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

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HIGHLIGHTS

- Interference competition can positively affect population demographic properties.
- Maturation size responds differently to different types of interference competition.
- All four types of interference competition can promote initial diversification.
- Diversity of emergent communities varies with types of interference competition.

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ABSTRACT

We investigate how four types of interference competition – which alternatively affect foraging, metabolism, survival, and reproduction – impact the ecology and evolution of size-structured populations. Even though all four types of interference competition reduce population biomass, interference competition at intermediate intensity sometimes significantly increases the abundance of adult individuals and the population's reproduction rate. We find that foraging and metabolic interference evolutionarily favor smaller maturation size when interference is weak and larger maturation size when interference is strong. The evolutionary response to survival interference and reproductive interference is always larger maturation size. We also investigate how the four types of interference competition impact the evolutionary dynamics and resultant diversity and trophic structure of size-structured communities. Like other types of trait-mediated competition, all four types of interference competition can induce disruptive selection and thus promote initial diversification. Even though foraging interference and reproductive interference are more potent in promoting 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, while reproductive interference can only support relatively smaller communities with simpler trophic structure. Taken together, our results show how the type and intensity of interference competition jointly affect coexistence patterns in structured population models.

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1. Introduction

An important aspect of individual life history that has received comparatively little attention is the interference that takes place between individuals when they compete for resources (Le Bourlot et al., 2014). Interference competition is hypothesized

to be a major force driving natural selection (Rosenzweig, 1978; Dieckmann et al., 2004; Bolnick, 2004). This belief is reinforced by recent theoretical studies on the evolutionary emergence of food webs (e.g., Caldarelli et al., 1998; Drossel et al., 2001; McKane, 2004; Loeuille and Loreau, 2005; Rossberg et al., 2008; Brännström et al., 2011, 2012), which demonstrate that

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interference competition can promote species diversity. These studies canonically assume that interference competition elevates individual mortality, but elevated mortality is in fact only one of several possible outcomes.

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

The four different types of interference competition are indistinguishable in unstructured population models, such as those used in several recent studies on food-web evolution (e.g., Loeuille and Loreau, 2005; Rossberg et al., 2008; Brännström et al., 2011). This is because interference competition in unstructured population models can essentially only be incorporated as a reduction of the per-capita growth rate which mathematically is equivalent to an increase in mortality. Any inherent differences between the four different types of interference competition considered here can thus only become apparent in physiologically structured population models that incorporate ontogenetic development of individuals from juvenile to adult (de Roos and Persson, 2013). As the widespread use and legacy of unstructured population models have favored a tradition in which interference competition is represented as increased mortality, little is currently known about how interference competition acting on other ecological processes impacts the ecology and evolution of size-structured populations and communities.

In this paper, we investigate how the aforementioned four types of interference competition affect the ecological and evolutionary dynamics of size-structured populations and communities. We base our investigation on a recently developed modeling framework for fish populations. First, we introduce the size-structured population model that we use in our investigation and phenomenologically model the four types of interference competition at the individual level. We then explore the effects of interference competition on the demography and evolution of a single population. After we have elucidated the effects on a single population, we consider the impact of interference competition on the diversity and trophic structure of evolved communities. Finally, we conclude with a discussion in which we recapitulate our main findings, aim to place them in a broader context, and identify promising directions for future research.

2. Methods

The size-structured population model used in this paper builds on the framework for aquatic food webs of fish populations by Hartvig et al. (2011) in which well-mixed individuals share a common habitat (Section 2.1 and Appendix A). Individuals can interfere with each in any of four qualitatively different ways, with the strength of interference in each case depending on the individuals' body size and maturation size (Section 2.2 and Appendix A). While the body size changes through the life time of an individual, the maturation size is assumed to be an evolving trait which is faithfully inherited from parents to offspring except for rare and small mutations at birth (Section 2.3). As our model is not concerned with reproductive isolation, we use the term

ecotype rather than species for a population of individuals with the same maturation size. We characterize the ecotype by maturation size which is generally recognized as one of the most important life history characteristics in fish populations (Charnov et al., 2012), because it determines how energy is allocated between growth and reproduction.

2.1. Size-structured population model

We briefly outline the size-structured population model below and refer to Appendix A for a more detailed description including model equations (Table A1) and parameters (Table A2). We consider a large number of individuals characterized by their body size w which each belong to any of several ecotypes. An ecotype i is characterized by the maturation size m_i . Individuals grow in size, reproduce, and die at rates that depend on their size, availability of resources, and antagonistic interference with other individuals. The growth rate ($g(w, m_i)$, Eq. M8 in Table A1) is food dependent and determined from size-based predation on both resource and consumer individuals, following the principle of “big-eat-small” (Ursin, 1973). This principle allows for within-population predation (cannibalism) which is a ubiquitous phenomenon in fish populations (Fox, 1975; Polis, 1981; Smith and Reay, 1991; Elgar and Crespi, 1992). The rate at which predators encounter prey depends on the volume that the predator can search in one unit of time. Following an established allometric relationship, this volume scales with predator body size (Appendix A). Individuals can die as a result of predation by larger individuals (Eq. M10 in Table A1), background mortality, or starvation mortality (Eq. M11 in Table A1), which together combine to give an individual mortality rate $\mu(w, m_i)$. Finally, mature individuals produce offspring at a food- and size-dependent rate $b(w, m_i)$ (Eq. M9 in Table A1).

