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Title: Four types of interference competition and their impacts on the ecology and evolution of size-structured populations and communities

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Abstract: We investigate how four types of interference competition that affect foraging, metabolism, survival, and reproduction impact the ecology and evolution of size-structured populations. Surprisingly, even though all four types of interference competition reduce population bio-mass, interference competition at intermediate strengths sometimes significantly increases the abundance of adult individuals and the population's reproduction rate. We find that the evolutionary response to foraging and metabolic interference is smaller maturation size at low to intermediate interference intensity and larger maturation size at high interference intensity. The evolutionary response to survival and reproductive interference is always larger maturation size. We also investigate how the four types of interference competition impact the evolutionary dynamics and resultant structure of size-structured communities. Like other types of trait-mediated competition, all four types of interference competition can induce disruptive selection and thus initial diversification. Even though foraging and reproductive interference are more prone to induce initial diversification, they catalyze the formation of diverse communities with complex trophic structure only at high levels of interference intensity. By contrast survival interference does so already at intermediate levels. Reproductive interference supports relatively smaller communities with simpler trophic structure. Taken together, our results demonstrate the importance of interference competition in ecology and evolution.



**Manuscript submission to *Journal of Theoretical Biology***

Dear Editor,

Please find enclosed for your consideration the manuscript

*“Four types of interference competition and their impacts on the ecology and evolution of size-structured populations and communities”*

by Lai Zhang, Ken Haste Andersen, Ulf Dieckmann, and Åke Brännström.

Recent theoretical advances in evolutionary ecology have highlighted interference competition between individuals as a key factor promoting species coexistence and the emergence of diverse communities over evolutionary time scales. Due to a fundamental limitation of traditional unstructured population models, these advances build on the assumption that interference increases individual mortality. This, however, is only one out of several possibilities.

In the submitted manuscript, we carry out the first systematic investigation of how different types of interference between individuals impact the ecology and evolution of populations and food webs. Building on an established physiologically structured population model, we show how four salient types of interference can be mechanistically modelled. We find that these differ significantly in their ecological and evolutionary impacts. In addition to providing new insights, we believe that this manuscript will be an important reference for future studies of interference competition and physiologically structured populations.

This work has not been published or accepted for publication elsewhere, and is not under consideration for publication in another journal or book. The submission of this work for publication has been approved by all authors and relevant institutions.

Thank you very much for your kind consideration!

Sincerely yours,

Lai Zhang

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1 **Four types of interference competition and their impacts on the ecology and**  
2 **evolution of size-structured populations and communities**

3

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18

19

20

21 **Abstract**

22 We investigate how four types of interference competition that affect foraging, metabolism,  
23 survival, and reproduction impact the ecology and evolution of size-structured populations.  
24 Surprisingly, even though all four types of interference competition reduce population bio-  
25 mass, interference competition at intermediate strengths sometimes significantly increases the  
26 abundance of adult individuals and the population's reproduction rate. We find that the evolu-  
27 tionary response to foraging and metabolic interference is smaller maturation size at low to  
28 intermediate interference intensity and larger maturation size at high interference intensity.  
29 The evolutionary response to survival and reproductive interference is always larger matura-  
30 tion size. We also investigate how the four types of interference competition impact the evolu-  
31 tionary dynamics and resultant structure of size-structured communities. Like other types of  
32 trait-mediated competition, all four types of interference competition can induce disruptive  
33 selection and thus initial diversification. Even though foraging and reproductive interference  
34 are more prone to induce initial diversification, they catalyze the formation of diverse com-  
35 munities with complex trophic structure only at high levels of interference intensity. By con-  
36 trast survival interference does so already at intermediate levels. Reproductive interference  
37 supports relatively smaller communities with simpler trophic structure. Taken together, our  
38 results demonstrate the importance of interference competition in ecology and evolution.

39

40 **Keywords:** Adaptive dynamics, biodiversity, evolutionary branching, food webs, size struc-  
41 tured populations

42

## 43 **1. Introduction**

44 An important aspect of individual life history that has received comparatively little attention is  
45 the interference that takes place between individuals when they compete for resources. Inter-  
46 ference competition is hypothesized to be a major force driving natural selection (Rosenz-  
47 weig, 1978; Dieckmann et al., 2004; Bolnick, 2004). This belief is reinforced by recent theo-  
48 retical studies on the evolutionary emergence of food webs (e.g., Caldarelli et al., 1998; Dros-  
49 sel et al., 2001; McKane, 2004; Loeuille and Loreau, 2005; Rossberg et al., 2008; Brännström  
50 et al., 2011, 2012), which demonstrate that interference competition can promote species di-  
51 versity. These studies canonically assume that interference competition elevates individual  
52 mortality, but elevated mortality is in fact only one of several possible outcomes.

53 Interference competition in general exerts negative effects on individuals (Miller, 1967; Goss-  
54 Custard, 1980; Smallegange et al., 2006), either directly through injury (Briffa and Sneddon,  
55 2007), loss of energy and foraging time (Briffa and Sneddon, 2007; Stillman et al., 1997), or  
56 indirectly through a reduction in food intake rate or in effective fecundity (Vahl et al., 2005).  
57 The outcome of interference competition may be any combination of (i) reduced foraging rate  
58 (e.g., due to reduced searching time), (ii) increased metabolic requirements (e.g., by interfe-  
59 rence activities), (iii) reduced survival rate (e.g., through fierce contests), and (iv) reduced  
60 reproduction rate (e.g., predation on egg or larvae). Foraging interference and metabolic inter-  
61 ference directly affects individual physiology while survival and reproduction interference  
62 directly affect population demographic quantities.

63 The four different types of interference competition are indistinguishable in unstructured pop-  
64 ulation models, such as those used in the recent studies on food-web evolution (e.g., Loeuille  
65 and Loreau, 2005; Rossberg et al., 2008; Brännström et al., 2011), but their inherent differenc-  
66 es become apparent in physiologically structured population models that incorporate the onto-

67 genetic development of individuals from juvenile to adult (e.g., Ylikarjula et al., 1999; de  
68 Roos and Persson, 2001, 2013; Claessen and Dieckmann, 2002; Claessen and de Roos, 2003;  
69 Gårdmark and Dieckmann, 2006; de Roos et al., 2006). The widespread use and legacy of  
70 unstructured population models have, however, favored a tradition in which interference  
71 competition is represented as increased mortality. Consequently, very little is currently known  
72 about how different forms of interference competition impact the ecology and evolution of  
73 size-structured populations and communities.

74 In this paper, we investigate how the aforementioned four types of interference competition  
75 affect the ecological and evolutionary dynamics of size-structured populations and communi-  
76 ties. We base our investigation on a recently developed modelling framework for fish popula-  
77 tions. First, we introduce the size-structured population model that we use in our investigation  
78 and, then we phenomenologically model the four types of interference competition at the in-  
79 dividual level. Finally, we explore the effects of interference competition on the demography  
80 and evolution of a single population and on the structure of evolved communities. The paper  
81 concludes with a discussion of the results achieved.

82

## 83 **2. Model**

### 84 *2.1 Size-structured population dynamics*

85 The size-structured population model used in this paper builds on the framework for aquatic  
86 food webs of fish populations by Hartvig et al. (2011). We use the terms ecotype and diversi-  
87 fication rather than species and speciation to reflect the fact that our model is not concerned  
88 with reproductive isolation. We characterize the ecotype by maturation size that is generally  
89 recognized as one of the most important life history in fish populations (Charnov et al., 2012).

90 The model is briefly outlined below, with a more detailed description including model equa-  
91 tions and parameter values given in Appendix A.

