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Incorporating Demographic Diversity into Food Web Models: Effects on Community Structure and Dynamics

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15 **Abstract**

16 Life history strategies affect population dynamics; however, their effects on community dynamics
17 remain poorly understood. A food web model with stage-structured populations (structured food web)
18 and an equivalent model with unstructured populations (unstructured food web) were developed, and
19 their structures and dynamics were compared. Both models incorporated energetic processes and
20 allowed populations to go extinct and invade over time. The results from the two models shared some
21 similarities. For example, all of the initial randomly-formed food webs were unstable, but the extinction
22 and invasion rates of populations declined over time. However, there were also clear differences
23 between them. For example, preventing trophic interactions among similar-sized organisms led to a
24 large increase in the number of persisting consumer populations under the unstructured food web, but
25 the number was almost unchanged under the structured food web. Furthermore, an increase in the
26 carrying capacity of primary producers caused an increase in the population extinction rate of
27 consumers under the structured food web, but the extinction rate declined under the unstructured food
28 web. Finally, the average trophic level of consumers in the unstructured food web was often at 2,
29 indicating the food web primarily consisted of herbivores. On the other hand, the average trophic level
30 in the structured food web was significantly higher, indicating the existence of trophic interactions
31 among consumers. These results suggest the importance of incorporating stage structures into food web
32 models to bridge the current theories of food web dynamics and empirical observations because nature
33 consists of structured populations. In particular, I conclude that if one wants to study trophic
34 interactions beyond herbivory, it is crucial to incorporate structured populations into food web models.

35 **Keywords:** Competition, Diversity, Life history evolution, Predator-prey, Structured population, Trophic
36 interactions

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38 **1. Introduction**

39 Nature is a full of diversity in terms of their durations of developmental stages, which are defined by
40 survival, reproduction, and developmental rates of individuals in a population (Cole, 1954). This type of
41 diversity is herein termed demographic diversity. Demographic diversity plays an important role in
42 determining population dynamics (e.g. Fujiwara, 2007; Jeppsson and Forslund, 2012; Neubert and
43 Caswell, 2000; Tuljapurkar et al., 2009b), and its importance on community dynamics has been
44 suggested (De Roos et al., 2003; Giacomini et al., 2013; Zhou et al., 2013). For example, Wollrab et al.
45 (2013) demonstrated that a stage-structured predator can promote the diversity of its prey because a
46 bottleneck in the life cycle of the predator can reduce predation pressure on some of its prey, which
47 otherwise may be competitively excluded. Their study demonstrated the potential importance of
48 demographic diversity on population interactions and motivated the current study to investigate how
49 demographic diversity plays a role in determining the structure and dynamics of a food web consisting
50 of a large number of structured populations.

51 Another set of recent studies also focused on how ontogenetic niche shifts affect food web
52 dynamics (Nakazawa, 2015). Ontogenetic niche shifts occur partly because individuals in a population go
53 through ontogenetic changes in their body size, which affects feeding relationships between consumers
54 and resources (Werner and Gilliam, 1984). For example, Rudolf and Lafferty (2011) argued that a
55 population as a whole may be a generalist, but each life stage within the population may be specialized
56 in a certain resource, making a stage-structured population more vulnerable to resource losses than an
57 unstructured population. This idea has been supported by a series of experimental studies (Rudolf and
58 Rasmussen, 2013a, b). In the current study, the food web model that incorporates ontogenetic niche
59 shifts and demographic diversity of consumers was developed. The model was motivated by the idea
60 that populations can adjust their reproductive values and densities among stages, which can experience
61 different niches, to optimize their life history strategies for their persistence (Fujiwara et al., 2011).

62 The current study also fits under a subset of ongoing studies investigating the relationships
63 between species diversity (number of populations of different species) and the properties of ecological
64 communities. Earlier studies argued that species diversity should increase the stability of a community
65 because an increased number of interactions would attenuate population fluctuations reducing the
66 chance of population explosions (Elton, 1927) or an increased number of energetic pathways to
67 consumers would reduce the chance of their population extinction (MacArthur, 1955). On the other
68 hand, a subsequent study using a mathematical model demonstrated that species diversity should

69 reduce stability (May, 1972). Since these pioneering works, numerous studies, both empirical
70 observations (e.g. Cohen et al., 1993; Gross et al., 2014; MacDougall et al., 2013; Martinson et al., 2012;
71 Mora et al., 2011; Winemiller, 1990) and mathematical modeling (e.g. Allesina and Tang, 2012;
72 DeAngelis, 1975; Ives and Carpenter, 2007; Lorrilliere et al., 2012; Otto et al., 2007; Petchey et al., 2008;
73 Yodzis, 2000) were conducted, and these studies have been reviewed by a number of researchers (e.g.
74 Hooper et al., 2005; McCann, 2000; Rooney and McCann, 2012). A majority of recent research has
75 focused on attempting to understand the properties of communities with adapted populations (e.g.
76 Otto et al., 2007; Rooney and McCann, 2012; Rooney et al., 2008) because natural communities are
77 comprised of selected populations (May, 2006; Yodzis, 1981). However, the investigations of the
78 dynamics of randomly assembled communities still continue (e.g. Allesina and Tang, 2012). Therefore, I
79 also investigated how the dynamics of food webs change as they are assembled through a series of
80 population extinctions and invasions.