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

$$\frac{\partial}{\partial t} N_i(w, t) + \frac{\partial}{\partial w} (g(w, m_i) N_i(w, t)) = \mu(w, m_i) N_i(w, t), \quad (1a)$$

$$g(w_0, m_i) N_i(w_0, t) = \frac{\epsilon}{2w_0} \int_{w_0}^{M_i} b(w, m_i) N_i(w, t) dw. \quad (1b)$$

Here, $N_i(w, t)$ is the size spectrum of ecotype i at time t , and $M_i = m_i/\eta$ is the maximally attainable size of ecotype i , where η is the ratio of maturation size to maximum size. Eq. (1a) describes how the size spectrums of the ecotype changes over time as a consequence of individual growth and mortality. Newborn individuals enter the populations through the boundary condition, Eq. (1b), in which the constituent elements can be understood as follows: Offspring of size w_0 are produced by adults at a size-dependent birth rate $b(w, m_i)$ and survive the larvae stage with probability ϵ . The fraction $1/2$ reflects an assumed equal sex ratio.

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

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

in which $r_0 w^{n-1}$ is the intrinsic renewal rate (Savage et al., 2004) and $\kappa_0 w^{-\lambda}$ is the equilibrium resource density in the absence of consumers, both scaling allometrically with the size of the resource organisms. The term $\mu_p(w)$ reflects the consumption of the resource by individuals of all ecotypes. Thus, the resource level is determined by its productivity and consumptions from all predators. The sizes of the resource organisms fall within a finite range with upper limit

w_{\max} . The lower limit is not important as long as it is far smaller than the size of newborn individuals, w_0 .

2.2. Four types of interference competition

We phenomenologically consider four types interference competition: a reduction of time spent searching for prey (foraging interference), an extra loss of energy for activity during encounter (metabolic interference), a risk of dying as a result of interference encounter (survival interference), and egg/larvae predation (reproductive interference). The first three interference types occur between individuals with similar body size and maturation size, while reproduction interference occurs primarily between individuals with similar maturation size. Here “similar” means the two individuals have similar body size and similar maturation size. These assumptions are partly supported by Werner (1988) who argued that an increase in body size often necessities a shift in ecological niche. Individuals with dissimilar size will interact through predator–prey interaction, but not through interference.

Foraging interference, metabolic interference, and survival interference occur when a focal individual encounters another individual or vice versa. As the volumetric search rate increases with body size, we assume that the larger individual encounters the smaller. From these considerations the rate of interference encounter for an individual of ecotype i is estimated as

$$r_i(w, m_i) = \sum_j I_m\left(\frac{m_i}{m_j}\right) \left(\int_{w_0}^w \nu(w') I_w\left(\frac{w}{w'}\right) N_j(w', t) dw' + \int_w^{M_j} \nu(w') I_w\left(\frac{w'}{w}\right) N_j(w', t) dw' \right), \tag{3}$$

in which $\nu(w) = \gamma w^q$ is the volumetric search rate (Eq. M3 in Table A1). Here, $I_w(w/w')$ and $I_m(m/m')$ are measures of similarity in body size and maturation size respectively, and are defined by

$$I_w(w/w') = \exp\left(-\frac{\ln^2 w/w'}{2\sigma_w^2}\right), \tag{4a}$$

$$I_m(m/m') = \exp\left(-\frac{\ln^2 m/m'}{2\sigma_m^2}\right). \tag{4b}$$

The parameters σ_w^2 and σ_m^2 describe how quickly interference will attenuate with differences in body size (Eq. (4a)) and in maturation size (Eq. (4b)).

For reproductive interference, we assume that eggs are vulnerable to individuals of any body size since eggs do not move (ignoring water turbulence). We further assume that the rate at which an individual with a given body size encounters eggs is proportional to its volumetric search rate. The rate at which eggs of ecotype i are encountered is then defined as

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

The four types of interference competition are modeled as follows:

- (1) Foraging interference, i.e., reduction in search rate. The volumetric search rate $\nu(w)$ is reduced by a factor $e^{-\gamma_c r_1(w, m_i)}$ so that $\nu(w) = \gamma w^q$ is replaced by $e^{-\gamma_c r_1(w, m_i)} \gamma w^q$. Here γ_c is a free parameter characterizing the interference intensity.
- (2) Metabolic interference, i.e., increase in metabolic costs due to interference. Following metabolic scaling (West et al., 2001), the metabolic cost arising from interference is $\kappa_c r_1(w, m_i) w^p$,

where κ_c is the interference intensity, a free parameter. This cost is added to individual maintenance cost.

- (3) Survival interference, i.e., death of individuals due to interference. The mortality rate increases with $\mu_c = p_c r_1(w, m_i)$ where p_c is a constant regulating the intensity survival interference. This mortality is added to the individual mortality rate.
- (4) Reproductive interference, i.e., egg or larvae predation. The recruitment rate (the right-hand side of Eq. (1b)) is reduced by a factor $e^{-\alpha_c f(m_i)}$ where α_c is a free parameter indicating the strength of interference and $f(m_i)$ is the rate at which eggs of ecotype i are encountered.

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

In principle, all four types of interference competition described above can simultaneously occur in a population, but to understand the role of each type of interference in population dynamics, they are here investigated separately. To facilitate comparison between different types of interference competition, after initial numerical experiments, we scale each of the interference-intensity parameters γ_c , κ_c , p_c , and α_c so that a value of 1 causes the biomass of a reference population to be exactly one percent of the interference-free biomass. A parameter value of zero corresponds to the interference-free case and the interference intensity increases with larger values. The trait value m_0^* of the reference population is chosen as the unique evolutionarily singular maturation size for single populations without interference (see Appendix B).