92 We consider a large number of individuals belonging to any of several ecotypes and which are  
93 characterized by their body size  $w$ . An ecotype  $i$  is exclusively characterized by the matura-  
94 tion size  $m_i$ . Individuals grow in size, reproduce, and die at rates that depend on their size,  
95 availability of resources, and antagonistic interference with other individuals. The growth rate  
96 ( $g_i(w)$ ) is food-dependent and determined from size-based predation on both resource and  
97 consumer individuals, following the principle of “big-eat-small” (Ursin, 1973). This principle  
98 allows for within-population predation (cannibalism) which is a ubiquitous phenomenon in  
99 fish populations (Fox, 1975; Polis, 1981; Smith and Reay, 1991; Elgar and Crespi, 1992). The  
100 rate at which predators encounter prey depends on the volume that the predator can search in  
101 one unit of time. Following an established allometric relationship, this volume scales with  
102 predator body size (Appendix A). Individuals can die as a result of predation by larger indi-  
103 viduals, background mortality, or starvation mortality, which together combine to give an  
104 individual mortality rate  $\mu_i(w)$ . Finally, mature individuals produce offspring at a food- and  
105 size-dependent rate  $b_i(w)$ . A complete specification of these functions is given in Table A1  
106 (Appendix A).

107 Building on the individual-level processes described above, the demographic dynamics of  
108 ecotype  $i$  can be described by the following equations (McKendrick, 1926; von Foerster,  
109 1959; de Roos, 1997),

$$110 \quad \frac{\partial}{\partial t} N_i(w, t) + \frac{\partial}{\partial w} (g_i(w) N_i(w, t)) = \mu_i(w) N_i(w, t), \quad (1a)$$

$$111 \quad g_i(w_0) N_i(w_0, t) = \frac{\varepsilon}{2w_0} \int_{w_0}^{M_i} b_i(w) N_i(w, t) dw. \quad (1b)$$

112 Here,  $N_i(w, t)$  is the size spectrum of ecotype  $i$  at time  $t$ . Eq. (1a) describes how the size  
113 spectrums of the different ecotypes change over time as a consequence of individual growth  
114 and mortality. Newborn individuals enter the populations through the boundary condition, Eq.  
115 (1b) that specify the population's reproduction rate. Offspring of size  $w_0$  are produced by  
116 adults at a size-dependent birth rate  $b_i(w)$ . They survive the larvae stage with probability  $\varepsilon$ .  
117 The fraction  $1/2$  reflects an assumed equal sex ratio.

118 The available resources,  $R(w, t)$ , are continuously distributed along a size spectrum and have  
119 dynamics that follow chemostatic growth,

$$120 \quad \frac{d}{dt}R(w, t) = r_0 w^{n-1} \left( \kappa_0 w^{-\lambda} - R(w, t) \right) - \mu_p(w)R(w, t), \quad (2)$$

121 where  $r_0 w^{n-1}$  is the intrinsic renewal rate of resource (Savage et al., 2004) and  $\kappa_0 w^{-\lambda}$  is the  
122 maximum resource density in the absence of consumers, both scaling allometrically with the  
123 size of the resource organisms. The term  $\mu_p(w)$  reflects the consumption of the resource by  
124 individuals of all ecotypes. The sizes of the resource organisms fall within a finite range with  
125 upper limit  $w_{\max}$ . The lower limit is not important as long as it is far smaller than the size of  
126 newborn individuals,  $w_0$ .

127

## 128 *2.2 Four types of interference competition*

129 In this section, we derive four possible outcomes of interference competition in a phenomeno-  
130 logical manner: a reduction of time spent searching for prey (foraging interference), an extra  
131 loss of energy for activity during encounter (metabolic interference), a risk of dying as a result  
132 of interference encounter (survival interference), and egg/larvae predation (reproductive inter-  
133 ference).

134 We assume that interference occurs when two similar individuals encounter one another for  
 135 the first three types of interference. Here “similar” means that the two individuals have similar  
 136 body size and similar maturation size. The reason for this similarity is the ontogenetic trophic  
 137 niche shifts (Werner, 1988), which means that only individuals of similar sizes share the same  
 138 feeding niche. The similarity between two individuals with respective body sizes  $w$  and  $w'$   
 139 and maturation sizes  $m$  and  $m'$  are governed by two interference kernels,

$$140 \quad I_w(w/w') = \exp\left(-\frac{\ln^2 w/w'}{2\sigma_w^2}\right), \quad (3a)$$

$$141 \quad I_m(m/m') = \exp\left(-\frac{\ln^2 m/m'}{2\sigma_m^2}\right). \quad (3b)$$

142 Here,  $\sigma_w^2$  and  $\sigma_m^2$  are parameters which respectively describe how quickly interference will  
 143 attenuate with differences in body size (Eq. 3a) and in maturation size (Eq. 3b).

144 Interference encounters between a focal individual and another individual can happen either  
 145 when the focal individual encounters the other individual or vice versa. As the volumetric  
 146 search rate increases with body size, it is expected that the larger of the two individuals en-  
 147 counters the smaller. From these considerations the rate of interference encounter for an indi-  
 148 vidual of ecotype  $i$  is estimated as

$$149 \quad r_1(w, m_i) = \sum_j I_m\left(\frac{m_i}{m_j}\right) \left( \int_{w_0}^w v(w) I_w\left(\frac{w}{w'}\right) N_j(w', t) dw' + \int_w^{M_j} v(w') I_w\left(\frac{w'}{w}\right) N_j(w', t) dw' \right), (4)$$

150 where  $v(w) = \gamma w^a$  is the rate of foraging encounters (Eq. M3 in Table A1).

151 For reproductive interference, we assume that offspring is vulnerable to individuals of any  
 152 body size and that encounter with offspring is proportional to individual encounter searching  
 153 volume. The rate of interference encounter for ecotype  $i$  is then estimated as

$$154 \quad f(m_i) = \sum_j I_m\left(\frac{m_i}{m_j}\right) \int_{w_0}^{M_j} v(w) N_j(w, t) dw, \quad (5)$$

155 The four types of interference competition are modeled as follows,

156 (1) Foraging interference, i.e., reduction in search rate  $v(w)$  by a factor  $e^{-\gamma_c r_1(w, m_i)}$   
157 such that  $v(w) = \gamma w^q$  is replaced by  $e^{-\gamma_c r_1(w, m_i)} \gamma w^q$ . Here  $\gamma_c$  is a free parameter  
158 characterizing the interference intensity.

159 (2) Metabolic interference, i.e., increase in metabolic costs due to interference, conse-  
160 quently decreasing energy available for growth and reproduction.. Following metabol-  
161 ic scaling (West et al., 2001), we model interference metabolic cost by  $\kappa_c r_1(w, m_i) w^p$ ,  
162 where  $\kappa_c$  is the interference intensity, a free parameter. This cost is added to individual  
163 maintenance cost.

164 (3) Survival interference, i.e., death of individuals due to interference. It is assumed  
165 that mortality increases with interference encounter, yielding an extra mortality risk of  
166  $\mu_c = p_c r_1(w, m_i)$  where  $p_c$  is the constant regulating survival interference intensity.  
167 This mortality is added to the individual mortality rate.

168 (4) Reproductive interference, i.e., egg or larvae predation. The consequence is that  
169 the recruitment  $R$  (the right-hand side of Eq. 1b) is reduced by a factor  $e^{-\alpha_c f(m_i)}$ . In  
170 this expression  $\alpha_c$  is a free parameter indicating the strength of interference while  
171  $f(m_i)$  is the predation rate of egg of ecotype with maturation size  $m_i$ .

172 We stress that the aforementioned descriptions of interference competition are phenomemo-  
173 logical rather than mechanistic, as the rate of interference encounters  $r_1(w, m_i)$  can only be  
174 estimated.

