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Evolution of specialization under non-equilibrium population dynamics

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Abstract

We analyze the evolution of specialization in resource utilization in a mechanistically underpinned discrete-time model using the adaptive dynamics approach. We assume two nutritionally equivalent resources that in the absence of consumers grow sigmoidally towards a resource-specific carrying capacity. The consumers use resources according to the law of mass-action with rates involving trade-off. The resulting discrete-time model for the consumer population has over-compensatory dynamics. We illuminate the way non-equilibrium population dynamics affect the evolutionary dynamics of the resource consumption rates, and show that evolution to the trimorphic coexistence of a generalist and two specialists is possible due to asynchronous non-equilibrium population dynamics of the specialists. In addition, various forms of cyclic evolutionary dynamics are possible. Furthermore, evolutionary suicide may occur even without Allee effects and demographic stochasticity.

Key words: Adaptive dynamics, Resource utilization, Trade-off, Specialist, Generalist, Evolution, Local adaptation

1. Introduction

2 Evolution of life history traits interacts with population dynamics. Especially well this interplay is known in the case of evolution of dispersal, where
3 non-equilibrium population dynamics may forge dispersal and even enable evolutionary
4 branching of dispersal strategies, but, on the other hand, dispersal
5 may stabilize population dynamics (Gyllenberg et al., 1993; Holt and McPeck,
6 1996; Parvinen, 1999; Ronce, 2007). However, recent results indicate that the
7 type of population-dynamical attractor may affect the evolution of other life
8 history traits as well (White et al., 2006; Hoyle et al., 2011). In this paper,
9 we analyze the interplay between population dynamics and the evolution of
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1 resource utilization using the adaptive dynamics approach (Metz et al., 1992;
2 Geritz et al., 1998).

3 In order to enable reasonable evolutionary analysis, we base our model on in-
4 dividual level processes (Rueffler et al., 2006a). We first assume continuous-time
5 resource-consumer dynamics within breeding seasons for consumers utilizing two
6 alternative resources. With specialization between two substitutable resources,
7 a trade-off is necessarily present: a consumer may utilize both resources, but
8 the more efficiently it uses one resource, the less efficiently it is able to use the
9 other.

10 Following Geritz and Kisdi (2004), we assume time-scale separation between
11 the dynamics of the resources and those of the consumers. This enables us to
12 obtain a discrete-time model for the consumer population between breeding seasons.
13 Different within-season resource dynamics result in different discrete-time
14 between-season dynamics for the consumer population. We commit the majority
15 of our analysis using a model that, in the case of only one resource, equates
16 to the discrete logistic model, which is known to exhibit a wide range of different
17 population-dynamical attractors from equilibrium to chaos (e.g. Holmgren
18 (1994)). For comparison, we present also results obtained from models that
19 correspond to the Ricker (1954) model and Hassell (1975) model. In all of these
20 models, the type of the population-dynamical attractor affects the evolutionary
21 dynamics of the consumers' resource utilization strategies. On the other hand,
22 different consumer strategies result in different types of population-dynamical
23 attractors.

24 The family of models we study has been extensively studied in the case of
25 equilibrium dynamics by Nurmi and Parvinen (2008) who found three qualitatively
26 different evolutionary scenarios: evolution to a monomorphic specialist
27 population, evolutionary branching resulting in the coexistence of two specialist
28 strategies, and evolution to a monomorphic generalist population. This is in
29 line with the majority of previous results (Levins, 1962, 1963; Meszéna et al.,
30 1997; Ma and Levin, 2006; Rueffler et al., 2006b; Ravigné et al., 2009). Previous
31 work on other traits has shown that, under non-equilibrium population
32 dynamics, evolutionary branching may be possible also in such ecological scenarios
33 that do not allow branching under equilibrium dynamics (Parvinen, 1999;
34 White et al., 2006; Hoyle et al., 2011). Thus, non-equilibrium dynamics may
35 result in enhanced biodiversity. In our model, evolutionary branching is possible
36 already under equilibrium dynamics. However, non-equilibrium dynamics may
37 still add in diversity by allowing a secondary evolutionary branching to occur,
38 which results in the trimorphic coexistence of generalists and specialists. Furthermore,
39 non-equilibrium dynamics may, in our model, result in evolutionary
40 suicide (Ferrière, 2000; Parvinen, 2005).

41 In the presence of only one resource, it is possible to investigate the evolution
42 of the rate at which the consumer uses the resource. In this case, there are no
43 costs involved in the utilization of the sole resource. Thus, in most cases, there
44 is selection for ever increasing values of this rate until a physical maximum is
45 reached. It is also possible that the resource population collapses or even goes
46 extinct, e.g., because of Allee-effects or demographic stochasticity. This in turn

1 can cause the extinction of the consumer population, i.e. evolutionary suicide.
2 In our model with logistic dynamics, too intensive use of resources can cause
3 their collapse and thus the evolutionary suicide of the consumer population even
4 in the absence of Allee-effects and demographic stochasticity.

5 There are several models where the ecological coexistence of a generalist and
6 two specialists is possible (Wilson and Yoshimura, 1994; Kisdi, 2002; Abrams,
7 2006b). However, such coexistence may be evolutionarily unstable. Even more
8 rarely is such trimorphic coexistence evolutionarily attainable, i.e. reachable
9 from an initially monomorphic population when mutations are assumed small.
10 Egas et al. (2004) showed that evolution always destroys the trimorphic coexis-
11 tence in the model of Wilson and Yoshimura (1994). Furthermore, Egas et al.
12 (2004) showed that even in moderately modified versions of this model, evolution
13 to the trimorphic coexistence is possible only in an extremely narrow param-
14 eter domain. Abrams (2006a) showed that, if the resource dynamics fluctuate
15 asynchronously and the time consumers need to handle the resources is taken
16 into account, evolution to the trimorphic coexistence is possible and, in the
17 parameter domain where the ecological coexistence is possible, even plausible.
18 Abrams (2006a) deduced that asynchrony in the resource dynamics gives gener-
19 alists an advantage due to reduced variance in resource intake. This advantage
20 may, however, disappear when the generalists become more common since this
21 may have a synchronizing effect on the resource dynamics. In spatially hetero-
22 geneous models with global dispersal, evolution to the trimorphic coexistence
23 is not possible under equilibrium dynamics (Nurmi and Parvinen, 2008; Nurmi
24 et al., 2008) when only specialization can evolve, but recently Nurmi and Parvi-
25 nen (2011) showed that the joint evolution of specialization and dispersal may
26 result in the coexistence of an abundantly dispersing generalist and two scarcely
27 dispersing specialists (see also Kisdi (2002)). Furthermore, when the resources
28 are spatially aggregated, also distance-limited dispersal may enable evolution
29 to the trimorphic coexistence where generalists live in the habitat boundaries
30 (Debarre and Lenormand, 2011; Karonen, 2011).

31 In this paper, we integrate the ideas concerning the adaptive dynamics un-
32 der non-equilibrium population dynamics (Parvinen, 1999; White et al., 2006;
33 Hoyle et al., 2011) and the idea that asynchronous resource dynamics may en-
34 able coexistence of the specialists and generalists (Abrams, 2006a,b) with the
35 mechanistic modeling approach used by Nurmi and Parvinen (2008, 2011) to
36 analyze the evolution of specialization.

37 2. Model and methods

38 Following Geritz and Kisdi (2004), we assume that consumers hatch at the
39 beginning of a breeding season and use resources to produce eggs that also
40 encounter mortality during the breeding season. At the end of the season, all
41 adults perish and only a fraction of the eggs survives to the following season.

42 In the absence of consumers, continuous-time within-season dynamics of
43 resource i are determined by the logistic differential equation with carrying
44 capacity K_i , i.e.,

$$\dot{R}_i = \alpha_i \left(1 - \frac{R_i}{K_i}\right) R_i, \quad (1)$$

1 where R_i denotes the density of the resource and $\alpha_i > 0$ denotes the resource
 2 renewal rate. Different resources affect each other only via shared consumers.
 3 We assume that between breeding seasons resource populations recover to their
 4 carrying capacities independent of the usage during previous seasons.

5 The consumers use resources according to the law of mass action. The con-
 6 sumer individuals are all identical except for the specialization strategy $s \in [0, 1]$
 7 that affects only the resource consumption rates. An individual with strategy s
 8 uses resource 1 with rate $\beta(s)$ and resource 2 with rate $\beta(1-s)$. The resource
 9 consumption (or trade-off) function β is an increasing function with $\beta(0) = 0$
 10 and $\beta(1) = 1$. Thus, case $s = 0$ corresponds to a devoted specialist using only
 11 resource 2 and case $s = 1$ to a devoted specialist using only resource 1. Case
 12 $s = 0.5$ corresponds to an unbiased generalist. For example, if a consumer pop-
 13 ulation is monomorphic with strategy s and population size x , the dynamics
 14 of resource 1 are $\dot{R}_1 = \alpha_1 \left(1 - \frac{R_1}{K_1}\right) R_1 - \beta(s)R_1x$. Within season, consumers
 15 produce eggs with rate proportional to their resource usage. The consumer pop-
 16 ulation in the following season consists only of eggs that survive the winter and
 17 hatch.

18 When we, furthermore, assume that the resource dynamics are fast compared
 19 to the consumer dynamics such that the resources are always at the quasi-
 20 equilibrium determined by the consumer population sizes and strategies, we
 21 finally obtain the following logistic-type difference equation for the consumer
 22 between-season dynamics (Geritz and Kisdi (2004), see also Nurmi and Parvinen
 23 (2008)):

$$\begin{aligned} x_{n+1} = & \lambda_1 K_1 \beta(s) x_n \max\left(0, 1 - \frac{\beta(s)}{\alpha_1} x_n\right) \\ & + \lambda_2 K_2 \beta(1-s) x_n \max\left(0, 1 - \frac{\beta(1-s)}{\alpha_2} x_n\right), \end{aligned} \quad (2)$$

24 where $\lambda_i \in \mathbb{R}_+$ are compound parameters that depend on the details of the
 25 within season dynamics (Geritz and Kisdi, 2004).

26 In order to illuminate the differences between specialists and generalists we
 27 assume that the resources are nutritionally equivalent ($\lambda_1 = \lambda_2 = \lambda$) and renew
 28 in equal rate ($\alpha_1 = \alpha_2 = \alpha$). In this case, both λ and α can be scaled out and,
 29 for several consumers, equation (2) takes form

$$\begin{aligned} x_{n+1}^{(j)} = & K_1 \beta(s^{(j)}) x_n^{(j)} \max\left(0, 1 - \sum_{i=1}^k \beta(s^{(i)}) x_n^{(i)}\right) \\ & + K_2 \beta(1-s^{(j)}) x_n^{(j)} \max\left(0, 1 - \sum_{i=1}^k \beta(1-s^{(i)}) x_n^{(i)}\right) \\ = & f(s^{(j)}, S, X_n) x_n^{(j)}, \end{aligned} \quad (3)$$

30 where $f(s, S, X_n)$ is the fecundity of a strategy s individual when strategies $S =$
 31 $(s^{(1)}, s^{(2)}, \dots, s^{(k)})$ are present with population sizes $X_n = (x_n^{(1)}, x_n^{(2)}, \dots, x_n^{(k)})$.
 32 A rare mutant with strategy s^{mut} and negligible population size X_n^{mut} will grow

1 according to $x_{n+1}^{\text{mut}} = f(s^{\text{mut}}, S, X_n)x_n^{\text{mut}}$. Under equilibrium dynamics, we can
 2 determine the fitness of a rare mutant in the environment set by the residents,
 3 in the spirit of Metz et al. (1992), as

$$r(s^{\text{mut}}, S, X^*) = \ln(f(s^{\text{mut}}, S, X^*)),$$

4 where X^* denotes the vector of the equilibrium population sizes of the resi-
 5 dent strategies. Under non-equilibrium dynamics, the calculation of the fit-
 6 ness function is more complicated: Assume that the resident population com-
 7 prising strategies $S = (s^{(1)}, s^{(2)}, \dots, s^{(k)})$ has settled to an attractor $X =$
 8 $(X_1, X_2, \dots, X_n, \dots)$, where each X_n is the vector of the population sizes at
 9 time n as above. Then

$$r(s, S, X) = \lim_{t \rightarrow \infty} \ln \left(\sqrt[t]{\prod_{i=1}^t f(s, S, X_i)} \right) = \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{i=1}^t \ln(f(s, S, X_i)). \quad (4)$$