81 Here, I investigated the properties of a food web model with stage-structured consumers
82 (hereafter structured model/food web) and an equivalent model with unstructured consumers
83 (hereafter unstructured model/food web). The models were formulated as a system of ordinary
84 differential equations (ODEs), which were treated as semi-continuous time models. The continuous-time
85 formulations allowed the incorporations of individual-level events occurring simultaneously within a
86 population (i.e. birth, death, predation, and development). The discrete-time nature of the models
87 allowed the simple incorporations of population-level events (i.e. extinctions and invasions). The food
88 web models were built as a collection of interacting populations rather than individual-based models;
89 this allowed fast simulations of the models, permitting multiple replications of the model simulations.

90 **2. Methods**

91 The food web models in this study included 10 primary producers and 15 consumers although some of
92 the populations could go extinct (i.e. having a density of 0). The total number of populations was fixed
93 so that the total number of equations in a model remained the same over time. Each of the consumer
94 populations consisted of two stages under the structured food web and a single stage under the
95 unstructured food web. Under both models, primary producers were unstructured (i.e. consisting of a
96 single stage). Consumers fed on primary producers and/or other consumers (collectively referred to as
97 resources), and feeding interactions were determined by the body sizes of potential consumer and
98 resource stages (Fig. 1). The survival of individuals, development among stages, and reproduction were

99 governed by energetic processes. The basic idea behind the energetic model in this study originated
 100 from the dynamic energy budget models (Nisbet et al., 2000) although the processes were substantially
 101 simplified to accommodate the complexity of food webs. For example, to reduce the number of state
 102 variables, the models in this study did not keep track of energy reserve within individuals.

103 A simulation of a model food web begun with populations with randomly selected individual
 104 body sizes (traits), but it experienced the extinctions of populations and resettlements of previously
 105 extinct populations. Furthermore, consumer populations with new traits (i.e. new species) invaded the
 106 system by replacing some of the extinct populations. Consequently, the composition of life history
 107 strategies, which were determined by individual body sizes, and the number of persisting populations in
 108 the food web changed over time. During this food web assembly process, changes in the properties of
 109 the food web were recorded; these properties included the number and biomass of persisting
 110 populations, rates of extinctions and invasions, number of population interactions, and mean trophic
 111 level of consumers. These properties were compared between the structured and unstructured food
 112 webs under five different scenarios that were different in the niche width of consumers (as determined
 113 by the range of resource body size that consumers can feed) and the carrying capacity for primary
 114 producers.

115 The food web models included three basic processes: population dynamics, population
 116 interactions, and energetics. These processes, along with the algorithm for simulating the models, are
 117 described in more detail.

118 **2.1 Population Dynamics**

119 A stage-structured consumer population consisted of juvenile and adult stages. Only adults could
 120 reproduce, and their offspring were assumed to become juveniles immediately. Individuals in each stage
 121 could die from three possible causes: being consumed by others (consumption death), starvation
 122 (starvation death), and other natural causes (natural death). Suppose $n_{i,s}$ was the density of individuals
 123 in stage i (1: juveniles and 2: adults) of population s , then the dynamic equations were as following:

$$\begin{aligned}
 \frac{dn_{1,s}}{dt} &= b_s(N, W) - g_s(N, W)n_{1,s} - f_{1,s}(N, W)n_{1,s} - p_{1,s}(N, W)n_{1,s} - mn_{1,s}, \\
 \frac{dn_{2,s}}{dt} &= g_s(N, W)n_{1,s} - f_{2,s}(N, W)n_{2,s} - p_{2,s}(N, W)n_{2,s} - mn_{2,s},
 \end{aligned}
 \tag{1}$$

125 where N was a vector of stage densities ($n_{i,s}$), W was a vector of stage-specific individual mass ($w_{i,s}$),
 126 $b_s(N, W)$ was a per-population birth rate, $g_s(N, W)$ was a per-capita (per-juvenile) development
 127 rate from juvenile to adult, $f_{i,s}(N, W)$ was a per-capita starvation-death rate, $p_{i,s}(N, W)$ was a per-
 128 capita consumption-death rate, and m was a per-capita “natural” death rate (Table 1). Because
 129 starvation- and predation-deaths were modeled separately, the natural deaths excluded these
 130 processes. The natural death rate was also independent of size and density; however, the two
 131 dependencies were incorporated into the starvation death rate $f_{i,s}(N, W)$ and the consumption death
 132 rate $p_{i,s}(N, W)$. The model was not individual-based; therefore, it did not keep track of the transitions
 133 of any particular individuals among stages. Instead, it modeled changes in the stage-specific densities of
 134 individuals. However, conceptually, the incorporation of the natural death rate reduced the possibility of
 135 individuals remaining in any one stage for perpetuity.

136 Under the unstructured food web, consumer populations consisted of only one stage (adults),
 137 and offspring were assumed to become adults immediately. Their dynamics were given by

$$138 \quad \frac{dn_{3,s}}{dt} = b_s(N) - f_{3,s}(N)n_{3,s} - p_{3,s}(N)n_{3,s} - mn_{3,s}. \quad (2)$$

139 The notations were the same as those for the structured food web except $i = 3$ was used as a subscript
 140 to denote unstructured consumers.