2.3. Evolutionary dynamics

We employ adaptive dynamics theory to study the evolution of maturation size (e.g., Metz et al., 1996; Geritz et al., 1997; Dercole and Rinaldi, 2008; Brännström et al., 2013). The evolution of maturation size is governed by the canonical equation under the assumption of mutation-limited evolution (Dieckmann and Law, 1996). For a single population, evolution is always directional towards a unique singular maturation size at which directional selection ceases (Hartvig, 2011; see also Appendix B). At the singular maturation size, evolution either comes to halt or undergoes evolutionary branching, leading to emergence of dimorphic populations. This process of gradual evolution and evolutionary branching often continues, resulting in the emergence of an ecological community (c.f., Loeuille and Loreau, 2005; Dieckmann et al., 2007; Brännström et al., 2011; Brännström et al. 2013). The emerging community is generally evolutionarily stable except at low intensity of interference competition (Appendix B). In this latter case, we define the ecotype diversity and the trophic level as the minimum over the evolutionary attractor. We assume a strict separation between the ecological and evolutionary time scales typical of many studies in adaptive dynamics (e.g., Doebeli and Dieckmann, 2000) with ecological dynamics proceeding faster than the evolutionary dynamics, meaning that the resident community dynamics has settled on its demographic attractor before the next mutation occurs. Further details of the canonical equation and the community-assembly process are provided in Appendix C.

3. Results

We numerically explore how the four modeled types of interference competition affects the ecology and evolution of populations and communities. We start with a single population and explore how this population's demographic properties (i.e., population biomass, abundance, reproduction rate, and adult abundance) are influenced by

interference competition (Section 3.1). We then continue with this single population and investigate how the maturation size evolves in response to the interference competition (Section 3.2). Finally, moving beyond a single population, we examine how interference competition affects the diversity and trophic structure of evolutionarily assembled communities (Section 3.3). The section ends with a brief summary of the results (Section 3.4).

3.1. Demographic impacts of interference competition

Fig. 1 shows that three out of four demographic indicators are positively correlated with at least one type of interference competition. Foraging interference positively affects adult abundance for a range of interference intensities (Fig. 1C) but negatively affects the three other demographic indicators considered. Metabolic interference negatively affects all four of the considered demographic indicators. Survival interference causes a considerable initial increase in population abundance followed by a decline as survival-interference intensifies (Fig. 1B). The increase in abundance comes in spite of a monotonous decline in population biomass with survival-interference intensity. From this, we infer an increase in the number of juveniles. This is corroborated by a reduction in adult abundance (Fig. 1C). In stark contrast to the decrease in adult abundance is the rise in the population reproduction rate (Fig. 1D). Finally, reproductive interference raises the population reproduction rate at low interference intensity (Fig. 1D), although it decreases all of the three other indicators considered.

The positive impact that some types of interference competition have on the demographic indicators under consideration is primarily due to the change in the size-structure of consumer population. This is corroborated by Fig. 1A, which shows consistent declines of total

population biomass with increased interference. Thus an increase in adult, total population abundance or reproduction rate can then only come about through a changed size distribution of the consumer. Take the increased reproduction rate by survival interference for example, interference competition raises individual mortality rates, relieving exploitative competition and hence enhancing resource abundance. Surviving juveniles grow faster, potentially compensating for the loss of adult abundance. The population's reproduction rate depends on the adult size distribution and the adults' size-dependent birth rate. As the latter increases with the resource abundance, while the former is fairly constant when there is little interference competition, the sum of these two changes explains the observed increase in reproduction rate. However, this advantage of resource availability is lost when interference competition intensifies and fast-growing juveniles can no longer compensate for higher mortality.

3.2. Evolutionary impacts of interference competition on populations

Fig. 2A shows that among the four types of interference, survival interference gives rise to the largest maturation size, followed by the reproductive interference. Both foraging and metabolic interference decrease maturation size considerably when interference intensity is small but this tendency is reversed when interference is continuously intensified. An opposite situation for foraging interference is observed where sufficiently strong intensity drives the maturation size slightly down. The presented evolutionarily singular maturation size is convergence stable for all four types of interference competition across the entire range of interference strengths, meaning that a single population always gradually evolves towards the singular maturation size (see Fig. B1 in Appendix B).