175 In principle, all four types of interference competition described above can simultaneously  
176 occur in a population, but to understand the role of each type of interference in population  
177 dynamics, they are here investigated separately. The interference-intensity parameters  $\gamma_c, \kappa_c,$

178  $p_c$ , and  $\alpha_c$  are nonnegative scalars whose values are difficult to estimate due to the problem of  
179 disentangling interference competition and exploitative competition (Nakayama and Fuiman,  
180 2010). To facilitate comparison between different types of interference competition, we scale  
181 each interference-intensity parameter so that a value of 1 causes the biomass of a reference  
182 population to be exactly one percent of the interference-free biomass. The trait value  $m_0^*$  of  
183 the reference population is chosen as the unique evolutionarily singular maturation size for  
184 single populations without interference, as described in the next subsection..

### 185 *2.3 Evolutionary dynamics*

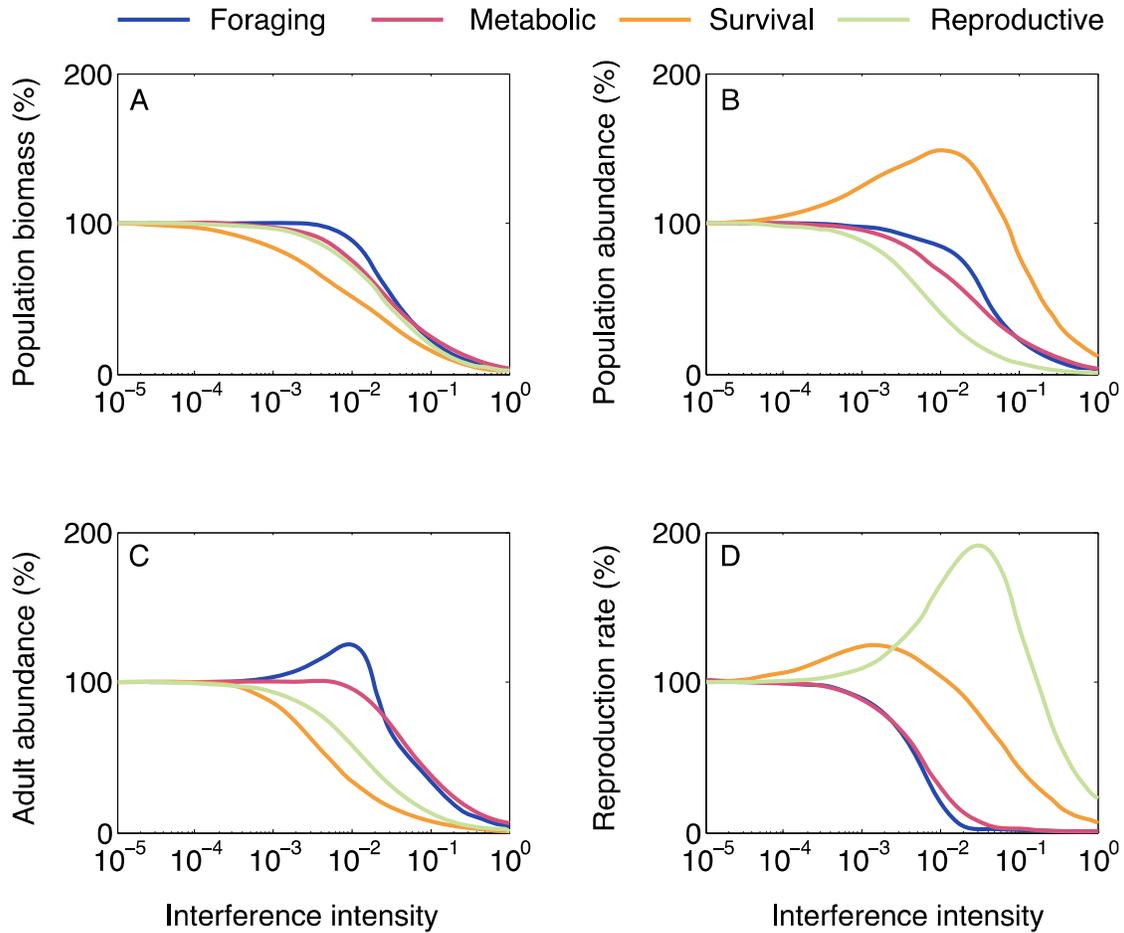
186 We employ adaptive dynamics theory to study the evolution of maturation size (e.g., Metz et  
187 al., 1996; Geritz et al., 1997; Brännström et al., 2013). The evolution of maturation size is  
188 governed by the canonical equation under the assumption of mutation-limited evolution (Di-  
189 eckmann and Law, 1996). For a single population, evolution is always direction towards a  
190 unique singular maturation size at which directional selection disappears (Hartvig, 2011; see  
191 also Appendix B). At the singular maturation size, evolution either comes to halt or undergoes  
192 evolutionary branching, leading to emergence of dimorphic populations. This process of gra-  
193 dual evolution and evolutionary branching often continues, resulting in the emergence of eco-  
194 logical communities (e.g., Loeuille and Loreau, 2005; Dieckmann et al., 2007; Brännström et  
195 al., 2011; Brännström et al. 2013). We assume a strict separation between the ecological and  
196 evolutionary time scales typical of many studies in adaptive dynamics (e.g., Doebeli and Di-  
197 eckmann, 2000) with ecological dynamics proceeding faster than the evolutionary dynamics,  
198 meaning that the resident community dynamics has settled on its demographic attractor before  
199 the next mutation occurs. Further details of the canonical equation and the community-  
200 assembly process are used are provided in Appendix C.

## 201 **3. Results**

202 The effects that the four types of interference competition have on the ecology and evolution  
203 of populations and communities are explored below. We first study the demographic impacts  
204 of interference competition and then we examine the evolution of maturation size  $m^*$  in a  
205 population under different types and intensities of interference competition. Finally, moving  
206 beyond a single population, we consider the importance of interference competition for the  
207 diversity and trophic structure of evolved communities.

### 208 *3.1 Demographic impacts of interference competition*

209 Figure 1 shows that, unexpectedly, three out of four demographic indicators are positively  
210 correlated with at least one type of interference competition. Foraging interference positively  
211 affects adult abundance for a range of interference intensities (Fig. 1C) but negatively affects  
212 the three other demographic indicators considered. Metabolic interference negatively affects  
213 all four of the considered demographic indicators. Survival interference causes a considerable  
214 initial increase in population abundance followed by a decline as survival-interference intensi-  
215 fies (Fig. 1B). The increase in abundance comes in spite of a monotonous decline in popula-  
216 tion biomass with survival-interference intensity. From this, we infer an increase in the num-  
217 ber of juveniles. This is corroborated by a reduction in abundance (Fig. 1C). In stark contrast  
218 to the decrease in adult abundance is the rise in the population reproduction rate (Fig. 1D).  
219 Finally, reproductive interference raises the population reproduction rate at low interference  
220 intensity (Fig. 1D), although it decreases all of the three other indicators considered.



221

222 **Fig. 1:** Influence of interference competition on four demographic indicators. (A) Population  
 223 biomass decreases for all types of interference competition. (B) Population abundance de-  
 224 clines for all interference types except survival. (C) Adult abundance declines for all interfe-  
 225 rence types except foraging. (D) Both survival interference and reproduction interference can  
 226 increase the population's reproduction rate. All demographic quantities are scaled in relation  
 227 to the interference-free quantities. In case of oscillations, long-term averages of mean popula-  
 228 tion quantities were considered, which usually happens to the foraging and metabolic interfe-  
 229 rence with high intensity. The reference population has maturation size  $m_0^*$ , which is the  
 230 unique evolutionarily singular maturation size in the absence of interference competition (see  
 231 Appendix B). Parameter values are as in Table A2 (Appendix A) with interference-intensity  
 232 ranging from  $10^{-5}$  to 1.