141 Under both the structured and unstructured food webs, the dynamics of primary producers
 142 were given by the logistic equation with a consumption-death rate:

$$143 \quad \frac{dn_{0,s}}{dt} = r_s n_{0,s} \left(1 - \frac{n_{0,s}}{k} \right) - p_{0,s}(N, W) n_{0,s}, \quad (3)$$

144 where r_s was the intrinsic per-capita population growth rate, k was the carrying capacity, and
 145 $p_{0,s}(N, W)$ was the per-capita consumption-death rate. The subscript $i = 0$ was used for denoting
 146 primary producers. The carrying capacity was set to an arbitrary value 10 for all primary producers as a
 147 reference case (Scenario 1; Table 2), and, for a comparison purpose, it was increased to 100 (Scenario 4)
 148 or allowed to fluctuate periodically (Scenario 5). This formulation assumed that each primary producer
 149 was limited by a different environmental resource so that they could co-exist when they did not

150 experience consumption-deaths. Competitions among primary producers for an available resource were
 151 a potentially interesting factor to incorporate; however, they were omitted in the current study so that
 152 the investigation could be focused on the effect of the demographic diversity of consumers on food web
 153 structure and dynamics.

154 **2.2 Population Interaction**

155 Individuals in a consumer population could feed on individuals in other populations (both primary
 156 producers and other consumers). I assumed no cannibalism; therefore, adults and juveniles of the same
 157 population could not eat each other. I also assumed that all individuals in the same stage had the same
 158 body size. The existence of a feeding interaction was determined by the body sizes of potential
 159 consumer and resource stages. Suppose $l_{i,s}$ was the length of individuals in stage i of population s .
 160 Then, individuals in stage y of population A (potential consumers) could feed on individuals in stage
 161 x of population B (a potential resource) if

$$162 \quad c_1 l_{y,A} < l_{x,B} < c_2 l_{y,A}, \quad (4)$$

163 where $0 < c_1 < c_2$. Therefore, the fundamental niche width for a consumer was determined by the two
 164 parameters c_1 and c_2 along with the length(s) of the consumer. I explored different values of c_1 and
 165 c_2 to determine a potential role of niche width in determining the structure and dynamics of food webs
 166 (Scenarios 1-4; Table 2; Fig. 1).

167 The per-capita consumption-death rate of stage x of population B was given as

$$168 \quad p_{x,B}(N) = \alpha_{x,B} \sum_{\{i,s\} \in \Omega_{consumer}} \beta_{i,s} n_{i,s} \quad (5)$$

169 where $\Omega_{consumer}$ was the set of stage and population indices (i and s , respectively) of the consumers
 170 that satisfy inequality (4) for stage x of population B as a resource, and $\alpha_{x,B}$ and $\beta_{i,s}$ were the
 171 vulnerability of a resource and consumption efficiency of a consumer, respectively (Table 1). The
 172 vulnerability $\alpha_{x,B}$ was assumed to decline with the body size of a resource stage and asymptotes to 0,
 173 and the consumption efficiency was assumed to increase with the body size of a consumer stage.
 174 Choosing the simplest forms, I allowed $\alpha_{x,B}$ to change inversely with the length of a resource, and $\beta_{i,s}$
 175 to change linearly with the length of a consumer.

176 2.3 Energetic Model

177 Development, birth, and starvation-death rates were based on the energy intake and expenditure of
 178 individuals. First, consumed energy was used for satisfying maintenance. The per-capita energetic
 179 requirement for stage y of population A , denoted by $E_{y,A}$, was a function of mass-specific energy
 180 requirement (μ) and the mass of an individual ($w_{y,A}$) as following:

$$181 \quad E_{y,A} = \mu w_{y,A}^{3/4}. \quad (6)$$

182 This formulation assumed that the energy requirement scaled with the power of $\frac{3}{4}$ of body mass,
 183 which had been demonstrated with endotherms (Kleiber, 1947).

184 A per-capita intake rate $I_{y,A}$ was given as

$$185 \quad I_{y,A} = \gamma \beta_{y,A} \sum_{\{i,s\} \in \Omega_{resource}} \alpha_{i,s} w_{i,s} n_{i,s}, \quad (7)$$

186 where γ was the assimilation efficiency and $\Omega_{resources}$ was the set of stage and population indices (i
 187 and s , respectively) of the resources that satisfy inequality (4) for stage y of population A as a
 188 consumer.

189 When the intake rate was smaller than the expenditure ($I_{y,A} < E_{y,A}$), the mortality rate
 190 increased exponentially with the energy deficiency

$$191 \quad f_{y,A}(N) = e^{0.1 \times (E_{y,A} - I_{y,A})} - 1. \quad (8)$$

192 Because the energy expenditure exceeded the input, there was no development or birth (i.e.

$$193 \quad g_s(N) = 0 \text{ or } b_s(N) = 0).$$

194 On the other hand, when the energy intake was greater than or equal to the energy expenditure
 195 ($I_{y,A} \geq E_{y,A}$), the per-capita instantaneous mortality from starvation was 0 (i.e. $f_{y,A}(N) = 0$), and the
 196 excess energy was used for development or reproduction. The per-capita development rate from a
 197 juvenile to an adult was

198

$$g_s(N) = \frac{\delta \times (I_{1,s} - E_{1,s})}{w_{2,s} - w_{1,s}}, \quad (9)$$

199 where $1 - \delta$ was a proportion of the energy used for an overhead energetic cost for development. In
 200 this study, 50% of the energy ($\delta = 0.5$) was assumed to become available for development. The
 201 development rate was a function of the difference between the sizes of the two stages. The larger the
 202 size difference, the longer it took to develop from one stage to the next. These rates also depended on
 203 the energy intake. As more food became available, development from one stage to the next became
 204 faster. These were two of the important features of the model in this study. Consequently, the life
 205 history of a population was determined by the size distribution of individuals within a population (trait)
 206 as well as food availability (environment). Equation (8) was similar to the one derived from a detailed
 207 individual-based physiological model by De Roos et al. (2008) except that their model predicted
 208 compensatory non-linearity of the development rate with the available energy. I omitted the non-linear
 209 multiplier in De Roos et al. (2008) to make the model simpler on the basis that we still have uncertainty
 210 in how individuals' physiology and behavior compensate for starvation or excess energy availability.

