Evolutionary Predictions Should Be Based on Individual-Level Traits

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ABSTRACT: Recent theoretical studies have analyzed the evolution of habitat specialization using either the logistic or the Ricker equation. These studies have implemented evolutionary change directly in population-level parameters such as habitat-specific intrinsic growth rates r or carrying capacities K. This approach is a shortcut to a more detailed analysis where evolutionary change is studied in underlying morphological, physiological, or behavioral traits at the level of the individual that contribute to r or K. Here we describe two pitfalls that can occur when such a shortcut is employed. First, population-level parameters that appear as independent variables in a population dynamical model might not be independent when derived from processes at the individual level. Second, patterns of covariation between individual-level traits are usually not conserved when mapped to the level of demographic parameters. Nonlinear mappings constrain the curvature of trade-offs that can sensibly be assumed at the population level. To illustrate these results, we derive a two-habitat version of the logistic and Ricker equations from individual-level processes and compare the evolutionary dynamics of habitat-specific carrying capacities with those of underlying individual-level traits contributing to the carrying capacities. Finally, we sketch how our viewpoint affects the results of earlier studies.

Keywords: development, logistic equation, optimization, Ricker equation, specialization, trade-off.

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Long-term evolution by mutation and selection is largely driven by invasion of novel genotypes into resident populations. Invasion is a population dynamical process and therefore, when evolution is studied by means of mathematical models, has to be inferred from a population dynamical model. In the recent literature, several studies have appeared that analyze the evolution of habitat specialization by using either the Ricker equation (Wilson and Yoshimura 1994; Egas et al. 2004) or the logistic equation (Parvinen and Egas 2004; de Mazancourt and Dieckmann 2004) to describe habitat-specific population growth. In these models, habitat specialization is subject to a trade-off: a high value in the carrying capacity or the intrinsic growth rate in one habitat is bought at the expense of a low carrying capacity or growth rate in the other habitat. Evolution and coexistence are then studied by assuming variation in the degree of habitat specialization in terms of either r or K. These parameters have an interpretation only at the level of populations, while mutations causing evolutionary change occur at the level of the individual. Therefore, the models mentioned above employ a shortcut because a description of how variation at the level of the individual is linked to variation in population-level parameters is skipped. Such a shortcut is permissible only when the assumed patterns of variation at the level of the demographic parameters can be derived from variation in underlying individual-level traits, an issue that can be evaluated only with models that are based on an explicit mapping from processes at the level of individuals to population-level parameters.

Although our study is motivated by the specific problem introduced above, the issue at hand is of a much more general nature. Genetic variation occurs at the level of DNA sequences and ultimately affects the makeup of a population. The step from individual sequences to population-level characteristics can be described by a cascade of mappings. Genotypes are mapped to enzymes and their regulation. During development, these characteristics might be mapped to, for example, the morphometrical properties of a bird's beak, which determine its handling

times for different seeds, which determine energy uptake, which determines offspring production, which determines population growth rate. The general question then becomes how patterns of variation and covariation at one level are mapped to the next level.

The aim of this article is to show how an explicit mapping from individual-level traits to population-level parameters can help us to understand how evolution is likely to work by informing us about how patterns of variation and covariation at lower levels can constrain resulting patterns of variation at higher levels. In the next section, we discuss two pitfalls that can occur when an explicit description of the mapping from individual-level traits to demographic parameters is skipped. We then continue by illustrating these issues by means of two examples, and we conclude by sketching how our viewpoint affects the results of the studies mentioned above.

Population-Level Parameters Derive from Underlying Traits at the Level of the Individual

In this section, we use the logistic equation to illustrate two separate issues that emerge when patterns of variation and covariation at the level of population-level demographic parameters are derived from variation in underlying individual-level traits. The logistic equation is given by

$$\frac{1}{N}\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right), \quad (1)$$

where N denotes population density, r is the intrinsic rate of increase, and K is the carrying capacity. The logistic equation is widely used to describe density-dependent population growth of a single species with only two parameters. The fact that r and K do not have an interpretation at the level of the individual has triggered a series of derivations from first principles at the level of the individual. Such derivations assume density dependence either in the birth rate b (MacArthur 1972, p. 56; Schoener 1973; Edelstein-Keshet 1988, p. 119; see also Kooi et al. 1998) or the death rate m (Gyllenberg 2005). For derivations that do not describe the dynamics of individuals but describe the fraction of either inhabited patches in a metapopulation or infected individuals in a population of susceptible and infected individuals, see Hanski (1999, p. 56) and Diekmann and Heesterbeek (2000, p. 212). The derivations that assume a density-dependent birth rate have a limited scope because they predict a negative birth rate when the population size passes some threshold, and we do not consider these derivations any further. All derivations that assume a density-dependent death rate im-

plement the idea that the death rate is linearly increasing with population density:

$$\frac{1}{N}\frac{dN}{dt} = b - (m + \alpha N) = (b - m)\left(1 - \frac{\alpha}{b - m}N\right), \quad (2)$$

where the biological interpretation of the positive proportionality constant α depends on the specific derivation. From comparing equation (2) with equation (1), we see that $r = b - m$ and $K = (b - m)/\alpha$.