233

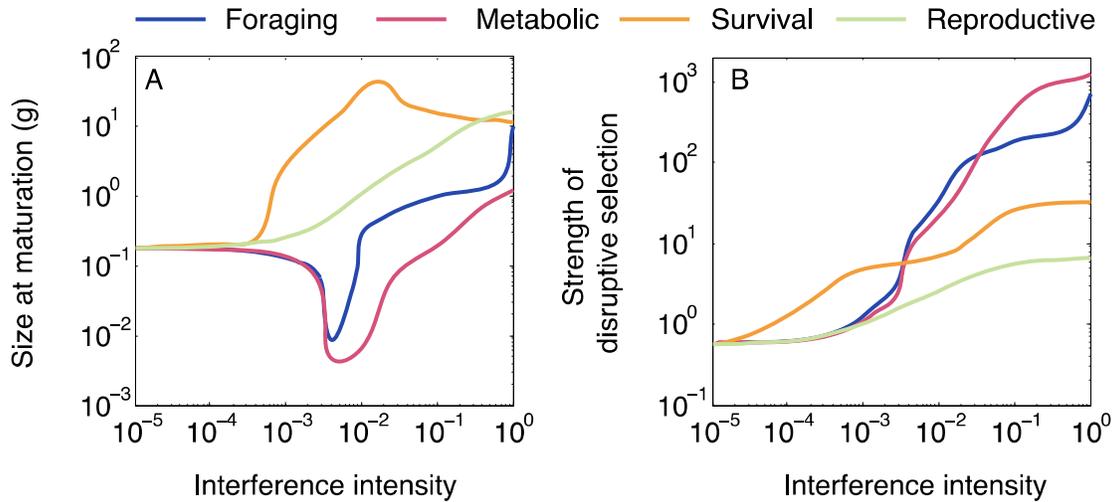
234 The surprising positive impact that some types of interference competition have on the demo-  
235 graphic indicators under consideration is primarily due to the change in the size-structure of  
236 consumer population. This is corroborated by Fig. 1A, which shows consistent declines of  
237 total population biomass with increased interference. Thus an increase in adult, total popula-  
238 tion abundance or reproduction rate can then only come about through a changed size distri-  
239 bution of the consumer. Take the increased reproduction rate by survival interference for ex-  
240 ample, interference competition raises individual mortality rates, relieving exploitative com-  
241 petition and hence enhancing resource abundance. Surviving juveniles grow faster, potentially  
242 compensating for the loss of adult abundance. The population's reproduction rate depends on  
243 the adult size distribution and the adults' size-dependent birth rate. As the latter increases with  
244 the resource abundance, while the former is fairly constant when there is little interference  
245 competition, the sum of these two changes explains the observed increase in reproduction  
246 rate. However, this advantage of resource availability is lost when interference competition  
247 intensifies and fast-growing juveniles can no longer compensate for higher mortality.

248

### 249 *3.2 Evolutionary impacts of interference competition on populations*

250 Figure 2A shows that among the four types of interference, survival interference gives rise to  
251 the largest maturation size, followed by the reproductive interference. Both foraging and me-  
252 tabolic interference decrease maturation size considerably when interference intensity is small  
253 but this tendency is reversed when interference is continuously intensified. An opposite situa-  
254 tion for foraging interference is observed where sufficiently strong intensity drives the matu-  
255 ration size slightly down. The presented evolutionarily singular maturation size is conver-  
256 gence stable for all four types of interference competition across the entire range of interfe-

257      rence strengths, meaning that a single population always gradually evolves towards the singu-  
258      lar maturation size (see Fig. B1 in Appendix B).



259

260      **Fig. 2:** Influence of interference competition on the evolution of populations. (A) Survival  
261      and reproductive interference promotes maturation at smaller size at low to intermediate inter-  
262      ference intensity and larger size at high interference intensity. (B) All four types of interfe-  
263      rence competition promote diversification of the population. Foraging, metabolic, and surviv-  
264      al interference are more likely to induce diversification than reproductive interference. The  
265      strength of disruptive selection is assessed by the second order derivative of the invasion fit-  
266      ness at the resident trait value. Parameter values are as in Table A2 (Appendix A) with inter-  
267      ference-intensity ranging from  $10^{-5}$  to 1.

268

269      Once a population has evolved to the singular maturation size, disruptive selection can cause  
270      the ancestral population to diversity into two new ecotypes in our model. Figure 2B shows  
271      that selection is always disruptive at the evolutionarily singular maturation size and that the  
272      strength of disruptive selection increases with interference intensity. This implies that the four  
273      types of interference all promote diversification, albeit to different extents. Foraging, metabol-

274 ic, and survival interference are more likely to enable diversification than reproductive inter-  
275 ference.

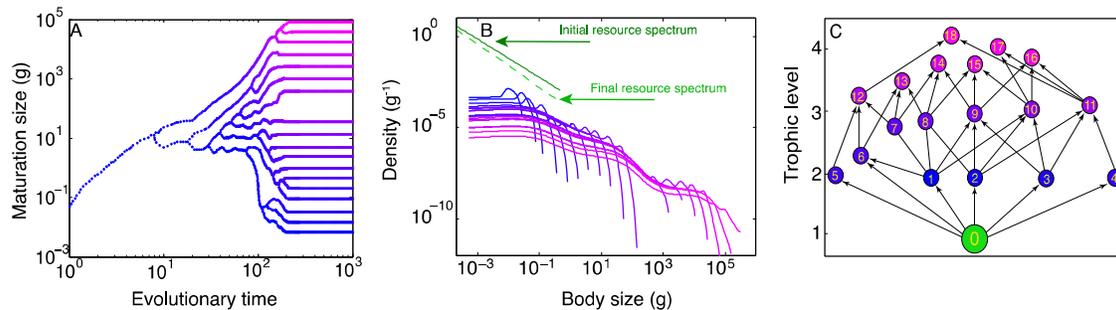
276 The effect of interference competition on the singular maturation size  $m^*$  can be understood  
277 from changes in size-dependent consumption rates. Foraging interference reduces individuals'  
278 volumetric search rates and hence also their foraging rates. The reduced foraging rate increas-  
279 es resource abundance. When interference is weak, the net increment of food intake resulting  
280 from reduced foraging rate and increased resource abundance is negative, which cause indi-  
281 viduals to grow slower. As a consequence, maturation is delayed, leading to higher risk of  
282 dying before the onset of reproduction. Directional selection reduces the maturation size until  
283 a new evolutionarily singular maturation size is reached at which the gain of short juvenile  
284 stage from lower maturation size exactly balances the loss from the associated lower fecundi-  
285 ty rate. However this tendency is reversed when the net increment of food intake turns out to  
286 be positive, which happens at the intermediate levels of interference intensity. A similar me-  
287 chanism explains the effects of metabolic interference.

288 For survival and reproductive interference, an increase in interference intensity relieves ex-  
289 ploitative competition for resource among the remaining consumer individuals. The increased  
290 resource availability results in faster individual growth rates, leading to lower risk of dying  
291 before the onset of reproduction. Directional selection increases the maturation size until a  
292 new evolutionarily singular maturation size is reached at which the gain of higher fecundity  
293 rate exactly balances the loss of longer juvenile stage from increased maturation size.