211 Finally, the population birth rate was given as

$$b_s(N) = \frac{\delta (I_{2,s} - E_{2,s})}{w_{1,s}} n_{2,s}. \quad (10)$$

213 Therefore, the birth rate was a function of the size of juveniles. In this study, 50% of the energy
 214 ($\delta = 0.5$) was also assumed to become available for reproduction. In two extreme cases, a large
 215 number of small offspring or a small number of large offspring could be produced. For an unstructured
 216 population, per-capita birth rate was given by equation (10) after replacing all of the stage indices
 217 (including that of the mass) with 3, indicating unstructured consumers.

218 2.4 Simulations

219 Each simulation consisted of solving the system of ODEs from time $t=0$ to 500, allowing existing
 220 populations to go extinct and new populations to invade, and iterating these processes 300 times (Fig. 2).
 221 Treating the system of ODEs as a semi-continuous time model alleviated a problem associated with
 222 numerical rounding errors when state variables were near 0. Although the equations were deterministic,
 223 they were used for simulations. Apart from the initial random assembly of the food web, the
 224 randomness in the simulation was introduced in the body sizes of invading consumers and initial

225 population densities of invading consumers and resettled populations (Table 1). The process of
226 simulating a food web is described in more detail below.

227 Initially, food web was randomly assembled. First, the intrinsic growth rates and body sizes of
228 primary producers were assigned randomly (Table 1). In this simulation, the primary producers
229 maintained the same intrinsic growth rates and body sizes over time. Then, the body sizes of consumer
230 stages were randomly assigned (Table 1). Finally, the initial stage densities of both consumers and
231 primary producers were randomly assigned by simulating uniform random distribution between 0 and
232 10.

233 Once the initial random food web was formed, the system of the ODEs was solved from $t=0$ to 1.
234 At $t=1$, if stage densities were less than a quasi-extinction threshold (1×10^{-6} , which was also the
235 maximum tolerance level of the ODE solver used in this study), those densities were set to 0. Then, the
236 processes of solving the ODEs and setting the densities of quasi-extinct stages to 0 at every integer time
237 were continued until $t=500$.

238 After solving the system of ODEs from $t=0$ to 500, the extinctions of populations were
239 determined, and new populations were introduced as invading populations. In this simulation, if the
240 sum of the stage densities of a population was below 1×10^{-6} , the population was considered extinct.
241 Although populations did not always reach the asymptotic dynamics, which were either stable at an
242 equilibrium point or exhibiting periodic dynamics, I still considered all of the populations above the
243 threshold to be persisting in the system because such populations would not be considered extinct
244 under *in situ* observations. Then, among the extinct populations, five populations were randomly
245 selected, and they were replaced with invading populations with randomly assigned body sizes. The rest
246 of extinct populations were allowed to resettle into the system with the same body sizes as before.
247 Under almost all occasions, more than five consumers were extinct. However, when less than five
248 consumers were extinct, all extinct consumers were replaced with invading populations to maintain the
249 maximum number of consumers rather than changing the number of equations. Stage densities of the
250 invading and resettling populations received new randomly assigned small densities (uniformly
251 distributed between 1×10^{-6} and 1×10^{-2}). Then, the food web was solved from $t=0$ to 500 again, and
252 this was iterated 300 times. This process was treated as if a food web was projected by one “time step”
253 by solving ODEs from time $t=0$ to 500, and this projection was iterated over 300 time steps. The results
254 were only evaluated at the end of each time step (i.e. at 300 time steps).

255 Finally, each scenario of each model was simulated independently 80 times to yield food web
256 replicates. Unless otherwise noted, the means and associated standard errors were calculated over the
257 80 replicates under the same scenario. To reduce the effects of differences in the properties of primary
258 producers, 80 sets of intrinsic population growth rates of primary producers were simulated once, and
259 the same sets were used for structured and unstructured food webs of all scenarios.

260 All calculations were done with MATLAB (MATLAB, 2012). For pseudo-random number
261 generations, command “rand” was used. A different seed for the random number generator was used
262 each time the software was started in order to avoid using the same seed for the random number
263 generations among replicates under the same scenario. For solving the system of ordinary differential
264 equations, function “ode45” with the default options was used.

265 **3 Results**

266 The results under Scenario 1 are presented first as a reference case. These results are, then, compared
267 with the results under other scenarios. Because a large number of results exist, selected results are
268 presented in the main text, and additional results are provided online as Supplementary Material.

