consumer*, D) *total*. White nodes are basal foundation species, gray nodes are other basal  
529 species, and black nodes are consumers. Solid black lines with arrows represent trophic  
530 interactions and dashed lines are non-trophic interactions (i.e., reduction in metabolic rate).

531

532 Fig. 2. Saturating functions (eqn. 6) relating metabolic rate to foundation species  
533 biomass. A) In the absence of a foundation species, species have the baseline, allometrically-  
534 scaled metabolic rate (dashed line; eqn. 5b). Increasing the biomass of the foundation species  
535 results in an asymptotic decline in metabolic rate to  $0.5\times$  (green),  $0.2\times$  (magenta), or  $0.01\times$   
536 (cyan) the baseline. B) When foundation species biomass = 0, species have metabolic rates  $10\times$   
537 (blue),  $5\times$  (red), or  $2\times$  (orange) the baseline, allometrically-scaled metabolic rate (dashed line).  
538 As the biomass of the foundation species increases, metabolic rate declines asymptotically to the  
539 baseline. These functions are the six metabolic rate treatments that we applied to the predator-  
540 prey model.

541 Fig. 3. ANCOVA plots illustrating species richness (A) and principal axis scores (B, C)  
542 of food-web structure after food-web assembly (at  $t = 2,000$  modeled time steps) as a function of  
543 metabolic rate and the four types of foundation species models. Green lines and points  
544 correspond to the *basal* model, Pink = *consumer* model, Blue = *total* model, and Orange =  
545 *control* model.

546

547

548 Fig. 4. Principal component biplots of food-web metrics for assembled food webs (at  $t =$   
549 2,000 modeled time steps). Illustrations along each PC axis depict representative individual  
550 webs.

551 Fig. 5. ANCOVA plots illustrating species richness (A) and principal axis scores (B, C)  
552 of food-web structure after foundation species removal (at  $t = 4,000$  modeled time steps) as a  
553 function of metabolic rate and the four types of foundation species models. Green lines and  
554 points correspond to the *basal* model, Pink = *consumer* model, Blue = *total* model, and Orange =  
555 *control* model.

556 Fig. 6. Principal component biplots of standardized change in food-web metrics for food  
557 webs after foundation species removal (i.e.,  $\Delta Z = z_{t=2001} - z_{t=4000} / z_{t=2001}$ ). Text along each PC axis  
558 show general change in food web complexity and richness associated with each axis.

559

560