### 294 ***3.3 Evolutionary impacts of interference competition on communities***

295 A single ecotype eventually evolves to the evolutionarily singular maturation size at which  
296 point it experiences disruptive selection. Evolutionary branching may then result in the emer-  
297 gence of two coexisting ecotypes from the single ancestor. Through directional selection and

298 further evolutionary branching, an entire community of coexisting ecotypes is eventually es-  
 299 tablished. Figure 3 shows an example of evolutionary community assembly under survival  
 300 interference. Through evolutionary branching, a community of 18 coexisting ecotypes in evo-  
 301 lutionary equilibrium eventually emerges (Fig. 3A). Among the emergent ecotypes, the larg-  
 302 est maturation size can be 100 kg, 6 orders of magnitude larger than its distant ancestor. The  
 303 size spectra of ecotypes are shown in figure 3B, which shows that the body size of large eco-  
 304 types covers a broad range from newborn to adult. Individuals in these ecotypes undergo an  
 305 ontogenetic niche shift as they grow, eventually switching their primary dietary source from  
 306 the resource to other consumer individuals including conspecifics based on the size-dependent  
 307 predation (Eq. M1 in Table A1). Characterizing ecotype trophic level via the averaged trophic  
 308 positions of adults facilitates an illustration of the community's trophic structure (Fig. 3C).  
 309 The ecotypes span three trophic levels with the largest ecotype having trophic level greater  
 310 than 4, assuming that the basal resource has trophic level 1.

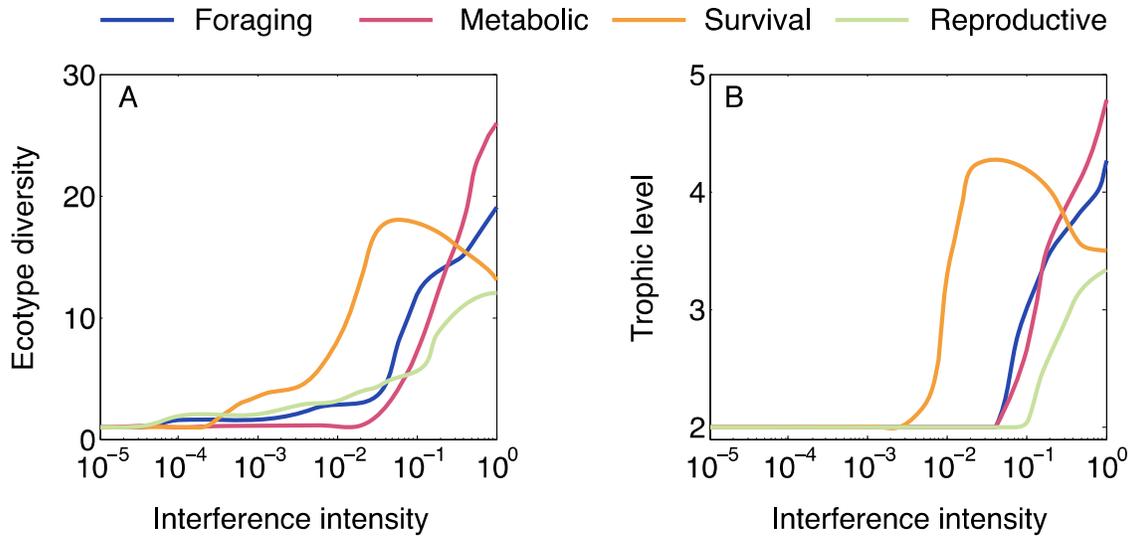


312 **Fig. 3:** An example of an evolved community under survival interference. (A) A single ances-  
 313 tor eventually gives rise to a community of 18 coexisting ecotypes at evolutionary equili-  
 314 brium. (B) Ecotype size spectra (solid lines), together with the initial (solid dark-green line)  
 315 and final (dashed-green line) resource size spectra. (C) Trophic structure of the evolved com-  
 316 munity. We identify an ecotype's trophic level with the trophic position of adults of that eco-  
 317 type, to account for the change in trophic level that individuals experience as they grow. The  
 318 arrows between ecotypes (nodes) indicate the presence and direction of energy flows account-

319 ing for more than 15% of the recipient ecotypes' diet. Trophic level (vertical axis) is defined  
320 as the average path length from a focal ecotype down to the resource (node 0), weighted by  
321 the proportion of energy along each path relative to the total energy that is consumed by the  
322 adult individuals of the focal ecotype (Levine, 1980). The nodes are ordered according to  
323 ascending maturation size. Parameter values are in Table A2 (Appendix A) with survival-  
324 interference intensity set to 0.03.

325

326 We investigate how two salient measures of the evolved communities, ecotype diversity (Fig.  
327 4A) and maximum trophic level (Fig. 4B), are affected by interference competition. Figure  
328 4A shows that all types of interference competition promote large communities, but metabolic  
329 interference most strongly promotes diverse communities with high trophic levels, followed  
330 by foraging and survival interference. Reproductive interference gives rise to less diverse  
331 communities with simpler trophic structure. In addition, for each type of interference competi-  
332 tion, the most diverse community emerges at intermediate levels of interference intensity for  
333 survival interference while they only emerge at high levels of interference intensity for the  
334 other three types of interference competition. Finally, by comparing the ecotype diversity and  
335 the maximum trophic level of evolved communities, we find that the most diverse communi-  
336 ties usually have the highest maximum trophic level.



337

338 **Fig. 4:** Influence of interference competition on the evolution of communities. (A) Survival  
 339 interference promotes diverse communities at intermediate interference strength. The three  
 340 other types of interference promote diverse communities only at high levels of interference  
 341 competition. (B) The maxim trophic level of the evolved communities follows a similar pat-  
 342 tern as the evolved diversity. The trophic level of the resource species is assumed to be 1. Pa-  
 343 rameter values are as in Table A2 (Appendix A) with interference intensity ranging from  
 344  $10^{-5}$  to 1.

345

### 346 3.4 Summary

347 Our principal findings are summarized in Table 1. The four types of interference competition  
 348 generally have a negative impact on demographic indicators. As exceptions to this rule, forag-  
 349 ing interference can increase the adult abundance, survival interference can increase the total  
 350 abundance and the population's reproduction rate, and reproductive interference can increase  
 351 the population's reproduction rate. These exceptions are significant only at intermediate  
 352 strengths of interference competition. We find that a population's maturation size is first re-

353   duced then increased by foraging and metabolic interference, but it is always increased by  
354   survival and reproductive interference when compared to a population without interference.  
355   Interference competition also has profound impacts on communities. All four types of interfe-  
356   rence competition can induce disruptive selection and support the emergence of diverse com-  
357   munities, though survival interference might be more likely to drive the emergence of diverse  
358   communities in practice as it has large effects already at low and intermediate levels of inter-  
359   ference intensity.

**Table 1:** Summary of ecological and evolutionary impacts of the four types of interference competition

Interference	Ecological impacts				Evolutionary impacts				
	Biomass	Abundance	Adult abundance	Reproduction	Maturation size	Disruptive selection	Diversity	Trophic level	Communities
Foraging	↓	↓	↑↓	↓	↓↑	↑	↑	↑	↑
Metabolic	↓	↓	↓	↓	↓↑	↑	↑	↑	↑
Survival	↓	↑↑	↓	↑↑	↑↑	↑	↑↓	↑↓	↑↓
Reproductive	↓	↓	↓	↑↓	↑	↑	↑	↑	↑

Up (down) arrows mean interference exerts positive (negative) influence on the associated ecological and evolutionary property.