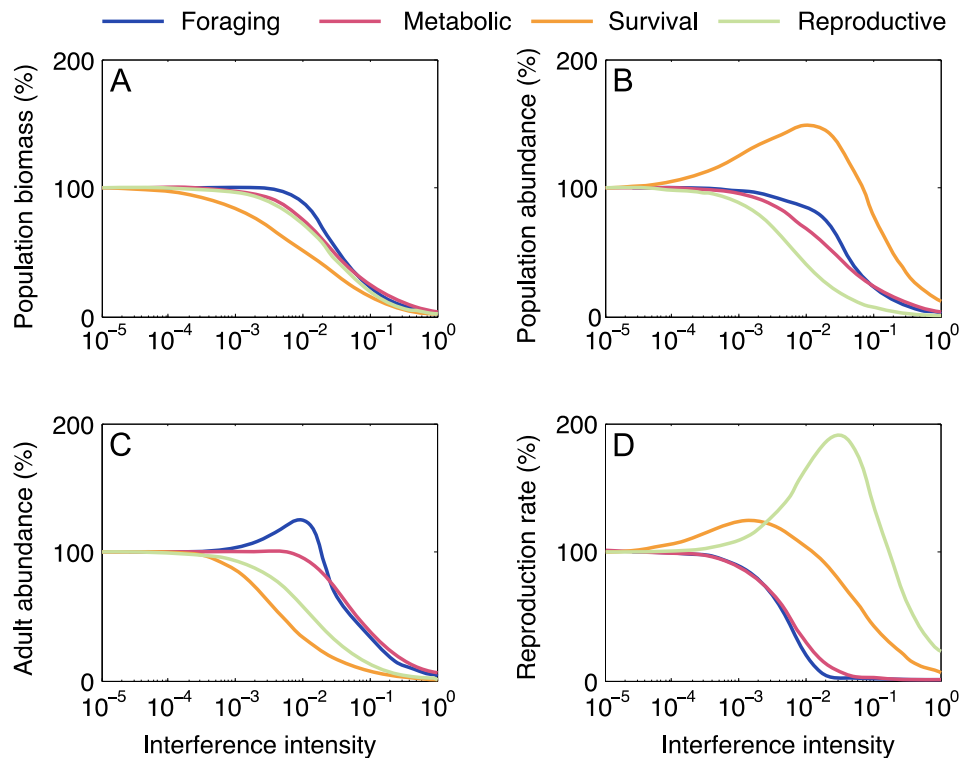


Fig. 1. Influence of interference competition on four demographic indicators. (A) Population biomass decreases for all types of interference competition. (B) Population abundance declines for all interference types except survival. (C) Adult abundance declines for all interference types except foraging. (D) Both survival interference and reproduction interference can increase the population's reproduction rate. All demographic quantities are scaled in relation to the interference-free quantities. In case of oscillations, long-term averages of mean population quantities were considered, which usually happens to the foraging and metabolic interference with high intensity. The reference population has maturation size m_0^* , which is the unique evolutionarily singular maturation size in the absence of interference competition (see Appendix B). Parameter values are as in Table A2 (Appendix A) with interference-intensity ranging from 10^{-5} to 1. Interference intensity below the range shown has negligible effects on population dynamics.

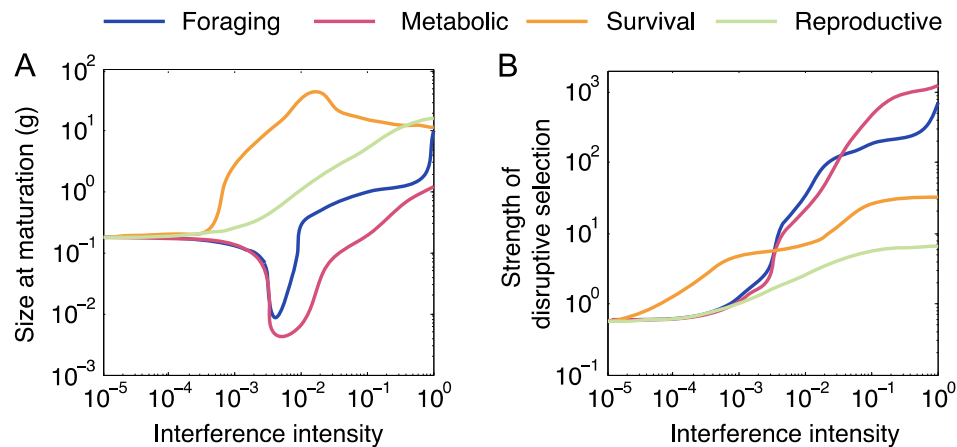


Fig. 2. Influence of interference competition on the evolution of populations. (A) Survival and reproductive interference promotes maturation at smaller size at low to intermediate interference intensity and larger size at high interference intensity. (B) All four types of interference competition promote diversification of the population. Foraging, metabolic, and survival interference are more likely to induce diversification than reproductive interference. The strength of disruptive selection is assessed by the second order derivative of the invasion fitness at the resident trait value. Parameter values are as in Table A2 (Appendix A) with interference-intensity ranging from 10^{-5} to 1 for the same reason as Fig. 1.

Once a population has evolved to the evolutionarily singular maturation size, disruptive selection can cause the ancestral population to diversify into two new ecotypes. Fig. 2B shows that selection is always disruptive at the evolutionarily singular maturation size and that the strength of disruptive selection increases with interference intensity. This implies that the four types of interference all promote diversification, albeit to different extents. Foraging, metabolic, and survival interference are more likely to enable diversification than reproductive interference.

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

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

3.3. Evolutionary impacts of interference competition on communities

A single ecotype eventually evolves to the evolutionarily singular maturation size at which point it experiences disruptive selection. Evolutionary branching may then result in the emergence of two coexisting ecotypes from the single ancestor. Through directional selection and further evolutionary branching, an entire community of coexisting ecotypes is eventually

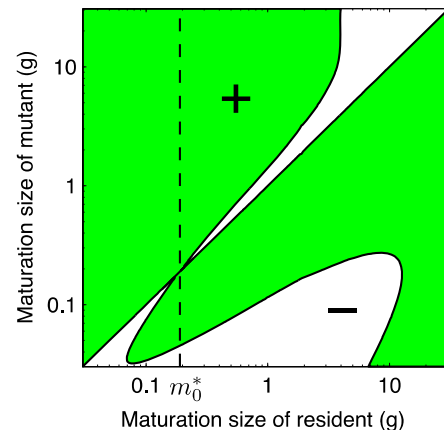


Fig. B1. Pairwise invasibility plot showing the evolutionary dynamics of a single population. There is exactly one evolutionarily singular maturation size, m_0^* (vertical dashed line). It is convergence stable, in the sense that any population will evolve towards the singular maturation size given sufficiently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

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

We investigate how two salient measures of the evolved communities, ecotype diversity (Fig. 4A) and maximum trophic

level (Fig. 4B), are affected by interference competition. Fig. 4A shows that all types of interference competition promote large communities, but metabolic interference most strongly promotes diverse communities with high trophic levels, followed by foraging and survival interference. Reproductive interference gives rise to less diverse communities with simpler trophic structure. Moreover, for each type of interference competition, the most diverse community emerges at intermediate levels of interference intensity for survival interference while they only emerge at high levels of interference intensity for the other three types of interference competition. For lower levels of interference intensity (approximately below 10^{-5} to 10^{-4}), only communities composed of at most two of ecotypes emerge, irrespective of the type of interference competition. This is because the two ecotypes which emerge after the initial diversification evolve to a state in which they are no longer able to coexist, starting the process over again from a single ecotype (see Appendix B). Finally, by comparing the ecotype diversity and the maximum trophic level of evolved communities, we find that the most diverse communities usually have the highest maximum trophic level.