10 If $r(s, S, X) > 0$, a mutant with strategy s is able to invade the resident popula-
 11 tion. In practice, it is possible to calculate fitness only in the case of p -periodic
 12 resident population dynamics. In this case,

$$r(s, S, X) = \frac{1}{p} \sum_{i=1}^p \ln(f(s, S, X_i)).$$

13 Some analytic results can be derived even without specifying the resource
 14 consumption function β (Nurmi and Parvinen, 2008). However, our results
 15 mostly rely on the numerical analysis of equations (3) and (4) together with
 16 evolutionary simulations. In the numerical explorations, we use

$$\beta(s) = \frac{1 - e^{-\theta s}}{1 - e^{-\theta}}, \quad \theta \neq 0. \quad (5)$$

17 This formula is not defined for $\theta = 0$, but since $\lim_{\theta \rightarrow 0} \beta(s) = s$ it is natural to
 18 define $\beta(s) = s$ when $\theta = 0$. The trade-off parameter θ determines whether the
 19 resource consumption function β is convex ($\theta < 0$), concave ($\theta > 0$), or linear
 20 ($\theta = 0$). In the case of concave resource consumption function, the resource
 21 consumption function increases deceleratingly. This case is sometimes referred
 22 as the case of weak trade-off since a generalist can use resources more efficiently
 23 than a linear combination of the two specialists ($\beta(0.5) > \frac{\beta(0) + \beta(1)}{2}$). Analo-
 24 gously, in the case of convex resource consumption function, the resource con-
 25 sumption function increases acceleratingly (strong trade-off, $\beta(0.5) < \frac{\beta(0) + \beta(1)}{2}$).
 26 In the terminology used by, e.g., White et al. (2006) and Hoyle et al. (2011),
 27 the case of concave resource consumption function corresponds to a trade-off
 28 with accelerating costs, and the case of convex resource consumption function
 29 corresponds to a trade-off with decelerating costs.

30 The resource consumption function is the only ingredient in our model that
 31 has no mechanistic interpretation. We use negative values of θ to phenomenolog-
 32 ically model the situations where there is an additional cost of generalism, and

1 positive values of θ to model those situations where there is an additional ben-
2 efit of generalism. The linear resource consumption function ($\beta(s) = s$, $\theta = 0$)
3 is an important special case since it can be interpreted, for example, as the
4 search time allocation between the two resources. With the formulation (5), we
5 obtain resource consumption functions that are almost similar to the case with
6 $\beta(s) = s^\theta$, but avoid artificial singularities in the borders of the strategy space.

7 The derivative of $r(s, S, X)$ with respect to the mutant strategy s (fitness
8 gradient), determines the direction of evolution in a monomorphic population.
9 The points where the fitness gradient vanishes are called evolutionarily singular
10 strategies. There exists no directional evolution at a singular strategy. If evo-
11 lution, in a neighborhood of a singular strategy, directs towards (or away from)
12 this strategy, it is called evolutionarily attracting (or repelling) strategy. If no
13 other nearby strategy cannot invade the resident population with this strategy,
14 it is called an evolutionarily stable strategy (ESS, Maynard Smith and Price
15 (1973)). In the case of frequency-dependent selection, however, it is possible
16 that an evolutionarily attracting singular strategy can be invaded by any other
17 nearby strategy. In this case, evolutionary branching occurs, i.e., the popula-
18 tion splits into two distinct morphs that start to evolve further apart from each
19 other. Evolutionary attractiveness and stability are independent properties, and
20 all combinations are possible. For more information on singular strategies and
21 their classification see Geritz et al. (1998).

22 Above, we assumed that the resources are equivalent, i.e. $\lambda_1 = \lambda_2$ and
23 $\alpha_1 = \alpha_2$. If we, furthermore, assume that $K_1 = K_2$, the environment becomes
24 completely symmetric with respect to the resources. In a symmetric environ-
25 ment, the unbiased generalist strategy $s = 0.5$ is always singular. We analyze
26 mainly the case of symmetric environments since in this case it is easy to illu-
27 minate the differences between specialists and generalists and to observe how
28 changes in the other ecological parameters affect the evolutionary dynamics.

29 **3. Evolution of specialization in the logistic model**

30 *3.1. Evolution of specialization under equilibrium population dynamics*

31 In our model, the trade-off parameter θ dominates the evolutionary dynam-
32 ics. Under equilibrium population dynamics, there are only three qualitatively
33 different evolutionary scenarios: if θ is assumed to have high enough values, the
34 evolution of a monomorphic population directs towards generalism, and if low
35 enough values, towards specialism. In other words, concave resource consump-
36 tion function promotes generalism whereas strongly convex resource consump-
37 tion function promotes specialism (compare with Nurmi and Parvinen (2008,
38 2011)). In the intermediate case with weakly convex resource consumption func-
39 tion, a monomorphic population evolves towards generalism where evolutionary
40 branching takes place. Figure 1 illustrates evolutionary simulations from all dif-
41 ferent evolutionary scenarios possible under equilibrium population dynamics.

42
43 When the parameter values are such that the population shows equilibrium
44 dynamics for all specialization strategies, we find the evolutionary bifurcation

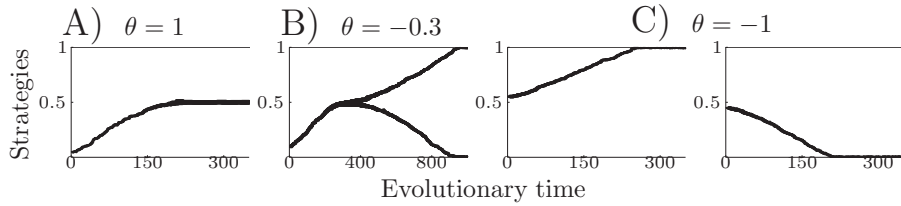


Figure 1: **Evolutionary scenarios under equilibrium population dynamics.**

Strategies present in the population as a function of the evolutionary time. One unit of evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix. Thus, it is only applicable for comparison between different simulations using the same procedure.

Panel A: Concave resource consumption function – Evolution leads to generalism.

Panel B: Weakly convex resource consumption function – Evolution of a monomorphic population leads to generalism where evolutionary branching takes place. The evolution of a dimorphic population leads to the combination of the two devoted specialists.

Panel C: Strongly convex resource consumption function – Evolution leads to the nearest devoted specialist strategy.

Other parameter values: $K_1 = K_2 = 1.5$, $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

1 diagrams illustrated in Figure 2. The generalist strategy turns from a branching
2 point to an evolutionarily stable strategy at $\theta = 0$ where the resource consump-
3 tion function turns from convex to concave. A simple calculation shows that
4 under equilibrium population dynamics this is a rather general result (Nurmi
5 and Parvinen, 2008). Under non-equilibrium dynamics, this relation no longer
6 holds (See e.g. Figure 9A). Corresponding results have been obtained also by
7 White et al. (2006); Hoyle et al. (2011). The parameter domains colored black
8 in Figure 2 are such that the population is not viable due to low resource intake:
9 when the resources are scarce, the additional cost of generalism (negative θ) may
10 cause extinction. When some strategies in the strategy space are not viable, it is
11 worthwhile to consider, whether evolutionary suicide is possible. Evolutionary
12 suicide may occur when evolution drives the strategy of the evolving population
13 towards the unviable part of the strategy space. This is possible when muta-
14 tions that are beneficial at the individual level are harmful at the population
15 level (e.g. "tragedy of commons" (Hardin, 1968)). At the extinction boundary,
16 it is possible that the resident population is invaded by a "kamikaze mutant"
17 that can outcompete the other strategies but is not viable alone and thus the
18 species dies out. However, if the population-dynamical attractor, as a function
19 of the resident strategy, approaches zero continuously, the resident population is
20 almost absent in the neighborhood of the extinction boundary. This means that
21 the invasion fitness of a mutant is the same as the fitness in a virgin environment.
22 Thus, only mutants that are viable alone are able to invade, and evolutionary
23 suicide is impossible. Therefore, a necessary condition for evolutionary suicide
24 is that the population-dynamical attractor drops discontinuously from a viable
25 non-trivial attractor to the trivial attractor corresponding to extinction. This
26 result has been proven algebraically for a wide class of models by Gyllenberg
27 et al. (2002), see also Parvinen (2005).

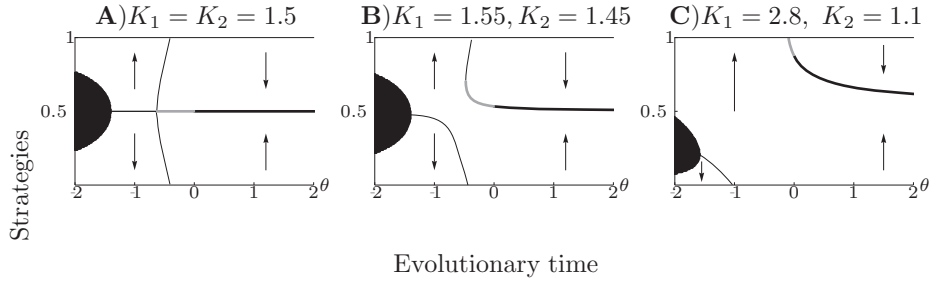


Figure 2: **Evolutionary bifurcation diagrams in the case of equilibrium population dynamics.** Singular strategies as a function of the trade-off parameter θ . Thin black curve indicates evolutionary repellors, thick grey curve branching points and thick black curve evolutionarily stable strategies. The arrows indicate the direction of evolution in a monomorphic population. In the black-colored parameter domain, the population is not viable due to low resource intake. Other parameter values: $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

1 In the case of equilibrium population dynamics (Figure 2), the transition to
 2 extinction takes place continuously: The equilibrium population size decreases
 3 continuously to zero when the specialization strategy approaches the extinction
 4 boundary (see Figure 4A). The continuous transition to extinction guarantees
 5 that the extinction boundary is evolutionarily repelling, and thus evolutionary
 6 suicide is not possible in the neighborhood of this parameter domain.

7 3.2. Non-equilibrium population dynamics

8 If resource carrying capacities have large values, the population dynamics
 9 may be periodic or even chaotic. Furthermore, the population-dynamical at-
 10 tractors may be qualitatively different for consumers using different strategies
 11 (see Figure 4). For a strategy $s = 1$ consumer utilizing solely resource 1, the
 12 type of the population-dynamical attractor is determined solely by the param-
 13 eter K_1 similarly to the logistic recurrence equation $x_{n+1} = K_1 x_n (1 - x_n)$. If
 14 $0 < K_1 < 1$, the corresponding specialist with strategy $s = 1$ is not viable. If
 15 $1 < K_1 < 3$, a monomorphic specialist population shows equilibrium dynamics.
 16 If $3 < K_1 < 4$, a monomorphic specialist population shows periodic or chaotic
 17 dynamics. If $4 < K_1$, a devoted specialist with $s = 1$ is not viable, because
 18 the population growth is fast enough to exhaust resource 1 (see equation (2)).
 19 Furthermore, note that the trade-off parameter θ does not affect the population
 20 dynamics of a monomorphic population of devoted specialist since $\beta(1) = 1$
 21 independent of θ . Analogous results hold for strategy $s = 0$ specialists.