Based on these derivations, two observations can be made. First, K depends linearly on those traits that underlie r, and any variation that affects r causes K to vary proportionally. Thus, seemingly independent parameters at one level are not necessarily independent when they are derived from an underlying level. A conclusion from the above derivation is that models that use the logistic equation as a building block and that assume variation in r while K is kept constant (e.g., Parvinen and Egas 2004) do not have an interpretation at the level of the individual. We do not claim that it is impossible to construct a derivation of the logistic equation from first principles such that individual-level traits exist that contribute to r but not to K. But even in this case, independent variation of r can be motivated only if genetic variation is likely to contribute only to exactly those traits that do not affect K.

Second, K can change independently of r only through a change in α. This parameter is inversely related to K, so any change in α affects K in a nonlinear way. This observation becomes important when studying the evolutionary dynamics of correlated traits. Assume a situation where an organism occupies two different habitats that require different adaptations and that population growth in each habitat can be described by the logistic equation (eq.[2]). In this situation, it is likely that a constraint exists that prevents a genotype from being optimally adapted to both habitats simultaneously. Here we adopt the viewpoint that such a constraint can be visualized as the outer boundary of the set of possible phenotypes that we will refer to as a trade-off curve (fig. 1). Assume further that adaptations to the habitats occur in traits α_1 and α_2. Since population growth increases with decreasing values of α_i (eq. [2]), selection will push a population's trait distribution from high values of α_i toward lower values until the trade-off is hit. From then on, selection will keep the phenotype distribution close to the trade-off, relative to the mutational step size. Patterns of covariation within a population will then depend on the shape of the outer boundary of the set of possible phenotypes, and different trade-off curves correspond to different such boundaries. Arnold (1992) refers to this scenario as the Charnov-Charlesworth
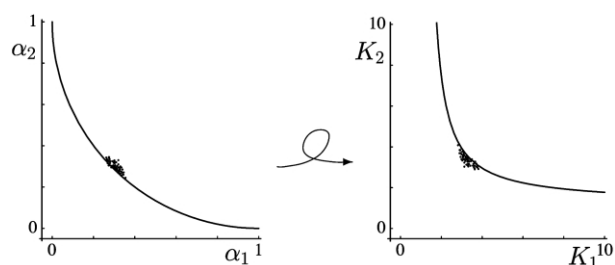
Figure 1: Distribution of phenotypes in the two-dimensional (α_1, α_2) trait space. Solid lines correspond to a constraint or trade-off beyond which no viable phenotypes can occur. Since fitness is decreasing in both α_1 and α_2, the set of possible phenotypes lies above and to the right of the constraint. The right panel shows the location of the phenotypes and the constraint after applying the mapping $(K_1, K_2) = [(b_1 - m_1)/\alpha_1, (b_2 - m_2)/\alpha_2]$. Because fitness is increasing in both K_1 and K_2, the distribution of phenotypes lies below and to the left of the constraint. Note that the trade-off has changed from weak to strong (see text for further explanation). In the (α_1, α_2)-space, the phenotypes have relative low values for both habitats, indicating a high degree of adaptation, while in the (K_1, K_2)-space, the phenotypes again correspond to low values, now indicating a low degree of adaptation. Parameter values are chosen such that $b_i - m_i = 1$.

model for equilibrium genetic covariance for a single pair of traits (cf. Charnov 1989; Charlesworth 1990). The pattern of covariation in individual-level traits causes specific patterns of covariation at the level of demographic parameters (fig. 1). In our example, phenotypes are mapped from the (α_1, α_2)-space to the (K_1, K_2)-space by $(K_1, K_2) = [(b_1 - m_1)/\alpha_1, (b_2 - m_2)/\alpha_2]$. In the same way, we can map the trade-off curve from one level to the next. The result of this mapping is shown in figure 1. Note that the phenotype distribution in the (K_1, K_2)-space lies below and to the left of the trade-off because population growth increases with increasing values of K_i.

The important message from this example is that properties of the phenotype distribution and the trade-off are not necessarily conserved when mapped from one level to the other. The phenotypes indicated by the dots in the (α_1, α_2)-space in figure 1 show relative low values of α_i for both habitats. The corresponding trade-off is called weak because the habitat generalist is only slightly inferior in each habitat when compared to the habitat specialists. On the other hand, phenotypes in the (K_1, K_2)-space show relative low carrying capacities in both habitats. In this case, the trade-off is called strong because habitat generalists are strongly inferior in each habitat in terms of their carrying capacity when compared to the corresponding specialist. From this observation, two questions emerge. First, can an a priori chosen curve for the trade-off between K_1 and K_2 be derived from a curve representing the underlying constraint between α_1 and α_2? Second, if we as-

sume that the answer to that question is yes, is it biologically plausible to assume the trade-off between α_1 and α_2, such that the curve becomes exactly mapped onto an a priori chosen curve for the trade-off between K_1 and K_2? In the following examples, we show that, in some cases, a weak trade-off between habitat-specific carrying capacities cannot be derived from any underlying trade-off and that, in other cases, specific curves for the trade-off at the higher level can be realized only by assuming rather extreme curvatures for the trade-off at the underlying level.