3.4. Summary

Our principal findings are summarized in Table 1. The four types of interference competition generally have a negative impact on demographic indicators. As exceptions to this rule, foraging interference can increase the adult abundance, survival interference can increase the total abundance and the population's reproduction rate, and reproductive interference can increase the population's reproduction rate. These exceptions are significant only at intermediate strengths of interference competition. We find that a population's maturation size is first reduced then increased by foraging and metabolic interference, but it is always increased by survival and reproductive interference when compared to a population without interference. Interference competition also has profound impacts on communities. All four types of interference competition can induce disruptive selection and support the emergence of diverse communities, though survival interference might be more likely to drive the emergence of diverse communities in practice as it has large effects already at low and intermediate levels of interference intensity.

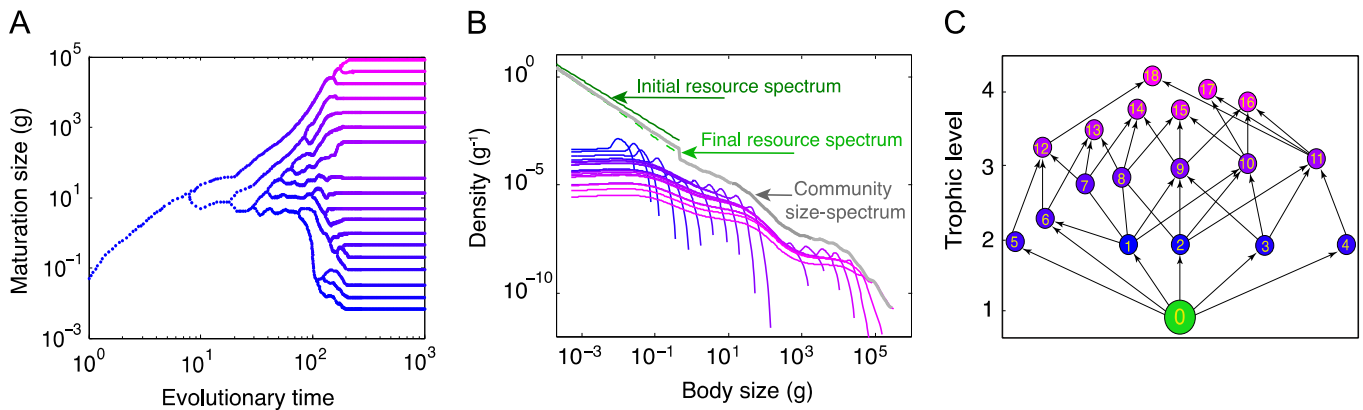


Fig. 3. An example of an evolved community under survival interference. (A) A single ancestor eventually gives rise to a community of 18 coexisting ecotypes at evolutionary equilibrium. (B) Ecotype size spectra (solid lines), together with the initial (solid dark-green line), final (dashed-green line) resource size spectra, and the community size-spectrum (gray line) which is a sum of all individual size spectra and resource spectrum. (C) Trophic structure of the evolved community. We identify an ecotype's trophic level with the trophic position of adults of that ecotype, to account for the change in trophic level that individuals experience as they grow. The arrows between ecotypes (nodes) indicate the presence and direction of energy flows accounting for more than 15% of the recipient ecotypes' diet. Trophic level (vertical axis) is defined as the average path length from a focal ecotype down to the resource (node 0), weighted by the proportion of energy along each path relative to the total energy that is consumed by the adult individuals of the focal ecotype (Levine, 1980). The nodes are ordered according to ascending maturation size. Parameter values are in Table A2 (Appendix A) with survival-interference intensity set to 0.03. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

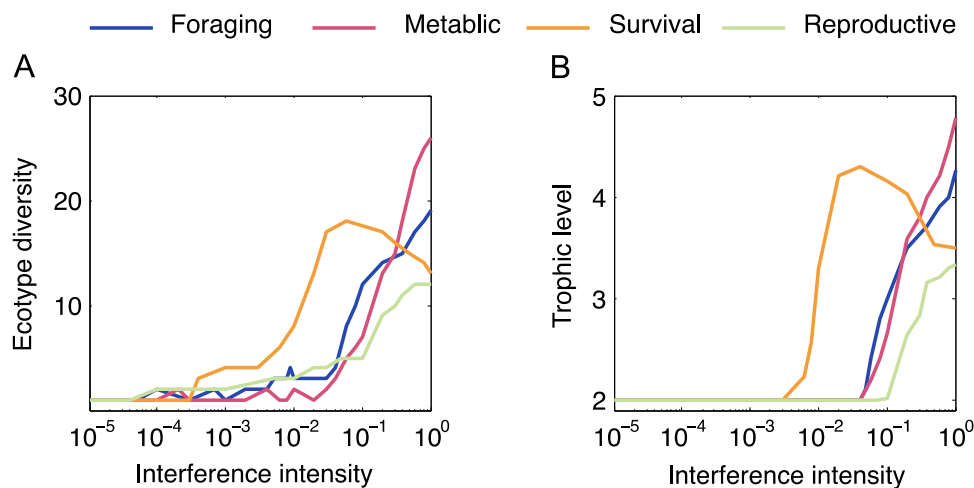


Fig. 4. Influence of interference competition on the evolution of communities. (A) Survival interference promotes diverse communities at intermediate interference strength. The three other types of interference promote diverse communities only at high levels of interference competition. (B) The maximum trophic level of the evolved communities follows a similar pattern as the evolved diversity. The trophic level of the resource is assumed to be 1. Parameter values are as in Table A2 (Appendix A) with interference intensity ranging from 10^{-5} to 1 for the same reason as Fig. 1.

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	Populations		Communities	
					Maturation size	Disruptive selection	Diversity	Trophic level
Foraging	↓	↓	↑↓	↓	↓↑	↑	↑	↑
Metabolic	↓	↓	↓	↓	↓↑	↑	↑	↑
Survival	↓	↑↓	↓	↑↓	↑↓	↑	↑↓	↑↓
Reproductive	↓	↓	↓	↑↓	↑	↑	↑	↑

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

4. Discussion

We have modeled four types of interference and investigated their impacts on the ecology and evolution of size-structured populations and food webs. Our results show that all four types of interference competition promote the emergence of diverse food webs with several trophic levels, but that only survival interference does so significantly at intermediate interference intensities, implying that survival interference may be more likely to drive the emergence of diverse communities than other types of interference.