269 **3.1 Reference Case (Scenario 1)**

270 The initial randomly assembled food web consisting of 10 primary producers and 15 consumers,
271 whether structured or unstructured, was unstable. It should be noted that, a food web (not a
272 population) was considered stable in this study when the number of persisting populations remained
273 steady; under a stochastic model, this was achieved when the mean number of extinctions was equal to
274 the mean number of successful invasions over a window of time. The average number of persisting
275 consumers at time step 1 (after the initial extinction process) was around 2 under the unstructured
276 model and around 3 under the structured model. However, as they experienced a series of invasions
277 and extinctions, the number of persisting consumers increased (Fig. 3a). The unstructured model
278 reached stability faster than the structured model. Under this particular scenario, the number of
279 persisting consumers under the structured food web was much greater than that under the
280 unstructured food web. The total biomass of consumers under both models also increased quickly with
281 time steps (Fig. 3b).

282 The average numbers of extinctions and invasions of consumers were greater at the beginning
283 (e.g. time steps 1-50) than latter time steps regardless of whether the populations were structured or

284 unstructured (Fig. 3c-d). This was true even though a food web consisted of a small number of persisting
285 populations initially (Fig. 3a), indicating a high turnover rate of consumers. A large number of extinctions
286 during the initial time steps were accompanied by an even larger number of successful invasions,
287 increasing the number of persisting populations. As the number increases, both extinctions and
288 successful invasions declined. Because the number of persisting populations was much greater under
289 the structured food web than the unstructured food web, per-population rate of extinction (i.e.
290 population extinction probability) was much lower under the structured food web than the unstructured
291 food web.

292 Primary producers exhibited slightly different temporal dynamics (Fig. 4a-b) compared with
293 consumers. Under both models, the initial randomly assembled food webs consisted of very small
294 number of primary produces. Under the unstructured model, the number of persisting primary
295 producers reached the maximum at time step 2 and declined thereafter, quickly reaching an asymptote.
296 Under the structured model, the number of primary produces increased initially and started to decline
297 after approximately 30 time steps. The total biomass of primary producers under both structured and
298 unstructured food webs declined with time steps even though the biomass of consumers increased with
299 time steps.

300 The mean trophic level of consumers (Fig. 5a) fluctuated widely under the structured model
301 whereas it remained at a constant level under the unstructured model. The number of interactions per
302 stage (Fig. 5b) rapidly reached stability under the unstructured food web whereas it took longer under
303 the structured model. The increase in the trophic level along with the change in the mean biomass of
304 consumers (Fig. 3b) indicated changing life history strategies of persisting consumers over time under
305 the structured model. The trophic level of consumers under the unstructured model was approximately
306 2, indicating they were mostly herbivorous; on the other hand, it was higher under the structured model,
307 indicating the consumptions of other consumers (predator-prey interactions) were occurring in the
308 system. The mean number of interactions under the unstructured food web was less than 1. This was
309 because a large number of persisting populations were primary producers and many of them persisted
310 without being preyed upon by any consumers (i.e. no population interaction).

311 **3.2 Comparisons of other scenarios with the reference case**

312 An increase in c_1 (the relative minimum resource size that consumers can feed; Scenario 2) allowed
313 more stages with a small body size to avoid consumption deaths. This had some similar effects on both

314 structured and unstructured food webs. The number and total biomass of both persisting consumers
315 (Fig. 6a, 6b) and primary producers (Fig. 6c, 6d) and the net primary production (Fig. 6e) increased
316 significantly whereas the rate of extinction declined under both models (Fig. 6f). However, the average
317 trophic level (Fig. 6g) increased significantly under the structured model, but it declined under the
318 unstructured model. Similarly, the number of population interactions per stage (Fig. 6h) declined under
319 the structured food web, but it remained the same under the unstructured food web.

320 A reduction in c_2 (the relative maximum resource size that consumers can feed; Scenario 3)
321 meant multiple stages could co-exist at similar body size without eating each other (e.g. stages with
322 length between 0.8 and 1.0 can co-exist without feeding interactions). The reduction in c_2 increased
323 the number of persisting consumers (Fig. 6a); this effect was especially pronounced under the
324 unstructured food web. On the other hand, the biomass of consumers was reduced under both models
325 (Fig. 6b). This reflected the reduction in the net primary production (Fig. 6e). On the other hand, the
326 number and biomass of primary producers changed only slightly (Fig. 6c, 6d). The average trophic level
327 (Fig. 6g) declined whereas the number of interactions increased under both models (Fig. 6g, 6h). Finally,
328 the rate of extinction increased under the structured food web whereas it declined substantially under
329 the unstructured food web (Fig. 6f).

330 An increase in k (the carrying capacity for primary producers; Scenario 4) resulted in different
331 consequences between the structured and unstructured food webs. Under the structured model, the
332 number of consumers (Fig. 6a) declined whereas the biomass of consumers (Fig. 6b) increased. On the
333 other hand, under the unstructured model, the number of consumers remained approximately the same
334 (Fig. 6a), but the total consumer biomass significantly increased (Fig. 6b). The number of primary
335 producers significantly declined under both structured and unstructured models (Fig. 6c); however, the
336 biomass of primary producers increased significantly under the structured food web whereas it
337 remained almost unchanged under the unstructured food web.

338 Finally, the periodic fluctuation in the carrying capacity for primary producers had the least
339 effect among the four scenarios when compared with the reference case. The major effect was in an
340 increase in the trophic level of consumers under the structured model.

341 **3.3 Comparison between structured and unstructured food webs**

342 The number of persisting consumers was often higher under the structured food web compared with
343 the unstructured food web. However, this relationship was reversed when c_2 (the relative maximum
344 resource size that consumers can feed) was reduced. On the other hand, the biomass of consumers was
345 almost always higher under the unstructured food web. The trophic level of consumers and the number
346 of interaction per stage were higher under the structured food web than unstructured food web (Fig. 6).