22 For an unbiased generalist strategy (which is singular if $K_1 = K_2$), the
 23 attractor type is analogously determined by the sum $\beta(0.5)(K_1 + K_2)$. Figure 3
 24 illustrates the population-dynamical attractors of the unbiased generalist ($s =$
 25 0.5) population as a function of the trade-off parameter θ . In panel A, the
 26 generalist population is unviable for low values of θ due to low resource intake
 27 (low resource carrying capacities and the additional cost of generalism) whereas
 28 in panel B, the population is unviable for large values of θ since both resources

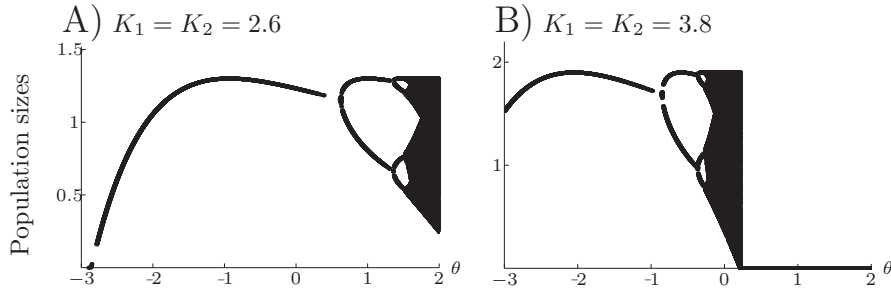


Figure 3: **Population-dynamical attractors of an unbiased generalist population** ($s = 0.5$) **as a function of the trade-off parameter** θ . The panels correspond to those of Figure 5. Other parameter values: $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

1 become exhausted because high resource carrying capacities and the additional
 2 benefit of generalism result in overly fast consumer population growth.

3 Figure 4 illustrates the population-dynamical attractors as a function of
 4 the specialization strategy s . In Figure 4A, the transitions to extinction at
 5 $\theta \approx 0.36$ and $\theta \approx 0.74$ occur continuously and thus evolutionary suicide is not
 6 possible, whereas in Figure 4D, these transitions at $\theta \approx 0.43$ and $\theta \approx 0.57$ occur
 7 discontinuously, which means that evolutionary suicide may be possible in this
 8 setting. Below we show that evolutionary suicide actually happens. Figures 4B
 9 and 4C illustrate that the resource consumption strategy may affect population
 10 dynamics in a variety of ways.

11 3.3. Evolution of specialization under non-equilibrium population dynamics

12 Figure 5 illustrates the evolutionary dynamics in the case of possibly periodic
 13 or chaotic population dynamics. It shows the evolutionary singular strategies
 14 as a function of the trade-off parameter θ together with the endpoints of the
 15 corresponding evolutionary simulations (see the Appendix for the description of
 16 the simulation procedure). In Figure 5A, devoted specialists have equilibrium
 17 population dynamics, whereas in Figure 5B, they have chaotic dynamics.

18 We are not aware of any algebraic means for calculating fitness under chaotic
 19 population dynamics. The population-dynamical route to chaotic dynamics
 20 takes place via a series of period-doubling bifurcations (see Figures 3 and 4).
 21 For the population-dynamical attractors of period 1, 2, 4, 8 or 16 we base our
 22 analysis on fitness gradient using equation (4). In (the neighborhood of) the
 23 parameter domain where population dynamics are chaotic, this method is not
 24 applicable. There we are forced to rely solely on evolutionary simulations. Such
 25 parameter domains are colored grey in Figure 5. Note, that in a dimorphic
 26 or polymorphic population, the parameter domains with chaotic population
 27 dynamics may be completely different. Note also that the search for attractors
 28 could be extended, but the increase in the size of the analytically treatable
 29 parameter domain would be rather small and the increase in computational
 30 time would be substantial.

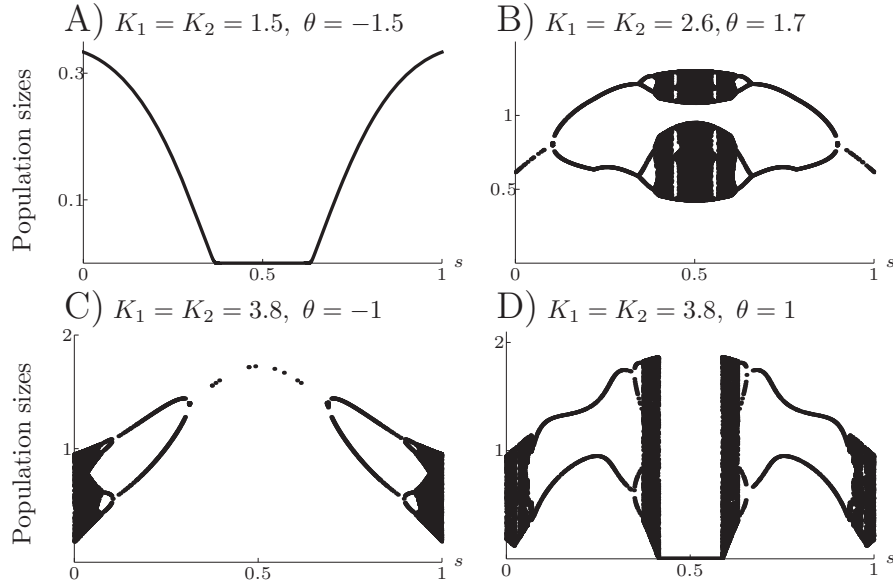


Figure 4: **Population-dynamical attractors as a function of the specialization strategy s .**

Panel A: Continuous transition to extinction when the resource carrying capacities are low such that, due to the additional cost of generalism, the resource intake by generalists is not high enough to maintain viability of the population (cf. Figure 2).

Panel B: Specialists have equilibrium population dynamics but, due to the additional benefit of generalism ($\theta > 0$), generalists have chaotic population dynamics (cf. Figure 5A).

Panel C: Specialists have chaotic population dynamics but the usage of two resources together with the additional cost of generalism stabilizes the population dynamics (cf. Figure 5B).

Panel D: Discontinuous transition to extinction. High resource carrying capacities and additional benefit of generalism accelerate the growth of the consumer population. Finally resources are exhausted and the consumer population goes abruptly extinct. Note, that biased usage of two resources may still stabilize population dynamics (cf. Figure 5B).

Other parameter values $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

1 All the simulations illustrated in Figure 5 start with an initially monomor-
 2 phic population with a random initial strategy and population size. When an
 3 evolutionary simulation ends in a monomorphic population, we illustrate this
 4 endpoint using a \diamond -sign. When evolutionary branching takes place, we illustrate
 5 the strategies present at the end of the simulation using $*$ -signs. Since all the
 6 simulations are run over only a finite time, it is possible that some of them have
 7 not yet reached an evolutionarily stable strategy.

8 The parameter domains colored black in Figure 5 are such that the popu-
 9 lation is not viable. In Figure 5A this unviability is caused by low resource
 10 intake (see Figure 4A), and as explained above, evolutionary suicide is not possi-
 11 ble. In Figure 5B unviability occurs since high resource carrying capacities
 12 together with the additional benefit of generalism result in population growth
 13 fast enough to exhaust the resources. As assumed in the model description, the
 14 resources recover next time unit after being exhausted. The consumer popula-
 15 tion, however, cannot recover, and extinction results. In this case, the transition
 16 from viable parameter domain to extinction occurs discontinuously (see Figure
 17 4D) and evolutionary suicide occurs whenever $\theta \gtrsim 0.3$. In Figures 5B and 9B
 18 the \dagger -sign at the boundary of this black area illustrates the last viable strategy
 19 before extinction in an evolutionary simulation.

20 When the resource consumption function is sufficiently convex (the trade-off
 21 parameter θ low), the evolution of specialization leads to a population compris-
 22 ing one or two devoted specialist strategies both under equilibrium population
 23 dynamics (Figures 2 and 5A) and under non-equilibrium population dynamics
 24 (Figure 5B). For weakly convex resource consumption function ($-1 \lesssim \theta \lesssim 0$
 25 in Figure 5), however, the evolutionary dynamics differ qualitatively between
 26 the cases with equilibrium (panel A) and non-equilibrium (panel B) population
 27 dynamics. Under equilibrium population dynamics, the evolution of a monomor-
 28 phic population leads to generalism where evolutionary branching takes place
 29 and finally evolution ends in a combination of the two devoted specialist strate-
 30 gies. Under non-equilibrium population dynamics, as well, the evolution of a
 31 monomorphic population leads to generalism and evolutionary branching takes
 32 place. However, after branching the evolution of the dimorphic population does
 33 not lead to the combination of the devoted specialist strategies. Instead, either
 34 another evolutionary branching results in the trimorphic coexistence of a gen-
 35 eralist and two devoted specialists, or the population remains dimorphic, but
 36 does not evolve to the coexistence of two devoted specialists. Next we discuss
 37 these two cases in detail.

38 3.4. *Dimorphic evolution of specialization under non-equilibrium population dy-* 39 *namics*

40 When the strategies $s^{(1)}$ and $s^{(2)}$ in a dimorphic population are symmetric
 41 ($s^{(1)} = 1 - s^{(2)}$), and the environment is symmetric ($K_1 = K_2$), then it follows
 42 directly from equation (3), that the diagonal $x^{(1)} = x^{(2)}$ in the population-
 43 dynamical state-space is invariant, i.e., if $x_n^{(1)} = x_n^{(2)}$, then also $x_{n+1}^{(1)} = x_{n+1}^{(2)}$.
 44 Such an in-phase orbit is called a symmetric orbit. It is possible to show al-
 45 gebraically (See the Appendix) that in such a case, the dimorphic population

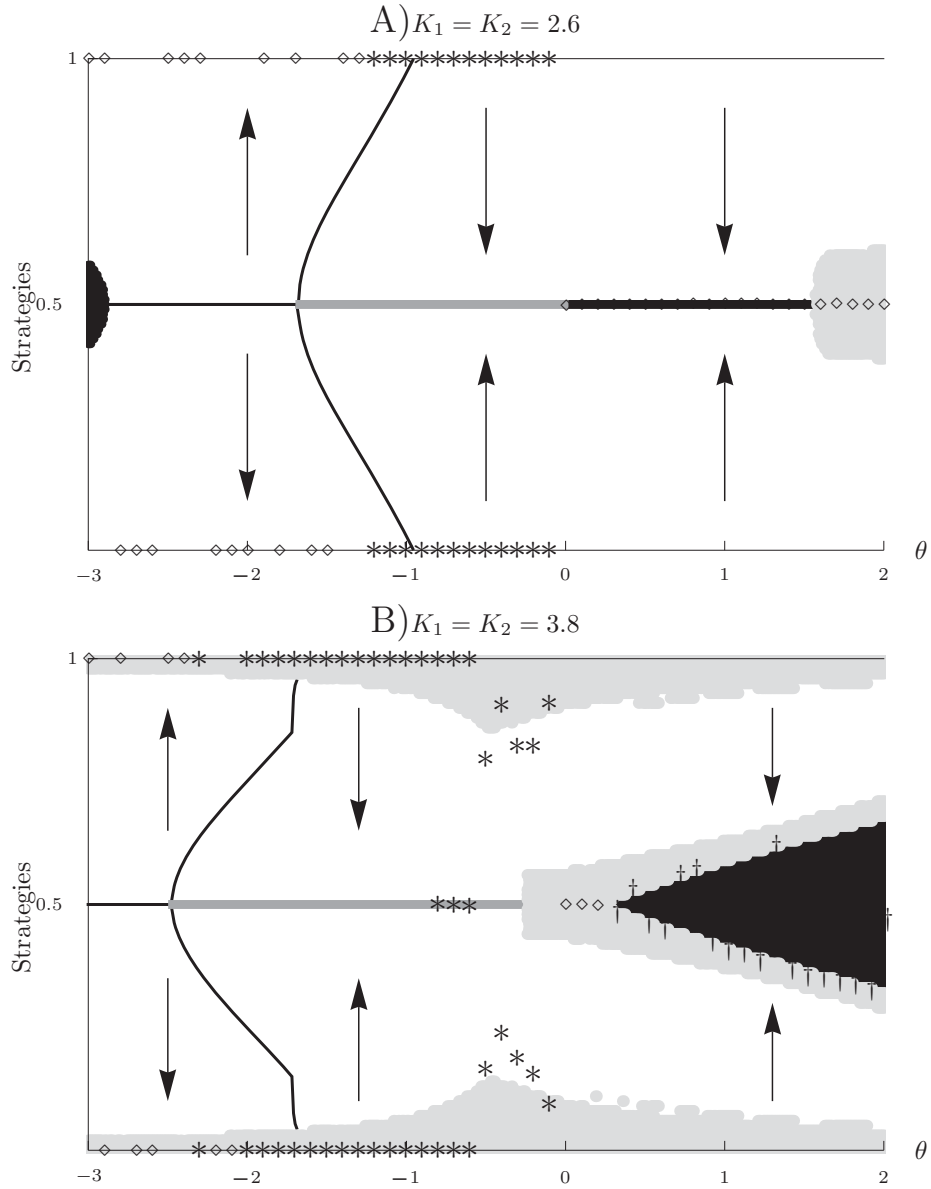


Figure 5: **Evolutionary bifurcation diagrams in the case of possibly non-equilibrium population dynamics.** Singular strategies and the endpoints of evolutionary simulations as a function of the trade-off parameter θ . Thin black curve indicates evolutionary repellers, thick grey curve branching points and thick black curve evolutionarily stable strategies. The arrows indicate the direction of evolution in a monomorphic population. In the black-colored parameter domain, the population is not viable. In the grey-colored parameter domain, the monomorphic population dynamics are (nearly) chaotic. If an evolutionary simulation ends in a monomorphic population, the end-strategy is denoted by \diamond . If it ends in a dimorphic or polymorphic population, the strategies comprising the endpoint are denoted by $*$ -signs. If evolutionary suicide occurs, the last viable strategy is denoted by \dagger -sign. The corresponding population dynamics are illustrated in Figures 3 and 4.