The four types of interference competition were modeled phenomenologically, building on an idealized expression for the interference encounter rate, which assumes that all individuals are available for interference encounters. A rigorous mechanistic derivation of interference competition which accounts for the fact that other individuals may already be tied up in interference encounters appears to be out of reach for general size-structured populations, as the interference encounter rate (i.e., Eq. (4)) must be solved from an integral equation. For populations with stage structure, Ruxton et al. (1992) mechanistically incorporated interference competition. They found that weak interference promotes unstable population dynamics. By contrast, we observed that interference competition generally has a stabilizing effect on the population dynamics. As the rare exception, we found that foraging and metabolic interference have a destabilizing effect when interference intensity is high (result not shown). This is primarily because these two types of interference competition reduce the energy available for individual growth, which consequently prolongs the growth journey from juvenile to adult. The longer the juvenile stage the more unstable the population is. Moreover, we note that our treatment of interference competition assumes that interference occurs between individuals having similar body size and/or maturation size. While this seems plausible for species in which individuals change diet as they grow in size, it cannot be excluded that interference may occur between individuals having different body size or maturation size. Elucidating the consequences of such “interference asymmetry” is an interesting topic for future research.

The four types of interference competition can be classified into two groups: physiologically-related interference (i.e., foraging interference and metabolic interference), which influences energy gains for individual ontogeny, and physiologically-unrelated interference (i.e., survival interference and reproductive interference), which influences individual survival. The latter are related to but differ from predation in that survival interference unlike predation occurs between individuals of similar body size and in that energy is not gained from neither survival interference nor reproductive interference. For these reasons, the results presented here on the effects of survival interference are likely to be quite different from predation, though the results on reproductive interference are likely to be rather similar to egg/larvae predation as long as the energy gained from predation is negligible for the species' demographic dynamics.

Interference affecting energy gain gives rise to qualitatively different ecological and evolutionary consequences. For instance, we found that physiologically-related interference can result in either evolution towards of smaller or larger maturation size depending on interference intensity, while physiologically-unrelated interference results in evolution towards larger maturation size (Fig. 2). This difference highlights that understanding and describing population dynamics require specifying not only the degree, but also the kind, of interference competition.

While many ways by which interference competition affects individuals can be modeled using size-structured population models, the range of options in unstructured population models is considerable smaller. Interference competition in unstructured population models is almost invariably represented as an increase in mortality, which negatively affects population demographic properties (e.g., Case and Gilpin, 1974; Schoener, 1976; Case et al., 1979; Vance, 1984; Amarasekare, 2002; Kuang et al., 2003). In size-structured population models, the negative effects of interference competition can, as we have seen, take different forms such as reducing energy for growth and reproduction. Importantly, these negative effects can partially or completely be compensated by changes in resource availability and population size structure. For instance, survival interference decreases consumer abundance, consequently relieving predation pressure on the resource, which in turn leads to higher resource abundance. Increased resource abundance makes surviving juveniles grow faster and surviving adults more productive, potentially compensating for the direct loss of consumer individuals through interference. This accounts for the increase in abundance seen from increased survival interference and foraging interference, as well as for the increase in reproduction rate seen from reproductive and survival interference. Such indirect benefits of interference competition cannot be realized in unstructured population models unless they are assumed a priori (e.g., Amarasekare, 2002).

That small to moderate intensity of interference competition promotes species coexistence in unstructured population models has been demonstrated by several studies (Loeuille and Loreau, 2005; Rossberg et al., 2008; Brännström et al., 2011, 2012). For size-structured population models, Hartvig and Andersen (2013) found that only a couple of species could coexist in the absence of interference competition. By incorporating interference competition in the model developed by Hartvig et al. (2011), we found that diverse evolutionarily assembled communities can emerge under all four types of interference competition that we considered, albeit to different extent. It should be noted that interference competition is but one mechanism which can promote species coexistence in size-structured population models. Other mechanisms capable of promoting coexistence include species-specific preferences (Hartvig et al., 2011; Rossberg et al., 2013), prey switching (Maury and Poggiale, 2013), stock-recruitment relationships (Andersen and Pedersen, 2010) and species-specific resources (Rossberg et al., 2013).

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

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Appendix A. Size-structured population model.

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

Each population *i*, henceforth denoted ecotype, is characterized by its maturation size *m_i*. Individuals within this ecotype are represented by body size *w* varying from *w₀* to *M_i* = *m_i*/η. Here, *w₀* is the size of offspring, which is assumed to be uniform among all ecotypes, and *M_i* is the maximum attainable body size of individuals in ecotype *i*. The ecotype size spectrum, i.e., the distribution of individual abundance as a function of body size, is denoted *N_i(w, t)* or simply *N_i*. The aggregated size spectra of all ecotypes in a community give rise to the community size spectrum (Andersen and Beyer, 2006).

Predation is size selective and mathematically formulated by a selection function (M1), which is lognormal (Ursin, 1973) and peaks when the size ratio of predator to prey equals the preferred predator–prey mass ratio β. The size range of prey individuals that a predator individual consumes is determined by the standard deviation σ. Interactions between individuals with size ratio that are several standard deviations from β are negligible and can be entirely ignored.

Encountered food for *w*-sized individuals comes from predation upon resource and consumer individuals (M2). The amount of food is proportional to the size-dependent volumetric search rate (M3). Satiation is described by the feeding level (M4), which multiplied with the maximum food intake (M5) gives rise to the ingested food. With assimilation efficiency α, ingested food is converted to energy (M6) that is utilized for life-history processes. Energy is in priority used for paying maintenance costs *k_sw^p* and then, if there is any, used for individual somatic growth and reproduction. The distribution of the remaining energy between these two processes is governed by an allocation function (M7). The growth equation (M8) indicates that the surplus energy after paying metabolic cost is entirely used for juvenile growth but drops at the onset of reproduction (M9). The growth of individuals ceases when they approach their maximum body size at which all energy is routed to reproduction.