## 1 **4. Discussion**

2 In this paper, we have modeled four types of interference and investigated their impacts on  
3 the ecology and evolution of size-structured populations and food webs. Our results show that  
4 interference competition is essential for promoting species diversity and the four types of in-  
5 terference competition have different impacts on the emerging population structure, the poten-  
6 tial for initial diversification, and the diversity of evolved food webs. All types of interference  
7 competition promote the emergence of diverse food webs with high maximum trophic level,  
8 but only survival interference does so significantly at intermediate interference intensities,  
9 implying that survival interference may be more likely to drive the emergence of diverse  
10 communities.

11 The four types of interference competition were modeled phenomenologically, building on an  
12 idealized expression for the interference encounter rate, which assumes that all individuals are  
13 available for interference encounters. A rigorous mechanistic derivation of interference com-  
14 petition which accounts for the fact that other individuals may already be tied up in interfe-  
15 rence encounters appears to be out of reach for general size-structured populations, as the in-  
16 terference encounter rate (i.e., Eq. 4) must be solved from an integral equation. For popula-  
17 tions with stage structure, Ruxton et al. (1992) mechanistically derived interference competi-  
18 tion. They found that weak interference promotes unstable population dynamics. We observed  
19 that interference competition generally has a stabilizing effect on the population dynamics. As  
20 the rare exception, we found that foraging and metabolic interference had a destabilizing ef-  
21 fect when interference intensity is high (result not shown).

22 While many ways by which interference competition affects individuals can be modeled using  
23 size-structured population models, the range of options in unstructured population models is  
24 considerable lower. In practice, interference competition in unstructured population models is

25 almost invariable represented as an increase in mortality, which negatively affects population  
26 demographic properties (e.g., Case and Gilpin, 1974; Schoener, 1976; Case et al., 1979;  
27 Vance, 1984; Amarasekare, 2002; Kuang et al., 2003). In size-structured population models,  
28 the negative effects of interference competition can take different forms. Importantly, these  
29 negative effects can partially or completely be compensated by changes in resource availabili-  
30 ty and population size structure. This accounts for the increase in abundance seen from in-  
31 creased survival interference and foraging interference, as well as for the increase in repro-  
32 duction rate seen from reproductive and survival interference. Such indirect benefits of inter-  
33 ference competition cannot be realized in unstructured population models unless they are as-  
34 sumed a priori (e.g., Amarasekare, 2002).

35 Theoretical studies of evolutionary impacts of interference competition mainly focus on the  
36 emergence of food webs of unstructured populations in which interference is represented as  
37 increased mortality. In the presence of interference competition, larger communities can be  
38 successfully evolved from a small ancestor (Loeuille and Loreau, 2005; Rossberg et al., 2008;  
39 Brännström et al., 2011). We observed similar results in the size-structured model. However,  
40 our study offers more insights into the role of interference in the evolution of both populations  
41 and communities. On the one hand, in addition to survival interference, foraging and metabol-  
42 ic interference also catalyze the formation of diverse communities and the formed communi-  
43 ties can even be more diverse than the communities evolved from survival interference, al-  
44 though this usually occurs at high levels of interference intensity. On the other hand, although  
45 all types of interference competition promotes species diversity, physiologically-related inter-  
46 ference (i.e., foraging interference and metabolic interference) can exert both negative and  
47 positive effects on the evolution of maturation size, depending on interference intensity, while  
48 physiologically-unrelated interference (i.e., survival interference and reproductive interfe-  
49 rence) generally exerts positive impacts (Fig. 2 and 4). The positive impact has been observed

50 in unstructured population models (Brännström et al., 2011). These findings reveal that inter-  
51 ference competition in size-structured population models can behave qualitatively differently  
52 from unstructured population models and that predictions of interference competition in size-  
53 structured population models are considerably more diverse than that in unstructured popula-  
54 tion models.

55 The emerging community in Fig. 3 is evolutionarily stable. This, however, is not always the  
56 case in particular for foraging and metabolic interference. We occasionally observed evolu-  
57 tionary limit cycles, reminiscent of Red Queen dynamics (Van Valen, 1973). Red Queen dy-  
58 namics can be triggered by diverse mechanisms, for instance, predator-prey interactions (Di-  
59 eckmann et al., 1995) or alternative ecotype-dynamical attractors (Kisdi et al., 2001). Since  
60 alternative steady states frequently appear in size-structured ecotype models with abundant  
61 resource supply (de Roos et al., 2003), we speculate that interference competition might cause  
62 the population dynamics to switch between distinct ecological steady states, thus, potentially  
63 favoring Red Queen dynamics at the evolutionary time scale (Kisdi et al., 2001). Elucidating  
64 the conditions that give rise to non-equilibrium evolutionary dynamics is an important chal-  
65 lenge for future work.

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81

## 82 **Appendix A:** Size-structured population model

83 We build on the recently developed food-web framework by Hartvig et al. (2011), which is a  
84 promising approach to construct food webs of continuously size-structured ecotypes. Table  
85 A1 and A2 summarize the model equations and model parameters. The framework is de-  
86 scribed in more detail below.

87 Each population  $i$ , henceforth denoted ecotype, is characterized by its maturation size  $m_i$ . In-  
88 dividuals within this ecotype are represented by body size  $w$  varying from  $w_0$  to  $M_i = m_i/\eta$ .  
89 Here,  $w_0$  is the size of offspring, which is assumed to be uniform among all ecotypes, and  $M_i$   
90 is the maximum attainable body size of individuals in ecotype  $i$ . The species size spectrum,  
91 i.e., the distribution of individual abundance as a function of body size, is denoted  $N_i(w, t)$  or  
92 simply  $N_i$ . The aggregated size spectra of all species in a community give rise to the commu-  
93 nity size spectrum (Andersen and Beyer, 2006).

94 Predation is size selective and mathematically formulated by a selection function (M1), which  
95 is lognormal (Ursin, 1973) and peaks when the size ratio of predator to prey equals the pre-  
96 ferred predator-prey mass ratio  $\beta$ . The size range of prey individuals that a predator individual

97 consumes is determined by the standard deviation  $\sigma$ . Interactions between individuals with  
98 size ratio that are several standard deviations from  $\beta$  are negligible and can be entirely ig-  
99 nored.

100 Encountered food for  $w$ -sized individuals comes from predation upon resource and consumer  
101 individuals (M2). The amount of food is proportional to the size-dependent volumetric search  
102 rate (M3). Satiation is described by the feeding level (M4), which multiplied with the maxi-  
103 mum food intake (M5) gives rise to the ingested food. With assimilation efficiency  $\alpha$ , ingested  
104 food is converted to energy (M6) that is utilized for life-history processes. Energy is in priori-  
105 ty used for paying maintenance costs  $k_s w^p$  and then, if there is any, used for individual so-  
106 matic growth and reproduction. The distribution of the remaining energy between these two  
107 processes is governed by an allocation function (M7). The growth equation (M8) indicates  
108 that the surplus energy after paying metabolic cost is entirely used for juvenile growth but  
109 drops due to the onset of reproduction (M9). The growth of individuals ceases when they ap-  
110 proach their maximum body size at which all energy is routed to reproduction.

111 In addition to the predation mortality (M10), individuals experience trait-dependent back-  
112 ground mortality at the rate  $\mu_0 m_i^{n-1}$ , as well as starvation mortality (M11) when the assimi-  
113 lated energy is insufficient to cover metabolic costs. The total mortality rate of  $w$ -sized indi-  
114 viduals is thus  $\mu_i(w) = \mu_p + \mu_0 m_i^{n-1} + \mu_s(w)$ . Moreover, in case of starvation, growth and  
115 reproduction stop instantaneously. The background mortality prevents unlimited growth of  
116 large individuals that do not experience predation.