Panel A: Specialists have equilibrium population dynamics but high benefit of generalism enables non-equilibrium population dynamics for generalists when θ is sufficiently large.

Panel B: Specialists have chaotic population dynamics. Biased usage of two resources may stabilize population dynamics, but high benefit of generalism enables chaotic dynamics and even evolutionary suicide.

Other parameter values: $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

1 always evolves towards the coexistence of the two devoted specialists given that
2 the resource consumption function is convex. This result holds also for other
3 models with similar underpinnings, e.g., the Ricker model (8).

4 When evolutionary branching occurs, the dimorphic population "inherits" its
5 population-dynamical attractor from the preceding monomorphic population.
6 For example, if the monomorphic population was on a two-periodic population-
7 dynamical attractor, the dimorphic population is, immediately after branching,
8 on an in-phase two-periodic orbit (See Geritz et al. (2002) for more information
9 on attractor inheritance. Corresponding phenomenon has also been observed by
10 Hoyle et al. (2011)). Thus, after evolutionary branching in a symmetric envi-
11 ronment, the dimorphic population is always initially on a symmetric attractor.
12 Therefore, the dimorphic population evolves towards the coexistence of the two
13 devoted specialists, as long as the population-dynamical attractors remain sym-
14 metric. However, the symmetry of the population-dynamical attractors may be
15 lost for several reasons:

- 16 • The symmetric population-dynamical orbit (equilibrium, cycle or chaotic)
17 may become population-dynamically unstable. In this case, population
18 switches to a new population-dynamical attractor with new, possibly dif-
19 ferent, evolutionary dynamics.
- 20 • Even though the symmetric population-dynamical orbit would remain
21 population-dynamically stable, it can be chaotic. In such a case, stochastic
22 mutations (although they are small) will eventually take the population
23 dynamics away from the domain of attraction of the symmetric orbit, and
24 again the population switches to another population-dynamical attractor.
- 25 • In the symmetric case $s^{(1)} = 1 - s^{(2)}$ the evolutionary forces acting on
26 these strategies are also symmetric, which means that average evolution-
27 ary trajectories would be along $s^{(1)} = 1 - s^{(2)}$ to full specialism. Due
28 to mutational stochasticity, the dimorphic population may evolve away
29 from this trajectory. Furthermore, deviations from this trajectory may be
30 enhanced by different evolutionary forces.

31 We have not found any means for algebraic analysis of the evolutionary dynamics
32 in the case of asymmetric chaotic population-dynamical attractors. Therefore,
33 we have to rely on evolutionary simulations. In symmetric environments, we
34 have found three qualitatively different evolutionary scenarios for the dimorphic
35 population:

- 36 • The population evolves to the coexistence of the two devoted specialists
37 similarly to the case with equilibrium dynamics (Figure 1B).
- 38 • The population remains dimorphic, but does not evolve to devoted spe-
39 cialism. Results of such evolutionary simulations are illustrated in Figures
40 6 and 7.
- 41 • Another evolutionary branching occurs and the population becomes tri-
42 morphic. One result of such an evolutionary simulation is illustrated in
43 Figure 8.

1 In order to illuminate how the population dynamics affect the evolution-
2 ary dynamics, we need to illustrate the population-dynamical attractors during
3 the evolutionary time together with the evolutionary tree in the strategy space.
4 However, the evolutionary simulations we present here are never completely mu-
5 tation limited. Instead, the population is, in practice, always polymorphic dur-
6 ing the simulation. Therefore, in order to illustrate the population-dynamical
7 attractor of the entire population, we need to calculate how much extant strate-
8 gies use resources, which in turn allows us to calculate the availabilities of the
9 resources. If strategies $(s^{(1)}, s^{(2)}, \dots, s^{(k)})$ are present at time unit n with pop-
10 ulation sizes $(x_n^{(1)}, x_n^{(2)}, \dots, x_n^{(k)})$, then the availabilities $A_1(n)$ and $A_2(n)$ of the
11 resources R_1 and R_2 , respectively, are

$$\begin{aligned} A_1(n) &= K_1 \max\left(0, 1 - \sum_{i=1}^k \beta(s^{(i)})x_n^{(i)}\right) \\ A_2(n) &= K_2 \max\left(0, 1 - \sum_{i=1}^k \beta(1 - s^{(i)})x_n^{(i)}\right). \end{aligned} \quad (6)$$

12 When the population is on a non-equilibrium attractor, these availabilities
13 fluctuate as the consumer population sizes fluctuate. Based on these availabili-
14 ties, it is often possible to deduce the type of the population-dynamical attractor
15 of the consumer population as a whole. For example, if the population is on
16 a two-periodic in-phase orbit (symmetric attractor), the sum of the resource
17 availabilities takes two different values on the population-dynamical attractor
18 whereas their difference is close to zero. If the population is on a two-periodic
19 out-of-phase orbit (asymmetric attractor), the differences alternate between a
20 positive and a negative value on the population-dynamical attractor whereas
21 the sum remains virtually constant. More generally: the more asynchronous
22 are the resource fluctuations the larger are the absolute values of the differences
23 in the resource availabilities.

24 Figure 6 illustrates the result of an evolutionary simulation ending in a sin-
25 gular dimorphic strategy pair (not devoted specialists) under periodic popu-
26 lation dynamics. Figure 6A illustrates the strategies present during an evo-
27 lutionary simulation: for each unit of the evolutionary time, we plot a black
28 point to each strategy present at that time unit. Panels B-D illustrate the
29 resource availabilities. At the end of each loop of the evolutionary simula-
30 tion procedure (i.e. for each evolutionary time unit) we observe the strategies
31 present $(s^{(1)}, s^{(2)}, \dots, s^{(k)})$ and their population sizes $(x_0^{(1)}, x_0^{(2)}, \dots, x_0^{(k)})$. The
32 population-dynamical attractor $((x_n^{(1)}, x_n^{(2)}, \dots, x_n^{(k)}), n = 0, 1, 2, \dots)$, that cor-
33 responds to this unit of evolutionary time, can then be calculated iteratively
34 using equation (3) (for 20 steps in Figure 6). Furthermore, we can calculate
35 the corresponding resource availabilities $A_1(n)$ and $A_2(n)$ using equation (6)
36 and calculate their sum $A_1(n) + A_2(n)$ and difference $A_1(n) - A_2(n)$ for each
37 population-dynamical step. For each evolutionary time unit in Figure 6B, we
38 plot a black point for each different sum of the resource availabilities observed
39 on the population-dynamical attractor at the end of the corresponding loop of
40 the evolutionary simulation. In Figure 6C, we plot the difference of the resource
41 availabilities in a similar way, and in Figure 6D, we plot the availability A_1 of

1 resource 1.

2 In Figure 6, evolutionary branching takes place while the population is on a
3 two-periodic attractor. As a consequence, after branching the dimorphic popu-
4 lation is on an in-phase two-periodic orbit, i.e. it is on a symmetric attractor.
5 However, as the two branches specialize further, this population-dynamical at-
6 tractor becomes unstable, and the population switches to a new, four-periodic
7 out-of-phase orbit (which is asymmetric). This creates asynchrony to the avail-
8 abilities of the resources, which in turn, benefits generalism and stops the evolu-
9 tion towards specialism. Finally, evolution leads to a dimorphic singular strategy
10 pair ($s^{(1)} \approx 0.16488$, $s^{(2)} \approx 0.83512$)

11 Also Figure 7 illustrates the result of an evolutionary simulation, where evo-
12 lution does not lead to the combination of the two devoted specialists. Contrary
13 to the simulation illustrated in Figure 6, the population dynamics in Figure
14 7 are chaotic, which ensures that the symmetry of the attractors in the di-
15 morphic population is lost almost immediately. However, the two branches
16 continue to specialize further until $0.13 \lesssim s^{(1)} \lesssim 0.23$ in one branch and
17 $0.77 \lesssim s^{(2)} \lesssim 0.87$ in the other. Once the strategies of the evolving population
18 have reached this dimorphic intermediate strategy region, they remain there.
19 However, the population does not settle to any evolutionarily singular strategy
20 combination. When the population dynamics are chaotic, several (even infinitely
21 many) different population-dynamical attractors may exist simultaneously, and
22 furthermore, even small random mutations may induce population-dynamical
23 attractor switchings. When the population-dynamical attractor changes, it is
24 possible that also the evolutionary forces acting on the population change. This
25 phenomena is exemplified also in Figure 6 where attractor switches from an
26 in-phase orbit to an out-of-phase orbit halts the dimorphic evolution towards
27 devoted specialism. Similar examples have also been observed for other traits
28 (Parvinen, 1999; Dercole et al., 2002; White et al., 2006; Hoyle et al., 2011).
29 In Figure 7, population-dynamical attractor switching sometimes affects the
30 evolutionary dynamics such that the dimorphic population evolves to a new
31 strategy combination within the same dimorphic intermediate strategy region.
32 Chaotic population dynamics prevent us from analyzing these switchings in de-
33 tail. Figures 7B and 7C suggest that attractor switching occur rather frequently.
34 However, from Figure 7A one can observe that only some of the seem to have
35 evolutionary effects. This is natural, because an attractor switching may be
36 evolutionarily ineffective, or it may be succeeded by another attractor switching
37 that balances its effects.

38 In Figure 5B, we observe evolutionary dynamics described above (Figure
39 7) within the parameter interval $-0.585 \lesssim \theta \lesssim 0$. The evolutionary simu-
40 lations lead to dimorphic populations where the strategies of the two branches
41 do not evolve to the devoted specialism. They do not evolve to any singular
42 strategy combination either. Instead, they remain in some intermediate strategy
43 region (which naturally depends on the trade-off parameter θ) and undergo infre-
44 quent evolutionary transitions within this strategy region caused by population-
45 dynamical attractor switchings. Therefore in Figure 5B, the endpoints of evo-
46 lutionary simulations do not form any clear pattern for $-0.585 \lesssim \theta \lesssim 0$.

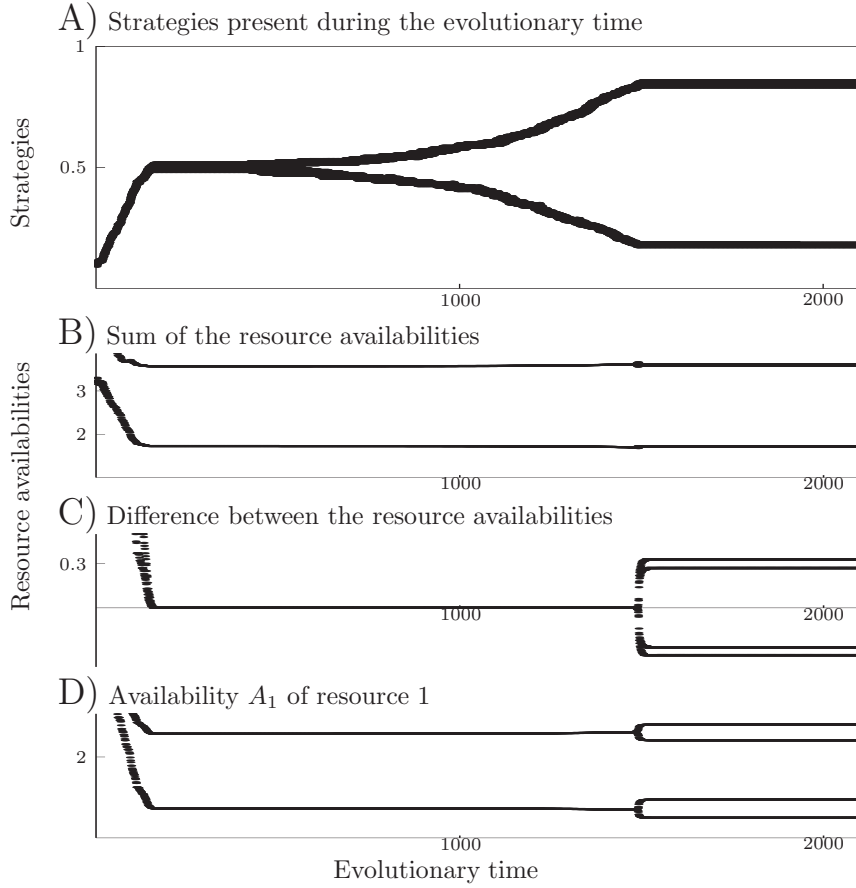


Figure 6: **The result of an evolutionary simulation leading to a dimorphic singular strategy pair under periodic population dynamics.**

Panel A: Strategies present in the population as a function of the evolutionary time. One unit of evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix. Thus, it is only applicable for comparison between different simulations using the same procedure.