347 **4 Discussion**

348 Nature consists of structured populations. Therefore, it is important to ask whether we can capture the
349 caricatures of real food webs with the models consisting of unstructured populations or we need to
350 include structured populations. For example, Rudolf and Lafferty (2011) investigated the potential
351 effects of ontogenetic niche shifts on food web dynamics and argued for its importance. My study
352 demonstrated that it is crucial to include stage structured populations because as simple as changing the
353 carrying capacity (k) for primary producers and how populations avoid consumptions (c_2) could lead
354 to conflicting results between the structured and unstructured food webs.

355 A reduction in c_2 (the relative maximum resource size that consumers can feed; Scenario 3)
356 increased the number of persisting consumers under the unstructured food web, but it only had a small
357 effect on the number of consumers under the structured food web. Under the unstructured model, a
358 reduction in c_2 meant an increase in the number of populations with larger adults to co-exist without
359 direct feeding interactions. Under the structured model, the effect was similar except that those
360 populations also had juveniles, which could be eaten by the adults of other populations, and without
361 juveniles, adults cannot be sustained. Consequently, the direct feeding interactions between
362 populations were not necessarily reduced by reduction in c_2 under the structured food web.

363 In addition to ontogenetic niche shifts, demographic diversity plays an important role in food
364 web structure and dynamics. For example, Fujiwara et al. (2011) showed that organisms can adjust their
365 life history strategies to improve their competitive strength against other populations. In this study,
366 populations with large adults tended to have delayed maturation because the difference in sizes between
367 adults and juveniles was large. Populations with large adults (i.e. delayed maturation) could exclude
368 populations with small adults (i.e. early maturation) or *vice versa* when the competition increased

369 between juvenile stages of the former and small adult stages of the latter. Therefore, simple partitioning
370 of available resources is probably not enough to account for complex food-web dynamics.

371 Body size is closely associated with energetic processes (Nisbet et al., 2000); therefore, it is
372 closely associated with life history strategy of populations. In this study, I also assumed that body size
373 determines the existence and strength of feeding interactions. This probably produced very strong
374 coupling of energetic process and feeding interactions. However, natural food webs vary greatly with
375 regard to how feeding interactions are determined. For example, trophic interactions are thought to be
376 structured more by body size under aquatic systems compared with terrestrial systems (Shurin et al.,
377 2006). Other factors, such as behavior, morphology, physiology, and anatomy of organisms, probably
378 play an important role in determining feeding interactions. In my model, consumers cannot feed on
379 larger organisms, but in reality, many examples of small predators feeding on larger prey exist (e.g. wolf
380 feeding on caribou). I suggest incorporating such variations is one of the important future directions of
381 the study toward understanding the structure and dynamics of food webs. The current model allows a
382 relatively easy incorporation of the complexity; it can be incorporated into vulnerability $\alpha_{i,s}$ and
383 consumption efficiency $\beta_{i,s}$ by making them functions of both specific consumer and resource
384 populations.

385 Determining the stability of randomly assembled food webs is still an active area of research (e.g.
386 Allesina and Tang, 2012). My analysis showed that the initial, randomly assembled food webs were
387 always unstable (Fig. 3), which is consistent with the results of May (1972). This is not surprising. For
388 example, if we were to select populations randomly from the global pool of species and assembled a
389 community, it would be very unlikely that the community is stable. Real-world food webs are, instead,
390 comprised of selected populations (May, 2006; Yodzis, 1981). Therefore, it is more informative to
391 investigate food webs consisting of selected populations. My model suggested such food webs have a
392 much reduced extinction rate. At the same time, they also have a reduced invasion rate, suggesting the
393 food webs consisting of selected populations can also resist invasions.

394 Fluctuations in environmental conditions are important mechanisms for the evolution of life
395 history strategies (Tuljapurkar et al., 2009a). Therefore, I expected that the food webs with structured
396 populations to become more stable compared with the ones with unstructured populations under
397 fluctuating environment. On the contrary to this prediction, the model suggested periodic fluctuations in
398 the carrying capacity of primary producers had only small effects on the structure and dynamics of food

399 webs. It is plausible that amplitude of the fluctuation was not large enough or the deterministic (i.e.
400 periodic) nature of the fluctuation made it easy for populations to adapt whether consumers were
401 structured or not. I suggest future studies to investigate the effects of large amplitude and/or stochastic
402 fluctuations in environmental conditions (e.g. Varughese, 2011) on food web structure and dynamics.

403 Because the purpose of this study was to show the difference between the structured and
404 unstructured food webs, I attempted to make the parameters consistent between the two models.
405 However, the actual values were not determined based on empirical studies, and the same parameter
406 values were used for all populations except their body sizes. In reality, the types of consumers (e.g.
407 ectotherms vs. endotherms, predators vs. herbivores) or the types of primary producers (e.g. terrestrial
408 plants vs. phytoplankton) would affect the parameters substantially (Hairston and Hairston, 1993; Yodzis
409 and Innes, 1992). Consequently, the use of any particular value for a parameter across all populations
410 would have not satisfied the complexity of the natural food webs regardless of how carefully the
411 parameter value was obtained, and incorporating population-specific parameters was beyond the scope
412 of the study at this stage. I believe attempts to develop more realistic food web models and to estimate
413 associated parameters empirically should be done in the future. The model in this study provides the
414 basic structure of a model that is balanced between complexity to represent the reality and simplicity to
415 allow multiple replications for accurate evaluations.