117 The ecotype dynamics are described by the McKendrick-von Foerster equation, Eq. (1a). The  
118 boundary condition, Eq. (1b), represents the recruitment of offspring. The resources are conti-  
119 nuously distributed along the size spectrum and have dynamics that follow chemostatic  
120 growth (Eq. 2). The resource spectrum is truncated at the lower size  $w_{\text{cut}}$ . This lower limit of

121 resource size does affect the results as long as it is far smaller than  $w_0$ . Both the resource car-  
 122 rying capacity (M12) and the resource regeneration rate (M13) are size-dependent.

123 In order to express units in integer powers, we scale individual body size and the maturation  
 124 size with a reference weight  $w_r = 1$  g, by setting  $\tilde{w} = w/w_r$  and  $\tilde{m} = m/w_r$ , respectively.  
 125 This gives rise to scaling constants in some of the equations listed in Table S1. For instance,  
 126 the volumetric search rate  $v(w) = \gamma w^q$  is transformed to  $v(\tilde{w}) = \gamma w_r^q \tilde{w}^q$  after which we  
 127 define  $\tilde{\gamma} = \gamma w_r^q$ . Other relevant equations and parameters are similarly scaled. From here on,  
 128 we will use the scaled variables although, for brevity, we will not write out the tilde. The  
 129 scaled parameters are presented in Table A2.

130 **Table A1: Model equations**

Num	Equation	Interpretation
M1	$\varphi(w/w') = \exp(-\log^2(w'\beta/w)/(2\sigma^2))$	Selection function
M2	$E(w) = v(w) \left( \int_0^{w_{\text{cut}}} w' R(w') \varphi\left(\frac{w}{w'}\right) dw' + \sum_j \int_{w_0}^{M_j} w' N_j(w') \varphi(w/w') dw' \right)$	Encountered food from resource and consumers
M3	$v(w) = \gamma w^q$	Encounter search rate
M4	$F(w) = E(w)/(E(w) + I_{\text{max}}(w))$	Feeding level
M5	$I_{\text{max}}(w) = hw^n$	Maximum food intake
M6	$S(w) = \alpha I_{\text{max}}(w) F(w)$	Assimilated energy
M7	$\psi(w, m) = (1 + (w/m)^{-10})^{-1} (w\eta/m)^{1-n}$	Allocation function
M8	$g(w, m) = \max\{0, (1 - \psi(w, m))S(w) - k_s w^p\}$	Individual growth rate
M9	$b(w, m) = \max\{0, \psi(w, m)(S(w) - k_s w^p)\}$	Individual birth rate
M10	$\mu_p(w) = \sum_j \int_{w_0}^{M_j} v(w') (1 - F(w')) N_j(w') \varphi(w'/w) dw'$	Predation mortality
M11	$\mu_s(w) = \max\{(S(w) - k_s w^p)/(\xi w), 0\}$	Starvation mortality
M12	$\kappa(w) = \kappa_0 w^{-\lambda}$	Maximum resource density
M13	$r(w) = r_0 w^{n-1}$	Resource generation rate

131

132 **Table A2: Parameters and values of the size-structured population model**

Parameter	Value	Unit	Interpretation
Consumer			
$\beta$	100	–	Preferred predator-prey mass ratio
$\sigma$	1	–	Width of selection function
$\alpha$	0.6	–	Assimilation efficiency
$\varepsilon$	0.1	–	Reproduction efficiency
$h$	85	g/yr	Scaled prefactor of maximum food intake
$k_s$	10	g/yr	Scaled prefactor of standard metabolism
$n$	0.75	–	Exponent of maximum food intake
$p$	0.75	–	Exponent of metabolic costs
$q$	0.8	–	Exponent of volumetric search rate
$\eta$	0.25	–	Ratio of maturation size to maximum size
$\mu$	0.84	g/yr	Scaled background mortality
$\xi$	0.1	–	Fraction of energy reserves
$w_0$	0.0005	–	Scaled egg size
$f_0$	0.6	–	Initial feeding level
$\gamma$	$\frac{f_0 h \beta^{2-\lambda} w_r}{\sqrt{2\pi(1-f_0)\kappa_0\sigma}}$	g/yr	Scaled factor of volumetric search rate
$w_r$	1	g	Reference weight for scaling <sup>a</sup>
Resource			
$\kappa_0$	0.005	$\text{g}^{-1}/\text{m}^3$	Scaled magnitude of resource size spectrum
$r_0$	4	1/yr	Scaled generate rate
$w_{\text{cut}}$	0.5	–	Upper limit of resource spectrum
$\lambda$	$2 + q - n$	–	Slope of resource spectrum
Interference			
$\sigma_w$	0.5	–	Interference variance in the direction of body size <sup>b</sup>
$\sigma_m$	0.5	–	Interference variance in the direction of maturation size <sup>b</sup>
$\sigma_\mu$	0.001	–	Standard deviation of mutation <sup>c</sup>

$\sigma_m$	0.001	–	Mutation rate <sup>c</sup>
$\gamma_c$	varied	–	Foraging interference intensity
$\kappa_c$	varied	–	Metabolic interference intensity
$p_c$	varied	–	Survival interference intensity
$\alpha_c$	varied	–	Reproductive interference intensity

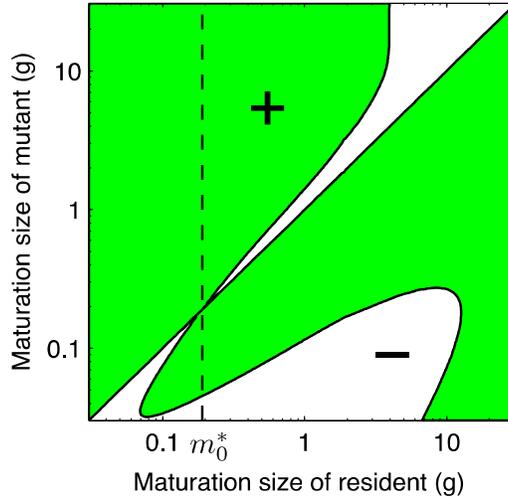
133 <sup>a</sup>Arbitrary. The remaining parameters are from Hartvig et al., 2011. <sup>b</sup>Ensure that interference occurs between  
134 individuals with similar trait and similar body size. <sup>c</sup>Dieckmann and Doebeli, 1999.

135

136 **Appendix B:** Adaptive dynamics of the size-structured population model without interference  
137 competition

138 In this appendix, we demonstrate the evolutionary dynamics of maturation size in a mono-  
139 morphic population (Fig. B1) and dimorphic population (Fig. B2) in the absence of interfe-  
140 rence competition.

141 Figure B1 shows that through a sequence of small mutations, the maturation size will ap-  
142 proach the evolutionarily singular maturation size  $m_0^*$ . Upon reaching  $m_0^*$ , mutant strategies  
143 with both higher and lower maturation size are able to invade and disruptive selection results.  
144 The singular maturation size  $m_0^* = 0.18$  g that is realized in the absence of interference com-  
145 petition and interspecific predation is evolutionarily unstable, and the ecotype undergoes evo-  
146 lutionary branching.