Panels B, C, and D: Resource availabilities A_1 and A_2 as defined in equation (6) as a function of the evolutionary time. For each evolutionary time unit, Panel B illustrates the sum of the resources availabilities during each step on the population-dynamical attractor. Panel C illustrates the differences of the resource availabilities and panel D the availability of resource 1.

Parameter values: $K_1 = K_2 = 3.5$, $\theta = -0.1$, $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

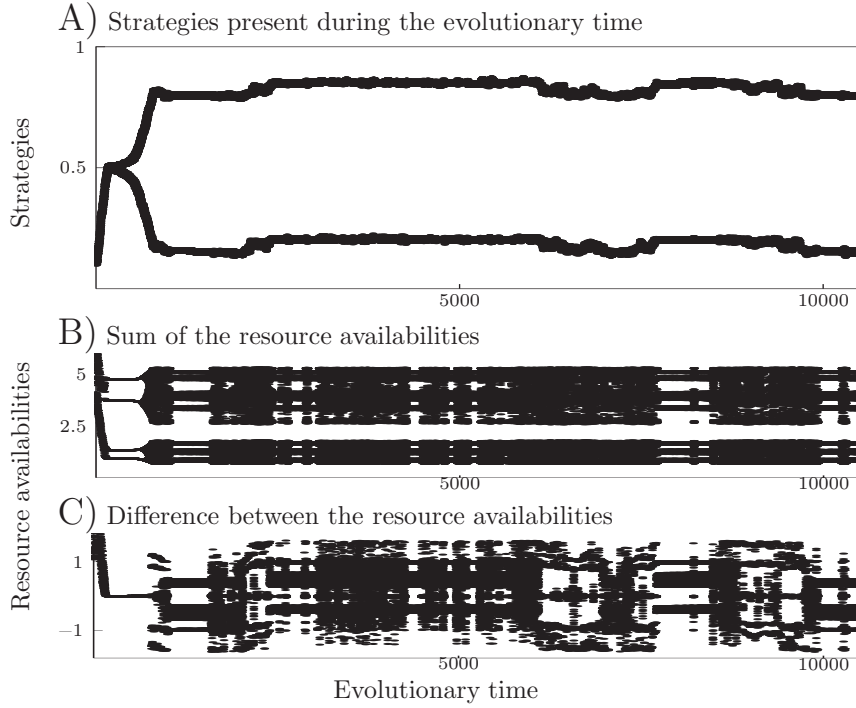


Figure 7: **The result of an evolutionary simulation where a singular strategy combination is never reached because the population-dynamical attractor switchings induced by chaotic population dynamics affect evolutionary dynamics.**

Panel A: Strategies present in the population as a function of the evolutionary time. One unit of evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix. Thus, it is only applicable for comparison between different simulations using the same procedure.

Panels B and C: Resource availabilities A_1 and A_2 as defined in equation (6) as a function of the evolutionary time. For each evolutionary time unit, Panel B illustrates the sum of the resources availabilities during each step on the population-dynamical attractor. Panel C illustrates the differences of the resource availabilities.

Parameter values: $K_1 = K_2 = 3.8$, $\theta = -0.3$, $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

1 In Figure 5B with $-0.86 \lesssim \theta \lesssim -0.586$, evolution leads to the trimorphic
2 coexistence of a generalist strategy and two devoted specialist strategies, as il-
3 lustrated in Figure 8. In well-mixed populations, evolution to this coexistence
4 has been shown possible when the resources fluctuate asynchronously (Abrams,
5 2006a). In our model, the resources have simple equilibrium dynamics in the
6 absence of consumers. However, the availability of the resources is determined
7 not only by the equilibrium value of the resource dynamics (resource carrying
8 capacity) but also by the population sizes and strategies of the consumers uti-
9 lizing the resources. When the population comprises two specialist branches
10 that fluctuate asynchronously, a generalist strategy may be viable due to the
11 reduced variance in the resource intake: due to the asynchronism in the fluctu-
12 ations of the resource availabilities, at least one of the two resources will usually
13 be available for the generalist whereas the specialists suffer frequently from low
14 resource availability. Therefore, the higher the absolute value of the difference
15 between the resource availabilities, the more likely the generalist strategy can
16 coexists with the specialists.

17 Based on Figure 8, it is possible to deduce the population-dynamical route
18 to the coexistence of a generalist and two specialists. The monomorphic pop-
19 ulation first evolves to generalism, where evolutionary branching occurs under
20 periodic population dynamics. After branching, the population-dynamical at-
21 tractors of the two branches are first symmetric (negligible difference between
22 the resource availabilities) due to attractor inheritance (Geritz et al., 2002). As
23 the branches specialize further, their population dynamics undergo a series of
24 period-doubling bifurcations and finally their population dynamics looks rather
25 chaotic. Meanwhile, the symmetry of the attractors is lost. However, the di-
26 morphic population dynamics are not completely chaotic, and after a while,
27 the population settles to an out-of-phase two-periodic orbit (the sum of the
28 resource availabilities remains constant whereas the difference alternates be-
29 tween two values). On the out-of-phase orbit, the generalists can coexist with
30 the specialists. The dimorphic population evolves to a singular strategy pair
31 ($s^{(1)} = 0$, $s^{(2)} \approx 0.919$), which is an evolutionary branching point for strategy
32 $s^{(2)} \approx 0.919$. Thus, second evolutionary branching starts slowly taking place.
33 The out-of-phase orbit maintains its population-dynamical stability during the
34 second branching and, finally, the population comprises the unbiased generalist
35 strategy together with two devoted specialist strategies. Although we illustrate
36 this phenomenon only for symmetric environments, it is present also in asym-
37 metric environments. The generalist in this trimorphic coexistence, however, is
38 the unbiased generalist only in symmetric environments.

39 *3.5. Evolution of specialization under non-equilibrium population dynamics and* 40 *asymmetric environments*

41 Figure 9 illustrates the case where the environment is asymmetric and chaotic
42 population dynamics are possible. In Figure 9A, chaotic population dynamics
43 are exclusively due to the high carrying capacity of resource 1, while the carrying
44 capacity of resource 2 is barely high enough to ensure the viability of the corre-
45 sponding devoted specialist. In Figure 9B, the carrying capacity of resource 2 is

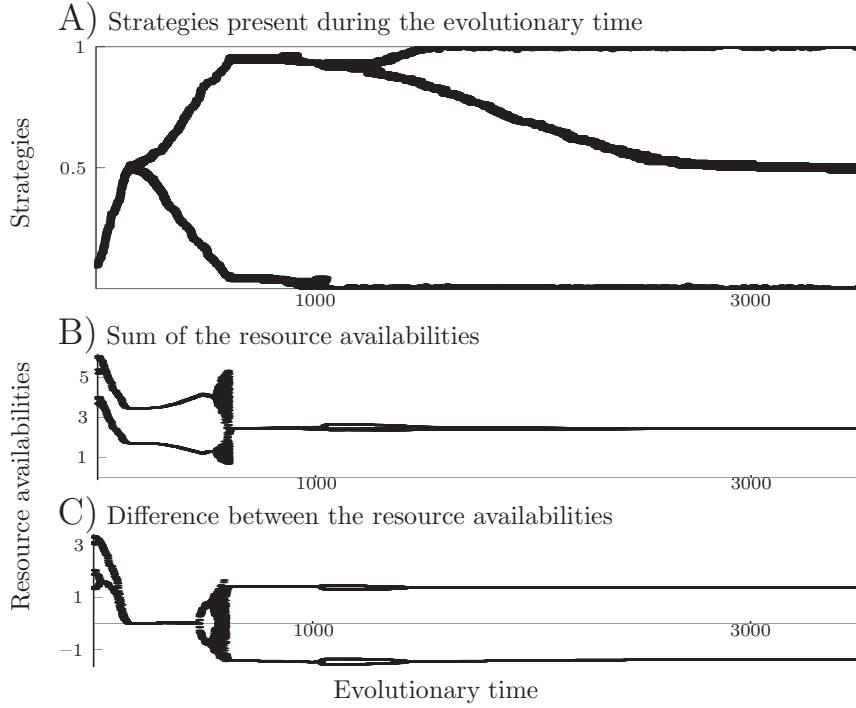


Figure 8: **The result of an evolutionary simulation leading to the coexistence of generalist and specialists.**

Panel A: Strategies present in the population as a function of the evolutionary time. One unit of evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix. Thus, it is only applicable for comparison between different simulations using the same procedure. Initial population is monomorphic practicing strategy $s = 0.1$. Simulation ended in a trimorphic population practicing strategies $s_1 = 0$, $s_2 = 0.5$, and $s_3 = 1$.

Panels B and C: Resource availabilities A_1 and A_2 as defined in equation (6) as a function of the evolutionary time. For each evolutionary time unit, Panel B illustrates the sum of the resources availabilities during each step on the population-dynamical attractor. Panel C illustrates the differences of the resource availabilities.

Parameter values: $K_1 = K_2 = 3.8$, $\theta = -0.72$, $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

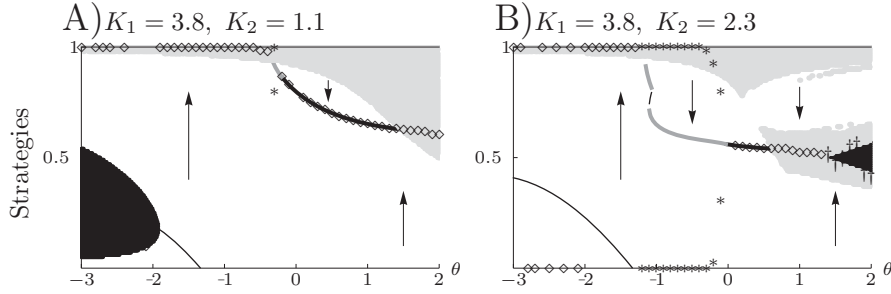


Figure 9: **Evolutionary bifurcation diagrams in the case of possibly chaotic population dynamics and asymmetric environments.** Singular strategies and endpoints of evolutionary simulations as a function of the trade-off parameter θ . Thin black curve indicates evolutionary repellers, thick grey curve branching points and thick black curve evolutionarily stable strategies. The arrows indicate the direction of evolution in a monomorphic population. In the black-colored parameter domain, the population is not viable. In the grey-colored parameter domain, the monomorphic population dynamics are (nearly) chaotic. If an evolutionary simulation ends in a monomorphic population, the end-strategy is denoted by \circ . If it ends in a dimorphic or polymorphic population, the strategies comprising the endpoint are denoted by $*$ -signs. If evolutionary suicide occurs, the last viable strategy is denoted by \dagger -sign.

Other parameter values: $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

1 higher. This stabilizes the population dynamics when consumers are partially
 2 specialized on resource 1 ($0.65 \lesssim s \lesssim 0.85$). On the other hand, in the cases with
 3 high benefit of generalism ($\theta \gg 0$), the sum of the resource carrying capacities
 4 is high enough to enable chaotic dynamics and even evolutionary suicide.