In addition to the predation mortality (M10), individuals experience trait-dependent background mortality at the rate μ₀*m_iⁿ*^{−1}, as well as starvation mortality (M11) when the assimilated energy is insufficient to cover metabolic costs. The total mortality rate of *w*-sized individuals is thus μ(*w, m_i*) = μ_p + μ₀*m_iⁿ*^{−1} + μ_s(*w*). Moreover, in case of starvation, growth and reproduction stop instantaneously. The background mortality prevents unlimited growth of large individuals that do not experience predation.

The ecotype dynamics are described by the McKendrick-von Foerster equation, Eq. (1a). The boundary condition, Eq. (1b), represents the recruitment of offspring. We assume an efficiency of reproduction ε which represents energy used during spawning migrations, energy losses in conversion of reserves to gonads, eggs

Table A1
Model equations.

Num	Equation	Interpretation
M1	$\varphi(w/w') = \exp(-\log^2(w'\beta/w)/(2\sigma^2))$	Selection function
M2	$E(w) = v(w)(\int_0^{w_{cut}} w'R(w')\varphi(w/w')dw' + \sum_j \int_{w_0}^{M_j} w'N_j(w')\varphi(w/w')dw')$	Encountered food from resource and consumers
M3	$\nu(w) = \gamma w^d$	Volumetric search rate
M4	$F(w) = E(w)/(E(w) + I_{max}(w))$	Feeding level
M5	$I_{max}(w) = hw^n$	Maximum food intake
M6	$S(w) = \alpha I_{max}(w)F(w)$	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	$\mu_p(w) = \sum_j \int_{w_0}^{M_j} \nu(w')(1 - F(w'))N_j(w')\varphi(w'/w)dw'$	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

Table A2
Parameters and values of the size-structured population model.

Parameter	Value	Unit	Interpretation
Consumer			
β	100	–	Preferred predator–prey mass ratio
σ	1	–	Width of selection function
α	0.6	–	Assimilation efficiency
ε	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 metabolic rate
p	0.75	–	Exponent of metabolic costs
q	0.8	–	Exponent of volumetric search rate
η	0.25	–	Ratio of maturation size to maximum size
μ	0.84	g/yr	Scaled background mortality
ξ	0.1	–	Fraction of energy reserves
w_0	0.0005	–	Scaled egg size
f_0	0.6	–	Initial feeding level
γ	$\frac{f_0 h \beta^2 - \lambda w_r}{\sqrt{2\pi(1-f_0)\kappa_0\sigma}}$	g/yr	Scaled factor of volumetric search rate
w_r	1	g	Reference weight for scaling ^a
Resource			
κ_0	0.005	g^{-1}/m^3	Scaled magnitude of resource size spectrum
r_0	4	1/yr	Scaled generate rate
w_{cut}	0.5	–	Upper limit of resource spectrum
λ	$2+q-n$	–	Slope of resource spectrum
Interference			
σ_w	0.5	–	Width of interference kernel in body size ^b
σ_m	0.5	–	Width of interference kernel in maturation size ^b
σ_μ	0.001	–	Standard deviation of mutations ^c
μ_m	0.001	–	Mutation rate ^c
γ_c	varied	–	Foraging interference intensity
κ_c	varied	–	Metabolic interference intensity
p_c	varied	–	Survival interference intensity
α_c	varied	–	Reproductive interference intensity

^a Arbitrary. The remaining parameters are from Hartvig et al. (2011).

^b Arbitrarily chosen value smaller than the width of the selection kernel to ensure that a given individual does not interfere against its prey.

^c Dieckmann and Doebeli (1999).

survival, etc. The resources are continuously distributed along the size spectrum and have dynamics that follow chemostatic growth (Eq. (2)). The resource spectrum is truncated at the lower size w_{cut} . This lower limit of resource size does affect the results as long as it is far smaller than w_0 . Both the resource carrying capacity (M12) and the resource regeneration rate (M13) are size-dependent.

In order to express units in integer powers, we scale individual body size and the maturation size with a reference weight $w_r = 1$ g, by setting $\tilde{w} = w/w_r$ and $\tilde{m} = m/w_r$, respectively. This gives rise to scaling constants in some of the equations listed in Table A1. For instance, the volumetric search rate $\nu(w) = \gamma w^q$ is transformed to $\nu(\tilde{w}) = \gamma w_r^q \tilde{w}^q$ after which we define $\tilde{\gamma} = \gamma w_r^q$. Other relevant equations and parameters are similarly scaled. From here on, we will use the scaled variables although, for brevity, we will not write out the superscript tilde. The scaled parameters are presented in Table A2.

Appendix B. Adaptive dynamics of the size-structured population model without interference competition.

In this appendix, we investigate the evolutionary dynamics of maturation size in a monomorphic population (Fig. B1) and dimorphic population (Fig. B2) in the absence of interference competition. The reported results also apply to populations with very low interference intensity.

Fig. B1 shows that through a sequence of small mutations, the maturation size will approach the evolutionarily singular maturation size m_0^* . Upon reaching m_0^* , mutant strategies with both higher and lower maturation size are able to invade and disruptive

selection results. The singular maturation size $m_0^* = 0.18$ g that is realized in the absence of interference competition and interspecific predation is evolutionarily unstable, and the ecotype undergoes evolutionary branching.