416 Under the unstructured models, consumers were almost always herbivores (i.e. the average
417 trophic level was 2). On the other hand, the trophic level of the consumers was higher under the
418 structured food web. Under the unstructured models, populations at a higher trophic level probably
419 could not persist because trophic interactions were so strong that no animal populations could persist as
420 a resource. On the other hand, under the structured models, if one of the stages could avoid being
421 consumed, the population might be able to persist even though the other stage was consumed by other
422 populations. This probably resulted in a higher average trophic level under the structured food webs.
423 Nature consists of food webs with varying maximum trophic levels, and in order to understand the
424 variation, it is important to investigate the balance between competition and consumer-resource
425 interactions (Hairston and Hairston, 1993). My study suggested that understanding these interactions
426 among structured populations is probably crucial for understanding the structure and dynamics of food
427 webs. I speculate that the existence of complex life history strategies and the existence of high trophic
428 levels are closely related with each other.

429 **Acknowledgement**

430 I thank C. Acres, C.B. Piper, K.O. Winemiller, and C. Zhou for valuable feedback on a previous version of
431 this manuscript. I also thank anonymous reviewers whose comments substantially improved the paper.
432 This project was funded in part by an Institutional Grant (NA14OAR4170102) to the Texas Sea Grant
433 College Program from the National Sea Grant Office, National Oceanic and Atmospheric Administration,
434 U.S. Department of Commerce.

435 **References**

- 436 Allesina, S., Tang, S., 2012. Stability criteria for complex ecosystems. *Nature* 483, 205-208.
- 437 Cohen, J.E., Pimm, S.L., Yodzis, P., Saldana, J., 1993. Body sizes of animal predators and animal prey in
438 food webs. *Journal of Animal Ecology* 62, 67-78.
- 439 Cole, L.C., 1954. The Population Consequences of Life History Phenomena. *Q. Rev. Biol.* 29, 103-137.
- 440 De Roos, A.M., Persson, L., McCauley, E., 2003. The influence of size-dependent life-history traits on the
441 structure and dynamics of populations and communities. *Ecol Lett* 6, 473-487.
- 442 De Roos, A.M., Schellekens, T., Van Kooten, T., van de Wolfshaar, K.E., Claessen, D., Persson, L., 2008.
443 Simplifying a physiologically structured population model to a stage-structured biomass model.
444 *Theoretical Population Biology* 73, 47-62.
- 445 DeAngelis, D.L., 1975. Stability and connectance in food web models. *Ecology* 56, 238-243.
- 446 Elton, C.S., 1927. *Animal Ecology*. The Macmillan Company, New York, U.S.A.
- 447 Fujiwara, M., 2007. Extinction-effective population index: Incorporating life-history variations in
448 population viability analysis. *Ecology* 88, 2345-2353.
- 449 Fujiwara, M., Pfeiffer, G., Boggess, M., Day, S., Walton, J., 2011. Coexistence of competing stage-
450 structured populations. *Scientific Reports* 1, 8.
- 451 Giacomini, H.C., DeAngelis, D.L., Trexler, J.C., Petrere, M., 2013. Trait contributions to fish community
452 assembly emerge from trophic interactions in an individual-based model. *Ecol. Model.* 251, 32-
453 43.
- 454 Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Polley, H.W., Reich, P.B., van Ruijven, J.,
455 2014. Species richness and the temporal stability of biomass production: a new analysis of
456 recent biodiversity experiments. *American Naturalist* 183, 1-12.
- 457 Hairston, N.G., Hairston, N.G., 1993. Cause-Effect Relationships in Energy-Flow, Trophic Structure, and
458 Interspecific Interactions. *American Naturalist* 142, 379-411.
- 459 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M.,
460 Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005.
461 Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological*
462 *Monographs* 75, 3-35.
- 463 Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. *Science* 317, 58-62.
- 464 Jeppsson, T., Forslund, P., 2012. Can life history predict the effect of demographic stochasticity on
465 extinction risk? *American Naturalist* 179, 706-720.
- 466 Kleiber, M., 1947. Body size and metabolic rate. *Physiol Rev* 27, 511-541.

467 Lorrilliere, R., Couvet, D., Robert, A., 2012. The effects of direct and indirect constraints on biological
468 communities. *Ecol. Model.* 224, 103-110.

469 MacArthur, R., 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology*
470 36, 533-536.

471 MacDougall, A.S., McCann, K.S., Gellner, G., Turkington, R., 2013. Diversity loss with persistent human
472 disturbance increases vulnerability to ecosystem collapse. *Nature* 494, 86-89.

473 Martinson, H.M., Fagan, W.F., Denno, R.F., 2012. Critical patch sizes for food-web modules. *Ecology* 93,
474 1779-1786.