5 Figure 10 illustrates the case with $K_1 > 4$. This means that specialists
 6 with strategy sufficiently close to 1 will exhaust resource 1. When resource 1
 7 is exhausted, devoted specialists with strategy $s = 1$ will vanish. If devoted
 8 specialists can invade the population and outcompete all the other strategies,
 9 evolutionary suicide may occur. However, there are several factors that may
 10 prevent evolutionary suicide in this setting. Most of all, when resource 1 is
 11 exhausted and devoted specialist wiped out, all the other strategies ($s < 1$) are,
 12 however, able to survive due to their ability to use resource 2. The population
 13 sizes of almost devoted resource 1 specialists will, naturally, drop to very low val-
 14 ues. However, since resource 1 recovers the next time unit after being exhausted,
 15 all the strategies that survived will start to increase in population size again.
 16 Furthermore, if $K_1 \gg 4$, resource 1 is frequently exhausted already by special-
 17 ists using strategy $s < 1$. The more specialized an individual is (on resource 1)
 18 the more vulnerable the individual is to these occasions. This, in turn, may halt
 19 evolution such that the devoted specialism never enters the population. In other
 20 words, there exists an almost devoted specialist singular strategy in the regime
 21 of the chaotic population dynamics. (compare with Hoyle et al. (2011)). Even
 22 when devoted specialist are able to invade the population, it is not guaranteed
 23 that they can outcompete the other strategies ($s < 1$) before being wiped out by
 24 the next resource depletion. Even in the cases where evolutionary suicide might

1 happen, it depends on the details of the simulation procedure whether evolu-
2 tionary suicide is observed or not: In "the standard simulation procedure" used
3 generally in the studies utilizing the adaptive dynamics approach (Kisdi, 1999;
4 White and Bowers, 2005; White et al., 2006; Nurmi and Parvinen, 2008, 2011),
5 the simulation step, where "extinct" strategies are removed from the popula-
6 tion, is usually immediately followed by a step where a new mutant (resembling
7 one of the extant strategies) is added to the population. This means that it is
8 never possible for the devoted specialist strategy to be the only strategy present
9 in the population when the population dynamics are iterated. If resource 1 is
10 exhausted, the devoted specialists vanish and the population size of the newly
11 added mutant becomes extremely small. However, this extremely rare mutant
12 now constitutes the whole population and thus it won't be considered extinct in
13 the "standart simulation procedure". In order to observe evolutionary suicide, it
14 is necessary to add to the simulation procedure some additional iteration of the
15 population dynamics (see the Appendix for details). Note that for evolution-
16 ary suicide to occur via generalist strategies, the situation is different (Figures
17 5B, 9B). There evolution directs towards generalism until both resources are
18 exhausted simultaneously and all consumers are wiped out which happens for
19 any reasonable simulation procedure.

20 When the evolution of a monomorphic population directs towards an evolu-
21 tionary branching point, even cyclic evolution is possible. After branching, the
22 two morphs evolve towards devoted specialism. When the branch specializing
23 on resource 1 reaches the strategy $s = 1$, it is wiped out due to the depletion
24 of resource 1. The other branch remains intact, but since the population has
25 become monomorphic, it starts to evolve towards generalism and a new branch-
26 ing results (compare with Kisdi et al. (2001); Dercole (2003)). This process is
27 illustrated in Figure 10B. Note that cyclic evolution does not have an endpoint.
28 Therefore in Figure 10A, we have chosen such a procedure for evolutionary sim-
29 ulations that evolutionary suicide is not possible. In Figure 10B, the simulation
30 procedure is chosen such that evolutionary suicide is possible.

31 Note furthermore that, the mechanisms described above may, also in the evo-
32 lutionary time-scale, enable the viability of populations that use two resources,
33 even in environments where both devoted specialists strategies are unviable due
34 to resource depletions caused by overly efficient resource usage.

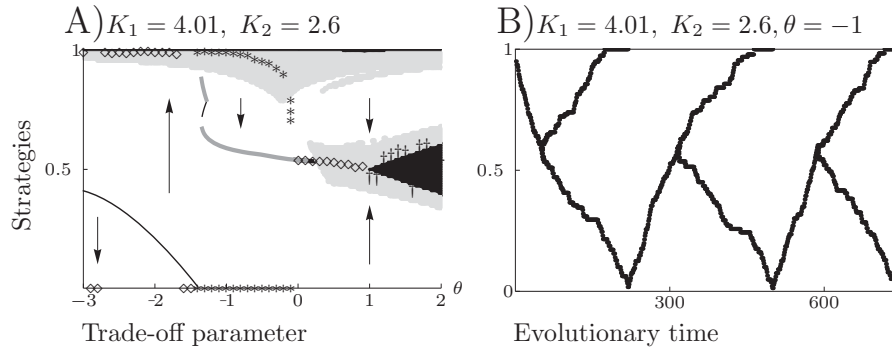


Figure 10: **Evolutionary bifurcation diagram in the case when devoted resource 1 specialist is not viable due to resource depletion.**

Panel A: Singular strategies and endpoints of evolutionary simulations as a function of the trade-off parameter θ . The simulation procedure does not enable evolutionary suicide via specialism. Thin black curve indicates evolutionary repellors, thick grey curve branching points and thick black curve evolutionarily stable strategies. The arrows indicate the direction of evolution in a monomorphic population. In the black-colored parameter domain, the population is not viable. In the grey-colored parameter domain, the monomorphic population dynamics are (nearly) chaotic. If an evolutionary simulation ends in a monomorphic population, the end-strategy is denoted by \diamond . If it ends in a dimorphic or polymorphic population, the strategies comprising the endpoint are denoted by $*$ -signs. If evolutionary suicide occurs, the last viable strategy is denoted by \dagger -sign.

Panel B: Strategies present in the population as a function of the evolutionary time when the simulation procedure enables evolutionary suicide via specialism. One unit of the evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix. Thus, it is only applicable for comparison between different simulations using the same procedure) Other parameter values: $\alpha_1 = \alpha_2 = 1$, $\lambda_1 = \lambda_2 = 1$.

1 **4. Evolutionary dynamics in other mechanistically underpinned pop-**
 2 **ulation models**

3 Following Geritz and Kisdi (2004), also other resource dynamics than the
 4 logistic differential equation (1) can be used to obtain discrete-time population
 5 models for the consumer. If the resources, in the absence of consumers, grow
 6 according to the Gompertz equation

$$\dot{R}_i = \alpha_i (\text{Ln}(K_i) - \text{Ln}(R_i)) R_i, \quad (7)$$

7 one obtains the famous Ricker (1954) model that, in the case of two resources
 8 (with $\alpha_1 = \alpha_2 = 1$) and k consumer strategies, has the form

$$\begin{aligned} x_{n+1}^{(j)} = & \lambda_1 K_1 \beta(s^{(j)}) x_n^{(j)} \exp \left(- \sum_{i=1}^k \beta(s^{(i)}) x_n^{(i)} \right) \\ & + \lambda_2 K_2 \beta(1 - s^{(j)}) x_n^{(j)} \exp \left(- \sum_{i=1}^k \beta(1 - s^{(i)}) x_n^{(i)} \right), \end{aligned} \quad (8)$$

9 where the notations correspond to the ones in equation (3). Analogously, one
 10 can derive, for example, different variants of Hassell (1975) or Beverton and Holt
 11 (1957) models. Beverton-Holt model that shows only equilibrium dynamics has
 12 been extensively analyzed by Nurmi and Parvinen (2008). We analyzed the
 13 evolutionary dynamics also in Hassell model (not illustrated). According to
 14 our observations, they are qualitatively similar to those of the Ricker model
 15 (illustrated below). Note, that our parametrization of the Gompertz equation
 16 (7) is slightly different from the parametrization used by Geritz and Kisdi (2004).
 17 In the parametrization used by Geritz and Kisdi (2004), it is not straightforward
 18 to interpret the parameters K_i as resource carrying capacities. This would
 19 unnecessarily complicate the evolutionary analysis and hence we have chosen to
 20 use parametrization (7) resulting in model (8).

21 Under equilibrium population dynamics, the evolutionary dynamics in the
 22 Ricker model are qualitatively similar to those of the logistic model (illustrated
 23 in Figure 2). Figure 11 illustrates the evolutionary dynamics in the Ricker
 24 model in the case of possibly periodic or chaotic population dynamics. The
 25 evolutionary dynamics are mainly qualitatively similar to those of the logistic
 26 model (illustrated in Figure 5). There are, however, some differences. The most
 27 obvious one is that the complete exhaustion of the resources is not possible in the
 28 Ricker model (compare equations (3) and (8)). Thus, deterministic evolutionary
 29 suicide is not possible. However, if demographic stochasticity was involved, evo-
 30 lutionary suicide would be possible. Another rather apparent difference between
 31 Figures 5B and 11 is that the bifurcation structure in the parameter domain
 32 where the generalist strategy turns from a repeller into a branching point, is
 33 different, with Ricker model showing even three alternative branching points for
 34 the same trade-off parameter value (e.g. $\theta = -4.5$). However, similar bifurca-
 35 tion structure can be found in the logistic model, as well, with slightly different
 36 parameter values (e.g. $\lambda = 1.1$ and other parameters as in Figure 5B).

1 Similarly to the logistic model, also in the Ricker model, there exists a pa-
2 rameter domain ($-2.7 \lesssim \theta \lesssim 0$) where evolutionary branching first takes place
3 and then the dimorphic population evolves neither to any singular strategy
4 combination nor to devoted specialism. Instead, the strategies of the dimorphic
5 population fluctuate in an intermediate strategy region, because chaotic popula-
6 tion dynamics result in frequent population-dynamical attractor switchings that
7 affect the evolutionary dynamics. When $-3.6 \lesssim \theta \lesssim -2.9$, another evolution-
8 ary branching takes place and evolution leads to the trimorphic coexistence of
9 generalists and specialists. These phenomena are qualitatively similar to those
10 observed in the logistic model even though they occur in different parameter
11 domains. However, the transition between these two phenomena is different. In
12 the logistic model, the transition occurs instantly without any intermediate phe-
13 nomena, whereas in the Ricker model, there exists an intermediate parameter
14 domain ($\theta \approx -2.8$). In this intermediate parameter domain, second evolutionary
15 branching takes place, but the appearance of the generalist strategy, however,
16 affects the population dynamics such that the generalist dies out. When the
17 population becomes dimorphic again, it evolves back to the singular dimorphic
18 strategy pair and a new evolutionary branching takes place. This results in
19 cyclic evolution as illustrated in Figure 12.

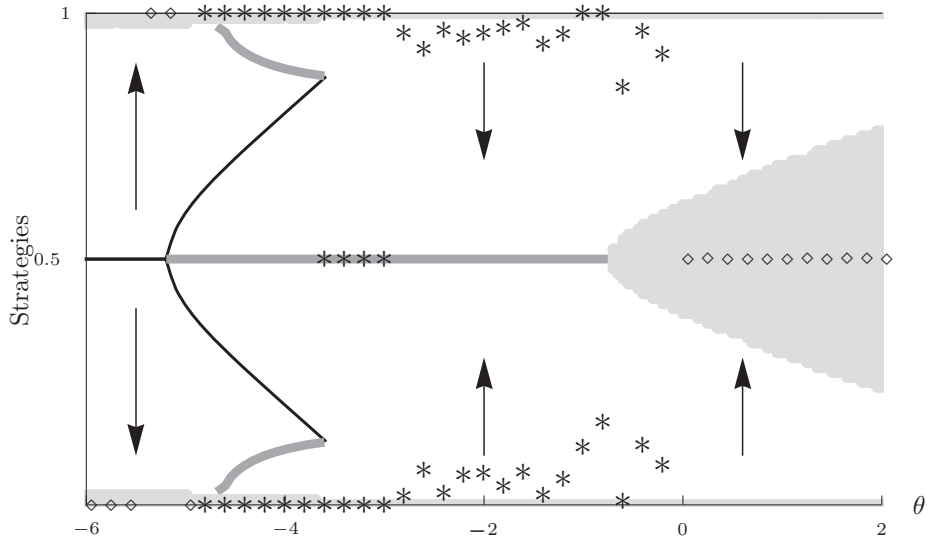


Figure 11: **Evolutionary bifurcation diagram of the Ricker model with possibly chaotic population dynamics.** Singular strategies and endpoints of evolutionary simulations as a function of the trade-off parameter θ . Thin black curve indicates evolutionary repellers, thick grey curve branching points and thick black curve evolutionarily singular strategies. The arrows indicate the direction of evolution in a monomorphic population. In the grey-colored parameter domain, the monomorphic population dynamics are (nearly) chaotic. If an evolutionary simulation ends in a monomorphic population, the end-strategy is denoted by \diamond , else the strategies comprising the endpoint are denoted by $*$ -signs. Other parameter values: $K_1 = 18$, $K_2 = 18$, $\lambda_1 = \lambda_2 = 1$, $\alpha_1 = \alpha_2 = 1$.