Evolutionary branching causes the emergence of two ecotypes with distinct maturation sizes. As the two ecotypes coevolve, their trait values diverge from each other in the direction indicated by the arrows in the two-dimensional trait evolution plot in Fig. B2. The deterministic evolving trajectories from the monomorphic population to the dimorphic community are shown by the dashed lines. The difference in maturation size between the two ecotypes increases until the pair crosses the thick solid isocline at which directional selection in the ecotype with the smaller maturation size ceases. The coevolving populations then stay within the region between the two isoclines until they reach the dark-green area. As they pass over the boundary, one of the two ecotypes will go extinct, depending on which ecotype first enters the dark-green area. When the population becomes monomorphic, the evolutionary dynamics starts over again, leading to a perpetual cycle of evolutionary branching and extinction reminiscent of Red Queen dynamics (Van Valen, 1973). Evolutionary diversification of the system beyond two ecotypes does not appear possible without introduction of interference competition.

Appendix C. Algorithm for evolutionary community assembly.

We use adaptive dynamics techniques to study the evolution of maturation size (e.g., Metz et al., 1996; Geritz et al., 1997; Dercole and Rinaldi, 2008; Brännström et al., 2013). Ecological

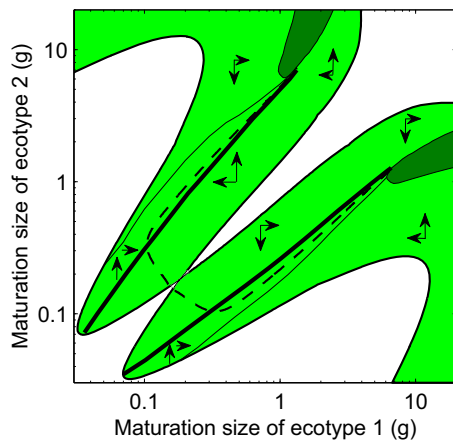


Fig. B2. Trait evolution plot showing the evolutionary dynamics of two coexisting ecotypes. Light-green areas indicate the coexistence region for two resident ecotypes, while the dark-green areas indicate that ecotype 1 and 2 can invade one another when rare, but still not coexist. The isoclines (continuous lines) indicate where gradual evolution ceases in one of the resident ecotypes. Thick and thin line styles indicate whether selection in the ecotype for which gradual evolution has ceased is stabilizing or disruptive, respectively. Horizontal (vertical) arrows indicate the direction of evolutionary change in maturation size of resident ecotype 1 (2). The dashed line is the predicted evolutionary trajectory of the dimorphic population following evolutionary branching at maturation size m_0^* . Upon entering the dark-green area, one of the two coexisting ecotypes become extinct and the population is again monomorphic, leading to a perpetual evolutionary cycle. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

communities emerge as a consequence of gradual evolution and evolutionary branching. The directional evolutionary change in an ecotype is determined under the assumption of mutation-limited evolution by the canonical equation of adaptive dynamics (Dieckmann and Law, 1996),

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

in which x and y are the logarithmical values of the traits of resident and mutant ecotypes, μ_m is the rate of mutations and σ_μ is standard deviation of mutations, $R(x)$ is the reproduction rate of the resident ecotype while $S_x(y)$ is the fitness of a mutant with trait value y invading a resident with trait value x (Dieckmann and Law, 1996). Differentiating and evaluating at $y=x$ then gives the selection gradient, $\partial_y S_x(y) |_{y=x}$. Positive selection gradient means that mutant ecotypes with trait value (maturation size) larger than the resident ecotype can invade. An important case is that the gradient vanishes. A trait value at which the selection gradient vanishes is called an evolutionarily singular maturation size. It is either a minimum or maximum of the invasion fitness $S_x(y)$. Being a minima (positive curvature of the fitness curve at the singular maturation size) implies that the singular maturation size is evolutionarily unstable and, if directional evolution leads up to the maturation size, evolutionary branching will eventually unfold and cause the population to become dimorphic. If all ecotypes have trait values that are located at maxima of the invasion fitness, then no further evolutionary change occurs. We say that the community has reached an evolutionarily stable state (ESS).

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

(1) Suppose there are multiple ecotypes in the current environment with trait values $x = (x_1, \dots, x_n)$. Their demographic dynamics are described by the McKendrick-von Foester (MvF) Eq. (1). The demographic equations are integrated

numerically using a first-order semi-implicit upwind scheme to a demographically steady state.

- (2) The selection gradient of each ecotype x_i , i.e., $D(x_i) = \partial_y S_x(y=x_i)$, is evaluated at the trait value of that ecotype. There are three cases¹: (i) Non-vanishing selection gradient. An ecotype with trait value $x_{n+1} = x_i + \delta_1$ is added to the environment with δ being a normally distributed random value with zero mean and standard deviation σ_μ . A corresponding MvF equation describing is added to describe the new ecotype's demographic dynamics, while the MvF equation associated with the parent ecotype is removed. (ii) Vanishing selection gradient with a corresponding maximum of the invasion fitness. There is nothing to do with this resident ecotype. (iii) Vanishing selection gradient with a corresponding minimum of the invasion fitness. In this case, the resident ecotype has reached an evolutionary branching point. Two mutants are inserted symmetrically around the parent ecotype's trait value, i.e., $x_{n+1} = x_i - \delta_1$ and $x_{n+2} = x_i + \delta_2$, where δ_1 and δ_2 are chosen at random from a Gaussian distribution with mean value 0 and standard deviation σ_μ^2 . In addition, two MvF equations corresponding to the two mutant ecotypes are added.
- (3) If all ecotypes have vanishing selection gradients corresponding to a maxima of the invasion fitness, then assembly ceases. Otherwise, change n to the new number of ecotypes and repeat from step 1.

In the algorithm above, the invasion fitness is calculated as the asymptotic exponential growth rate of mutant population (Metz et al., 1992), and the selection gradient (e.g., $\partial_y S_x(y=x_i)$) can then be approximated numerically using finite difference. The biomass of a new ecotype is initially set to 10^{-20} g/m³ and this value is also taken as the extinction threshold. Parameter values can be found in Table A2.

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

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