475 MATLAB, 2012. Ver. 7. The MathWorks, Inc., Natic, Massachusetts, U.S.A.

476 May, R.M., 1972. Will a large complex system be stable. *Nature* 238, 413-&.

477 May, R.M., 2006. Network structure and the biology of populations. *Trends in Ecology & Evolution* 21,
478 394-399.

479 McCann, K.S., 2000. The diversity-stability debate. *Nature* 405, 228-233.

480 Mora, C., Aburto-Oropeza, O., Bocos, A.A., Ayotte, P.M., Banks, S., Bauman, A.G., Beger, M., Bessudo, S.,
481 Booth, D.J., Brokovich, E., Brooks, A., Chabanet, P., Cinner, J.E., Cortes, J., Cruz-Motta, J.J.,
482 Magana, A.C., DeMartini, E.E., Edgar, G.J., Feary, D.A., Ferse, S.C.A., Friedlander, A.M., Gaston,
483 K.J., Gough, C., Graham, N.A.J., Green, A., Guzman, H., Hardt, M., Kulbicki, M., Letourneur, Y.,
484 Perez, A.L., Loreau, M., Loya, Y., Martinez, C., Mascarenas-Osorio, I., Morove, T., Nadon, M.O.,
485 Nakamura, Y., Paredes, G., Polunin, N.V.C., Pratchett, M.S., Bonilla, H.R., Rivera, F., Sala, E.,
486 Sandin, S.A., Soler, G., Stuart-Smith, R., Tessier, E., Tittensor, D.P., Tupper, M., Usseglio, P.,
487 Vigliola, L., Wantiez, L., Williams, I., Wilson, S.K., Zapata, F.A., 2011. Global human footprint on
488 the linkage between biodiversity and ecosystem functioning in reef fishes. *Plos Biology* 9, (DOI
489 10.1371/journal.pbio.1000606).

490 Nakazawa, T., 2015. Ontogenetic niche shifts matter in community ecology: a review and future
491 perspectives. *Population Ecology* 57, 347-354.

492 Neubert, M.G., Caswell, H., 2000. Density-dependent vital rates and their population dynamic
493 consequences. *Journal of mathematical biology* 41, 103-121.

494 Nisbet, R.M., Muller, E.B., Lika, K., Kooijman, S., 2000. From molecules to ecosystems through dynamic
495 energy budget models. *Journal of Animal Ecology* 69, 913-926.

496 Otto, S.B., Rall, B.C., Brose, U., 2007. Allometric degree distributions facilitate food-web stability. *Nature*
497 450, 1226-1229.

498 Petchey, O.L., Beckerman, A.P., Riede, J.O., Warren, P.H., 2008. Size, foraging, and food web structure.
499 Proc Natl Acad Sci U S A 105, 4191-4196.

500 Rooney, N., McCann, K.S., 2012. Integrating food web diversity, structure and stability. Trends in Ecology
501 & Evolution 27, 40-46.

502 Rooney, N., McCann, K.S., Moore, J.C., 2008. A landscape theory for food web architecture. Ecol Lett 11,
503 867-881.

504 Rudolf, V.H.W., Lafferty, K.D., 2011. Stage structure alters how complexity affects stability of ecological
505 networks. Ecol Lett 14, 75-79.

506 Rudolf, V.H.W., Rasmussen, N.L., 2013a. Ontogenetic functional diversity: Size structure of a keystone
507 predator drives functioning of a complex ecosystem. Ecology 94, 1046-1056.

508 Rudolf, V.H.W., Rasmussen, N.L., 2013b. Population structure determines functional differences among
509 species and ecosystem processes. Nature Communications 4, 7.

510 Shurin, J.B., Gruner, D.S., Hillebrand, H., 2006. All wet or dried up? Real differences between aquatic and
511 terrestrial food webs. Proceedings of the Royal Society B-Biological Sciences 273, 1-9.

512 Tuljapurkar, S., Gaillard, J.M., Coulson, T., 2009a. From stochastic environments to life histories and back.
513 Philosophical transactions of the Royal Society of London. Series B, Biological sciences 364,
514 1499-1509.

515 Tuljapurkar, S., Steiner, U.K., Orzack, S.H., 2009b. Dynamic heterogeneity in life histories. Ecol Lett 12,
516 93-106.

517 Varughese, M.M., 2011. A framework for modelling ecological communities and their interactions with
518 the environment. Ecological Complexity 8, 105-112.

519 Werner, E.E., Gilliam, J.F., 1984. The Ontogenetic Niche and Species Interactions in Size Structured
520 Populations. Annual Review of Ecology and Systematics 15, 393-425.

521 Winemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological
522 Monographs 60, 331-367.

523 Wollrab, S., de Roos, A.M., Diehl, S., 2013. Ontogenetic diet shifts promote predator-mediated
524 coexistence. Ecology [Ecology] 94, 2886-2897.

525 Yodzis, P., 1981. The stability of real ecosystems. Nature 289, 674-676.

526 Yodzis, P., 2000. Diffuse effects in food webs. Ecology 81, 261-266.

527 Yodzis, P., Innes, S., 1992. Body Size and Consumer-Resource Dynamics. American Naturalist 139, 1151-
528 1175.

529 Zhou, C., Fujiwara, M., Grant, W.E., 2013. Dynamics of a predator-prey interaction with seasonal
530 reproduction and continuous predation. *Ecol. Model.* 268, 25-36.

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532

Table 2. Scenarios investigated. Each scenario was applied to both structured and unstructured food webs.

Scenario	c_1^*	c_2^\dagger	k^\ddagger
1	0.125	1	10
2	0.25	1	10
3	0.125	0.8	10
4	0.125	1	100
5	0.125	1	$2.5(\cos(10\pi t) + 3)$

* Proportion of minimum size relative to consumer

† Proportion of maximum size relative to consumer

‡ Carrying capacity for primary producers.