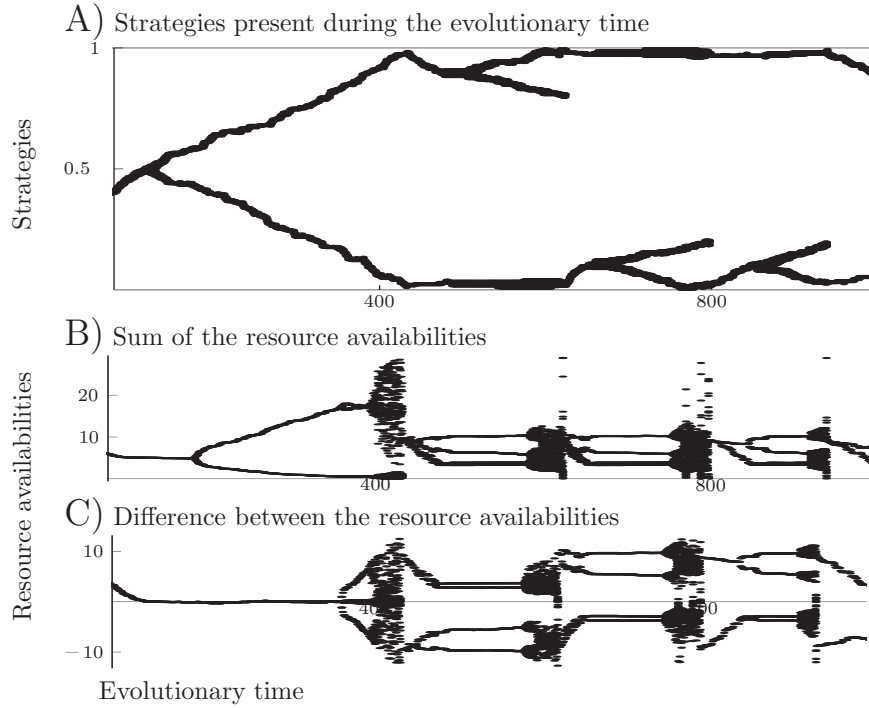


Figure 12: **The result of a cyclic evolutionary simulation in Ricker model.**
Panel A: Strategies present in the population as a function of the evolutionary time. One unit of the evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix. Thus, it is only applicable for comparison between different simulations using the same procedure. Initial population is monomorphic practicing strategy $s = 0.4$.
Panels B and C: Resource availabilities A_1 and A_2 (for the logistic model corresponding availabilities are defined in equation (6)). For each evolutionary time unit, panel B illustrates the sum of the resources availabilities during each step on the population-dynamical attractor. Panel C illustrates the differences of the resource availabilities on the population-dynamical attractor for each evolutionary time unit.
 Parameter values as in Figure 11 with $\theta = -2.8$.

1 5. Discussion

2 In this paper, we have examined the evolution of resource specialization
3 under non-equilibrium population dynamics. We use a model that is mechanis-
4 tically underpinned on individual level ingredients, which makes it suitable for
5 evolutionary analysis (Rueffler et al., 2006a). Furthermore, for a mechanisti-
6 cally underpinned model, it is easy to interpret parameters biologically, as well
7 as consider, whether the model assumptions are satisfied in different biological
8 scenarios. On the other hand, our model involves several simplifications that
9 may affect model predictions:

- 10 • In our evolutionary analysis, we focus exclusively on the resource con-
11 sumption rates β and assume that consumers use resources according the
12 law of mass-action with these rates. This allows us to focus on the evo-
13 lutionary effects of non-equilibrium population dynamics. However, the
14 model would be biologically more realistic if non-linear functional response
15 was assumed, or if the behavioral elements affecting the evolution of spe-
16 cialization were taken into account (Rueffler et al., 2007; Abrams, 2010).
- 17 • Our previous results concerning the evolution of specialization under equi-
18 librium metapopulation dynamics (Nurmi and Parvinen, 2008, 2011) sug-
19 gest a strong interplay between dispersal and specialization. Thus, one
20 should study also the consequences of non-equilibrium population dynam-
21 ics for the joint evolution of dispersal and specialization in metapopulation
22 models.
- 23 • We assume rather simple resource dynamics. However, the evolutionary
24 changes in the consumer strategies are likely to cause evolutionary changes
25 also in the resource populations resulting in co-evolution of resources and
26 consumers (see e.g. Abrams (2000) and references therein).
- 27 • Our evolutionary analysis is based on clonal reproduction and the rather
28 simple genetic architecture assumed by the adaptive dynamics approach.
29 There are several studies indicating that the phenotypic models of evo-
30 lution are capable to predict the course of evolution also in monomor-
31 phic sexually reproducing populations (Weissing, 1996; Kisdi and Geritz,
32 1999a,b; Geritz and Kisdi, 2000). However, when the monomorphic popu-
33 lation encounters disruptive selection, sexual reproduction usually hinders
34 branching in the absence of assortative mating or some other source of
35 reproductive isolation (Dieckmann and Doebeli, 1999; Geritz and Kisdi,
36 2000; Doebeli et al., 2007).
- 37 • We have studied a large family of resource consumption functions with
38 different curvature. However, the function is always either everywhere
39 concave or everywhere convex. Trade-offs play an essential part in the
40 evolution of specialization. Therefore, the usage of trade-off independent
41 methods (de Mazancourt and Dieckmann, 2004; Bowers et al., 2005; Geritz

1 et al., 2007) could reveal useful additional information concerning the
2 evolutionary dynamics.

3 Under equilibrium population dynamics in a well-mixed population, the evo-
4 lution of specialization, in the case of two alternative resources, always leads to
5 a monomorphic generalist population when the resource consumption function
6 is concave (trade-off weak, $\theta > 0$) and to a population comprising one or two
7 specialist strategies when the resource consumption function is convex (trade-off
8 strong, $\theta < 0$) (Levins, 1962, 1963; Schreiber and Tobiason, 2003; Ma and Levin,
9 2006; Nurmi and Parvinen, 2008; Zu et al., 2011a,b). Our results show that
10 under non-equilibrium population dynamics this result no longer holds (even
11 evolution to the trimorphic coexistence is possible). White et al. (2006) and
12 Hoyle et al. (2011) have reached a similar conclusion when analyzing the case
13 of trade-off between reproduction and survival. In fact, the results by Nurmi
14 and Parvinen (2008) indicate, that also spatial (metapopulation) structure may
15 break the relation between concavity of the resource consumption function and
16 evolution to a monomorphic generalist population.

17 Furthermore, White et al. (2006) and Hoyle et al. (2011) showed that ad-
18 ditional singular strategies may appear due to the non-equilibrium dynamics.
19 Similar phenomena is present in our model: evolution to the dimorphic sin-
20 gular strategy pair (Figure 6), as well as evolution to the trimorphic coexis-
21 tence (Figure 8) are evolutionary scenarios that are not possible under equilib-
22 rium population dynamics in a well-mixed population. Furthermore under non-
23 equilibrium population dynamics, cyclic evolution is possible (Figures 10 and
24 12), and evolution may even lead to a dimorphic population with evolutionary
25 fluctuations, where chaotic population dynamics enable population-dynamical
26 attractor switchings that affect the evolutionary forces such that the dimorphic
27 population evolves to another nearby intermediate strategy combination (Figure
28 7).

29 Hoyle et al. (2011) committed also thorough algebraic analysis of the tran-
30 sition from equilibrium to periodic population dynamics. Unfortunately, both
31 of the phenomena we observe involve dimorphic populations and chaotic pop-
32 ulation dynamics. This prevents the in-depth analysis in the spirit of Hoyle
33 et al. (2011). Especially, the interplay between evolutionary and ecological dy-
34 namics resulting in evolutionary fluctuations as depicted in Figure 7 would be
35 interesting, since it seems that rare randomly occurring mutations may disturb
36 the population dynamics and change the population-dynamical attractors such
37 that also the evolutionary dynamics are affected, and the population evolves to
38 another nearby strategy pair, but never to devoted specialism or to any singular
39 strategy combination. Within the scope of this article, we can only present sim-
40 ulations indicating that such evolutionary scenarios exist; to fully understand
41 them is an interesting task for further research.

42 Evolution starting from a monomorphic population may, under non-equilibrium
43 population dynamics, also lead to the trimorphic coexistence of a generalist and
44 two specialists. In such coexistence, each of the specialists uses the correspond-
45 ing resource more efficiently than the competing strategies. The viability of

1 the generalist strategy, on the other hand, is based on the asynchronous non-
2 equilibrium population dynamics of the specialists. The population sizes of the
3 specialist strategies fluctuate, and hence they are repeatedly rather low, which
4 means that the corresponding resource is abundantly available allowing the gen-
5 eralist to increase in population size. This phenomenon was originally observed
6 by Abrams (2006a) in a continuous-time model involving Holling type II func-
7 tional response in the case where the dynamics of the two resources are different,
8 which creates sufficient asynchrony to the resource dynamics. However, non-
9 linear functional response is known to have an essential part in allowing species
10 coexistence, e.g., several species can coexist even on a single resource under
11 non-equilibrium dynamics (Armstrong and McGehee, 1980; Kisdi and Liu, 2006;
12 Geritz et al., 2007; Tachikawa, 2008). In our model, consumers use resources
13 according to the law of mass-action with a linear functional response. Further-
14 more in our model, evolution to the trimorphic coexistence is possible also in the
15 case of similar resources. Thus, our results indicate that non-equilibrium pop-
16 ulation dynamics really is the main factor enabling evolution to the trimorphic
17 coexistence. As can be observed from Figure 5, evolution ends in the trimorphic
18 coexistence in a rather small parameter domain. It is, however a robust phe-
19 nomena that can be observed without fine-tuning of the parameters since it is a
20 fundamental part of the evolutionary dynamics on chaotic population-dynamical
21 attractors. It is always present in the parameter domain with transition from
22 the evolution dynamics leading to generalism into evolution to the combination
23 of the two devoted specialists.

24 It is also noteworthy that we observed evolution to the trimorphic coexis-
25 tence only for such ecological scenarios where monomorphic devoted specialist
26 populations have chaotic population dynamics. In these scenarios, the evolu-
27 tionary path to the out-of-phase two-periodic population-dynamical orbit that
28 allows the coexistence, always involves a series of period-doubling bifurcations
29 and seemingly chaotic population dynamics. However, we are not aware of any
30 theoretical reasons why chaotic population dynamics should necessarily be in-
31 volved with the evolutionary path to the trimorphic coexistence, because sym-
32 metric attractors may become population-dynamically unstable even without
33 chaos, and furthermore, the population-dynamical out-of-phase orbit is often
34 stable in scenarios where the in-phase orbit is unstable.

35 Under equilibrium population dynamics, evolution leading to a singular di-
36 morphic strategy pair comprising two partially specialized strategies is possible
37 in well-mixed populations, but requires rather complicated forms of trade-off
38 (Zu et al., 2011a,b). Under non-equilibrium dynamics, evolution to a singular
39 dimorphic strategy pair is possible even when the resource consumption func-
40 tion is everywhere convex (see e.g. Figure 5A). In metapopulation models with
41 equilibrium local dynamics, evolution to a singular strategy pair has been ob-
42 served, but evolution to the trimorphic coexistence requires joint evolution with
43 dispersal (Nurmi and Parvinen, 2008, 2011).

44 In our model with logistic resource dynamics, evolutionary suicide is possible
45 when resources are abundantly available (high resource carrying capacities K_1
46 and/or K_2). Evolutionary suicide may take place via generalist strategies (e.g.