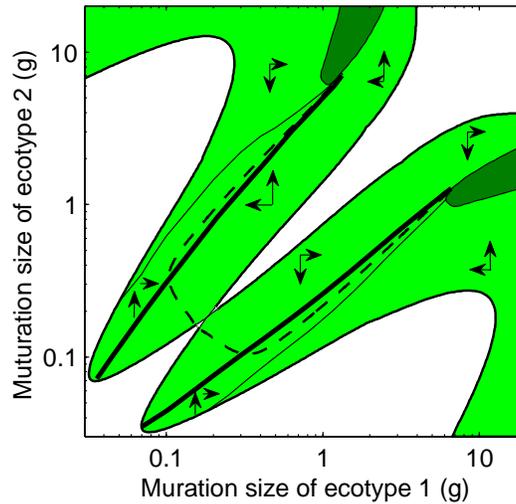


147

148 **Fig. B1:** Pairwise invasibility plot showing the evolutionary dynamics of a single population.  
 149 There is exactly one evolutionarily singular maturation size,  $m_0^*$ , (vertical dashed line). It is  
 150 convergence stable, in the sense that any population will evolve towards the singular maturation  
 151 size given sufficiently small mutational steps. Selection is disruptive at the singular maturation  
 152 size, eventually allowing the population to diversify and become dimorphic through  
 153 evolutionary branching. The positive and negative areas correspond to combinations of resident  
 154 and mutant trait values for which the mutant ecotype can invade the resident ecotype.  
 155 Parameter values are given in Table A2.

156 Evolutionary branching causes the emergence of two ecotypes with distinct maturation sizes.  
 157 As the two ecotypes coevolve, their trait values diverge from each other in the direction indicated  
 158 by the arrows in the two-dimensional trait evolution plot in figure B2. The deterministic  
 159 evolving trajectories from the monomorphic population to the dimorphic community are  
 160 shown by the dashed lines. The difference in maturation size between the two ecotypes increases  
 161 until the pair crosses the thick solid isocline at which directional selection in the ecotype with  
 162 the smaller maturation size ceases. The coevolving populations then stay within the region  
 163 between the two isoclines until they reach the dark-green area. As they pass the boundary,  
 164 one of the two ecotypes will go extinct, depending on which ecotype first overshoots the

165 boundary. When the ecotype becomes monomorphic, the evolutionary dynamics starts over  
 166 again, leading to a perpetual cycle of evolutionary branching and extinction reminiscent of  
 167 Red Queen dynamics (Van Valen, 1973). Evolutionary diversification of the system beyond  
 168 two ecotypes does not appear possible without introduction of interference competition.



169

170 **Fig. B2:** Trait evolution plot showing the evolutionary dynamics of two coexisting ecotypes.  
 171 Light-green areas indicate the coexistence region for two resident ecotypes, while the dark-  
 172 green areas indicate that ecotype 1 and 2 can invade one another when rare, but still not coex-  
 173 ist. The isoclines (continuous lines) indicate where gradual evolution ceases in one of the res-  
 174 ident ecotypes. Thick and thin line styles indicate whether selection in the ecotype for which  
 175 gradual evolution has ceased is stabilizing or disruptive, respectively. Horizontal (vertical)  
 176 arrows indicate the direction of evolutionary change in maturation size of resident ecotype 1  
 177 (2). The dashed line is the predicted evolutionary trajectory of the dimorphic population fol-  
 178 lowing evolutionary branching at maturation size  $m_0^*$ . Upon entering the dark-green area, one  
 179 of the two coexisting ecotypes become extinct and the population is again monomorphic,  
 180 leading to a perpetual evolutionary cycle.

181

182 **Appendix C:** Algorithm for evolutionary community assembly

183 We use adaptive dynamics techniques to study the evolution of maturation size (e.g., Metz et  
184 al., 1996; Geritz et al., 1997; Brännström et al., 2013). Ecological communities emerge as a  
185 consequence of gradual evolution and evolutionary branching. The directional evolutionary  
186 change in an ecotype is determined under the assumption of mutation-limited evolution by the  
187 canonical equation of adaptive dynamics (Dieckmann and Law, 1996),

188 
$$\frac{dx}{dt} = \frac{1}{2} \mu_m \sigma_\mu^2 R(x) \partial_y S_x(y) |_{y=x}, \quad (\text{C1})$$

189 in which  $x$  and  $y$  are the logarithmical values of the traits of resident and mutant ecotypes,  $\mu_m$   
190 is the rate of mutations and  $\sigma_\mu$  is standard deviation of mutations,  $R(x)$  is the reproduction rate  
191 of the resident ecotype while  $S_x(y)$  is the fitness of a mutant with trait value  $y$  invading a  
192 resident with trait value  $x$  (Dieckmann and Law, 1996). Differentiating and evaluating at  
193  $y = x$  then gives the selection gradient,  $\partial_y S_x(y) |_{y=x}$ . Positive selection gradient means that  
194 mutant ecotypes with trait value (maturation size) larger than the resident ecotype can invade.  
195 An important case is that the gradient vanishes. A trait value at which the selection gradient  
196 vanishes is called an evolutionarily singular maturation size. It is either a minimum or maxi-  
197 mum of the invasion fitness  $S_x(y)$ . Being a minima (positive curvature of the fitness curve at  
198 the singular maturation size) implies that the singular maturation size is evolutionarily unsta-  
199 ble and, if directional evolution leads up to the maturation size, evolutionary branching will  
200 eventually unfold and cause the population to become dimorphic. In a multi-species environ-  
201 ment, if all ecotypes have trait values that are located at maxima of the invasion fitness, then  
202 no further evolutionary change occurs. We say that the community has reached an evolutiona-  
203 rily stable state (ESS).

204 Evolutionary community assembly starts with the resource and a single ancestor ecotype in a  
205 demographic steady state. A community is then assembled algorithm as follows,

206 (1) Suppose there are multiple species in the current environment with trait values  
207  $x = (x_1, \dots, x_n)$ . Their demographic dynamics are described by the McKendrick-von  
208 Foester (MvF) equation (1). The demographic equations are integrated numerically to  
209 a demographically steady state.

210 (2) The selection gradient of each ecotype  $x_i$ , i.e.,  $D(x_i) = \partial_y S_x(y = x_i)$ , is evaluated  
211 at the trait value of that ecotype. There are three cases<sup>1</sup>: (i) Non-vanishing selection  
212 gradient. An ecotype with trait value  $x_{n+1} = x_i + \delta_1$  is added to the environment with  
213  $\delta$  being a random value proportional to  $D(x_i)$ . A corresponding MvF equation describ-  
214 ing is added to describe the new ecotype's demographic dynamics, while the MvF eq-  
215 uation associated with the parent ecotype is removed. (ii) Vanishing selection gradient  
216 with a corresponding maximum of the invasion fitness. There is nothing to do with  
217 this resident ecotype. (iii) Vanishing selection gradient with a corresponding minimum  
218 of the invasion fitness. In this case, the resident ecotype has reached an evolutionary  
219 branching point. Two mutants are inserted symmetrically around the parent ecotype's  
220 trait value, i.e.,  $x_{n+1} = x_i - \delta_1$  and  $x_{n+2} = x_i + \delta_2$ , where  $\delta_1$  and  $\delta_2$  are chosen at  
221 random from a Gaussian distribution with mean value 0 and standard deviation  $\sigma_\mu^2$ . In  
222 addition, two MvF equations corresponding to the two mutant ecotypes are added.

223 (3) If all ecotypes have vanishing selection gradients corresponding to a maxima of the  
224 invasion fitness, then assembly ceases. Otherwise, change  $n$  to the new number of  
225 ecotypes and repeat from step 1.

---

<sup>1</sup>Strictly speaking, there is also a fourth case in step 2 that of a vanishing selection gradient and while the inva-  
sion fitness is neither at a maximum nor a minimum. This degenerate case did not occur in our investigations.

226 In the algorithm above, the invasion fitness is calculated as the asymptotic exponential growth  
227 rate of mutant population (Metz et al., 1992), and the selection gradient (e.g.,  $\partial_y S_x(y = x_i)$ )  
228 can then be approximated numerically using finite difference. The biomass of a new ecotype  
229 is initially set to  $10^{-20}$  g/m<sup>3</sup> and this value is also taken as the extinction threshold. Parame-  
230 ter values can be found in Table A2.

231

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