1 Figure 5B) or via a specialist strategy (Figure 10). In the former case, both
2 resources are exhausted simultaneously, and all the strategies are wiped out.
3 This extinction occurs in all reasonable evolutionary simulation procedures. In
4 the latter case, only one resource is exhausted, and only the devoted specialists
5 are wiped out whereas all the other strategies survive and start to grow in pop-
6 ulation size again, even though the population size may visit very low values. It
7 depends on the details of the simulation procedure whether a devoted special-
8 ist is able to outcompete all the other strategies before being destroyed due to
9 the depletion of the only resource it is able to utilize. Especially, evolutionary
10 suicide is not possible in the "standard" simulation procedure used generally
11 in adaptive dynamics studies (see the Appendix). When evolutionary suicide
12 may take place via a specialist strategy, even evolutionary cycles of successive
13 branching events and extinctions of one branch are possible (Figure 10). Note
14 that the possibility of evolutionary suicide originates from the special charac-
15 teristics of discrete logistic population dynamics. For example, the bifurcation
16 diagram of the Ricker (as well as Hassell) equation (see equation (8)) is to large
17 extent similar to the one of the logistic equation (see equation (2)), but there
18 the resources are never completely exhausted, and evolutionary suicide is not
19 possible in the absence of Allee-effects and demographic stochasticity (compare
20 with Parvinen (2005)).

21 A large fraction of the studies combining evolutionary dynamics with fluctu-
22 ating population dynamics have focused on co-evolution in predator-prey models
23 (see e.g. a review by Abrams (2000)). Our model corresponds to these models in
24 the case where only predator can evolve. According to Abrams (1992, 2000), the
25 evolution of predator may sometimes cause predator-prey cycles, but usually it
26 stabilizes the population dynamics. Our results contrast with this since the con-
27 sumer evolution often destabilizes population dynamics. However, in line with
28 our results, Abrams (1992, 2000) concluded that increasing prey/resource carry-
29 ing capacity increased the probability for non-equilibrium population dynamics.
30 In fact, our results relate to the paradox of enrichment (Rosenzweig, 1971), since
31 increasing resource carrying capacity destabilizes population dynamics and may
32 even cause extinction.

33 To sum up, we have systematically analyzed the evolution of specialization
34 in resource utilization under non-equilibrium population dynamics. We have
35 shown, that several evolutionary phenomena that are not possible under equi-
36 librium population dynamics, may be possible under non-equilibrium population
37 dynamics: additional singular dimorphic strategy pairs may appear, and fur-
38 thermore, a secondary evolutionary branching may occur and evolution may
39 lead to the trimorphic coexistence of two specialist strategies and a generalist
40 strategy.

41 **A. Simulation procedure**

42 The simulations we commit are not individual based simulations. Instead,
43 we iterate the population dynamics (3) with infrequent insertions of new mutant
44 strategies and removals of strategies that have diminished sufficiently in order

1 to be considered extinct. The simulation procedure differs slightly from the
2 assumptions used by the adaptive dynamics machinery since simulations are not
3 completely mutation limited as new mutants may appear before the population
4 has reached an attractor. The simulation procedure is:

- 5 1. Iterate the population dynamics according to the equation (3). Here this
6 is typically done 2000 times.
- 7 2. Remove all the strategies that can be considered extinct. Note, that under
8 chaotic population dynamics, it is difficult to determine which strategies
9 to remove since the whole population may occasionally be very small. We
10 have chosen to base the removal of a strategy on its relative proportion of
11 the entire population. When strategies go extinct due to resource depletion
12 this is not a problem because in this case the population size is exactly
13 zero. Here we typically consider a strategy extinct if its population size is
14 less than 0.0001 times the total population size.
- 15 3. In order to speed up calculations, we set a maximum number of strategies
16 present in the simulation. If the number of strategies is not below this
17 limit, go back to step 1. Here the maximum number of strategies was
18 typically 20. However, this almost never affects results.
- 19 4. Pick one strategy that will mutate. The probability to pick a certain
20 strategy is determined by the strategy's population size divided by the
21 total population size.
- 22 5. Pick the size of the mutation using uniform distribution $U[-m, m]$, where
23 m is the largest possible mutation. Here typically $m = 0.01$.
- 24 6. Check that the new strategy belongs to the strategy space and differs suf-
25 ficiently from the extant strategies. If not, go back to step 4. Several
26 occurrences of almost similar strategies in a simulation would unneces-
27 sarily slow down the simulation. We usually require minimum difference
28 0.001.
- 29 (7.) Iterate the population dynamics.
- 30 (8.) Remove the extinct strategies. Now it is possible that the population
31 becomes monomorphic comprising devoted specialists only.
- 32 (9.) Iterate the population dynamics. Now it is possible that a resource deple-
33 tion wipes out devoted specialists and the population goes extinct.
- 34 10. Continue from step 1 if the population persists.

35 One loop of this procedure corresponds to one unit of the evolutionary time
36 in the figures that illustrate results of evolutionary simulations (Figures 1, 8,
37 10 and 12). In these figures, the illustrated length of the evolutionary time
38 has been chosen such that the figures illuminate the question in focus in the
39 optimal way. The actual simulations did run much longer than the illustrated

1 evolutionary time interval in order ensure that the system has really reached its
2 evolutionary endpoint (which can never be guaranteed, however).

3 When steps 7–9 are not included in the simulation procedure, it corresponds
4 to the "standard adaptive dynamics simulation" (Kisdi, 1999; White and Bowers,
5 2005; White et al., 2006; Nurmi and Parvinen, 2008, 2011) and evolutionary
6 suicide via specialism is not possible since the population never comprises solely
7 devoted specialists. Assume that the devoted specialists can outcompete the
8 other strategies in step 1. The other strategies are removed in step 2. However,
9 immediately in steps 3–6 a new mutant enters the population. Thus, when the
10 population dynamics are iterated again in step 1, the population comprises devoted
11 specialists and a rare mutant that is also a specialist, but not a devoted
12 one. If one resource is exhausted, the devoted specialists vanish. The mutant
13 population becomes extremely small, but it survives because of its ability to use
14 the other resource. However, this extremely rare mutant now constitutes the
15 entire population and it will not be removed in step 2. Devoted specialists may
16 later again outcompete this strategy, but devoted specialists can never constitute
17 the whole population. Thus, evolutionary suicide via specialism is possible
18 only when steps 7–9 are included to the simulation procedure. In step 7 devoted
19 specialists may outcompete other strategies that are then removed in step 8,
20 leaving only devoted specialists alive. If resource depletion is encountered during
21 the iteration of the population dynamics, devoted specialists are wiped out
22 and thus the whole population goes extinct.

23 Note that in step 2, we use a relative extinction threshold, i.e., we declare a
24 strategy extinct if its population size is small compared to the size of the entire
25 population. Alternatively, we could have used an absolute extinction threshold,
26 i.e., declare a strategy extinct when its population size is small (independent of
27 the size of the entire population). The type of the extinction threshold affects
28 essentially the possibility of evolutionary suicide as well as the evolutionary
29 dynamics under chaotic population dynamics. Using an absolute extinction
30 threshold involves the implicit assumption of demographic stochasticity: once
31 a population becomes extremely small, it will be wiped out by demographic
32 stochasticity. An absolute extinction threshold, although it might be biologically
33 more realistic, is problematic when combined with chaotic population dynamics,
34 since the chaotic population-dynamical fluctuations may then drive otherwise
35 viable strains or the entire population to extinction, and thus the size of the
36 extinction threshold might affect the evolutionary dynamics. Moreover, in this
37 paper, we considered the possibility for deterministic evolutionary suicide, and
38 hence we need to exclude stochasticity. Thus, we have chosen to use a relative
39 extinction threshold. It is noteworthy that this may slightly favor increased
40 efficiency in average resource usage (generalists in Figures 5, 9B, and 11, resource
41 1 specialists in Figure 10).

1 **B. Algebraic proof: Dimorphic evolution on symmetric population-**
2 **dynamical attractors directs towards devoted specialism.**

3 Assume that the environment is symmetric with $K_1 = K_2 = K$, $\lambda_1 = \lambda_2 =$
4 λ , $\alpha_1 = \alpha_2 = \alpha$ and the population is dimorphic with strategies $s^{(1)} = s^{\text{res}}$ and
5 $s^{(2)} = 1 - s^{\text{res}}$, where $s^{\text{res}} < 0.5$. Assume further that the dimorphic population
6 is on a symmetric attractor such that $x_n^{(1)} = x_n^{(2)} = x_n^{\text{res}}$ for each time unit n .
7 Then, for a mutant with strategy s^{mut} and population size x_n^{mut} , the equation
8 (3) determining fecundity has the form $x_{n+1}^{\text{mut}} = f(s^{\text{mut}}, S^{\text{res}}, X_n^{\text{res}})x_n^{\text{mut}}$, where

$$\begin{aligned} f(s^{\text{mut}}, S^{\text{res}}, X_n^{\text{res}}) &= K \max \{0, 1 - x_n^{\text{res}} (\beta(s^{\text{res}}) + \beta(1 - s^{\text{res}})) \} \\ &\quad \cdot (\beta(s^{\text{mut}}) + \beta(1 - s^{\text{mut}})) \\ &= H(S^{\text{res}}, X_n^{\text{res}}) (\beta(s^{\text{mut}}) + \beta(1 - s^{\text{mut}})), \end{aligned}$$

9 where $S^{\text{res}} = \begin{pmatrix} s^{\text{res}} \\ 1 - s^{\text{res}} \end{pmatrix}$, $X_n^{\text{res}} = \begin{pmatrix} x_n^{\text{res}} \\ x_n^{\text{res}} \end{pmatrix}$, and $H(S^{\text{res}}, X_n^{\text{res}})$ stands for a
10 shorthand notation for all the terms that do not involve the mutant strategy
11 s^{mut} . Other mechanistically underpinned models, such as (8), result in analo-
12 gous expressions with a different function H . Therefore, the following applies
13 to other models as well. The fitness of a mutant in the environment determined
14 by this dimorphic symmetric resident population is, according to the equation
15 (4),

$$\begin{aligned} r(s^{\text{mut}}, S^{\text{res}}, X^{\text{res}}) &= \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{i=1}^t \ln(f(s^{\text{mut}}, S^{\text{res}}, X_i^{\text{res}})) \\ &= \ln(\beta(s^{\text{mut}}) + \beta(1 - s^{\text{mut}})) \\ &\quad + \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{i=1}^t \ln(H(S^{\text{res}}, X_i^{\text{res}})). \end{aligned}$$

16 Now it is already obvious that the fitness function is convex whenever the re-
17 source consumption function β is convex ($\theta < 0$). Furthermore, the fitness
18 gradient at the strategy s^{res} is

$$\left. \frac{\partial r}{\partial s^{\text{mut}}} \right|_{s^{\text{mut}}=s^{\text{res}}} = \frac{\beta'(s^{\text{res}}) - \beta'(1 - s^{\text{res}})}{(\beta(s^{\text{res}}) + \beta(1 - s^{\text{res}}))},$$

19 which is negative for a convex resource consumption function since we assumed
20 that $s^{\text{res}} < 0.5$. Thus the strategy s^{mut} can invade and outcompete strategy
21 s^{res} if and only if $s^{\text{mut}} < s^{\text{res}}$. Analogously, the fitness gradient at the strategy
22 $1 - s^{\text{res}}$ is

$$\left. \frac{\partial r}{\partial s^{\text{mut}}} \right|_{s^{\text{mut}}=(1-s^{\text{res}})} = \frac{\beta'(1 - s^{\text{res}}) - \beta'(s^{\text{res}})}{(\beta(s^{\text{res}}) + \beta(1 - s^{\text{res}}))},$$

1 which is positive for a convex resource consumption function since $1 - s^{\text{res}} > 0.5$.
2 Thus the strategy s^{mut} can invade and outcompete strategy $1 - s^{\text{res}}$ if and only
3 if $s^{\text{mut}} > 1 - s^{\text{res}}$.

4 Altogether, the two branches will evolve further away from the unbiased gen-
5 eralist strategy until devoted specialism is reached, or the symmetry of strategies
6 is lost, or the symmetry of the population-dynamical attractors is lost.

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