Before we continue to illustrate our point, we want to emphasize that the very same two observations can be made for the Ricker equation $N_{t+1}/N_t = \exp[r(1 - N_t/K)]$. For derivations of the Ricker equation from first principles, see work by Royama (1992), Gatto (1993), Gurney and Nisbet (1998), Sumpter and Broomhead (2001), Thieme (2003), Geritz and Kisdi (2004), and Brännström and Sumpter (2005).

Two Examples

We want to illustrate by means of two examples how patterns of covariation between demographic parameters can be derived from an explicit model of individual-level processes that contribute to the demographic parameters. Our examples are strongly inspired by the models of Wilson and Yoshimura (1994), Egas et al. (2004), de Mazancourt and Dieckmann (2004), and Parvinen and Egas (2004). In this section, we develop a two-habitat version of the logistic and the Ricker equations from first principles. This provides us with explicit expressions for the carrying capacity in terms of individual-level traits. In the "The Mapping of Trade-Offs," we then investigate how specific curvatures for trade-offs between traits that contribute to the carrying capacities affect the curvature of the resulting trade-off between habitat-specific carrying capacities. In "Evolutionary Dynamics," we show how evolutionary predictions can differ when evolutionary change is directly assumed in the carrying capacities, as compared to evolutionary change in underlying individual-level traits.

Continuous Time: Fast Migration between Habitats

Assume that individuals migrate at a high rate between habitats and that travel time is negligible. This means that the environment is fine grained. Under the assumption that birth and death rates are small when compared to the migration rates, we calculate the probability for an individual to be in habitat 1, P_1, or in habitat 2, P_2, in appendix A. Furthermore, we assume that birth and death processes are determined instantaneously; that is, whether an individual dies or gives birth at a certain moment in time depends purely on its current habitat. If population growth

within each habitat can be described by the logistic equation (eq. [1]), then the population dynamics are given by

$$\frac{dN}{dt} = N\left[P_1 r_1\left(1 - \frac{P_1 N}{K_1}\right) + P_2 r_2\left(1 - \frac{P_2 N}{K_2}\right)\right], \quad (3)$$

with r_i and K_i as the habitat-specific intrinsic growth rates and carrying capacities, respectively. The dynamics have a single nontrivial, stable equilibrium at

$$\hat{N} = \frac{(P_1 r_1 + P_2 r_2)K_1 K_2}{P_1^2 r_1 K_2 + P_2^2 r_2 K_1}. \quad (4)$$

In order to give the parameters r_i and K_i, an interpretation at the level of the individual, we present in appendix A one possible derivation of equation (3) based on individual-level processes. This derivation is inspired by Royama's derivation (1992, p. 144; see "Discrete Time: Juvenile Dispersal") of the Ricker equation. We assume that individuals die at some minimum rate when they can exploit a competition neighborhood of size a on their own. The size of this neighborhood is determined by a variety of biological properties such as the conversion efficiency of food into energy or the efficiency with which resources are gathered. The minimum death rate increases incrementally by l, a positive constant, with each additional conspecific that enters the competition neighborhood of the focal individual. For a single habitat, this mechanism yields

$$\frac{dN}{dt} = N(b - m)\left(1 - \frac{la}{b - m}N\right), \quad (5)$$

where b and m are the density-independent birth and death rates, respectively. Equation (5) corresponds to equation (2), but now the demographic parameters r and K have an interpretation in terms of individual-level traits: $r = b - m$ and $K = (b - m)/la$. This holds for each habitat so that $r_i = b_i - m_i$ and $K_i = (b_i - m_i)/(l_i a_i)$. If we insert these descriptions into equation (3), we get the following two-habitat version:

$$\frac{dN}{dt} = N\left[P_1(b_1 - m_1)\left(1 - \frac{l_1 a_1}{b_1 - m_1}P_1 N\right)\right.$$
$$\left. + P_2(b_2 - m_2)\left(1 - \frac{l_2 a_2}{b_2 - m_2}P_2 N\right)\right]. \quad (6)$$

Discrete Time: Juvenile Dispersal

Here we assume that generations are discrete and non-overlapping. At birth, individuals are randomly distributed over two habitats with probabilities P_1 and $P_2 = 1 - P_1$. These probabilities are proportional to the relative sizes of the two habitats and independent of the habitat of birth. The latter is the case because of either very effective dispersal or a fine-grained environment. Once settled, individuals stay within their habitat until death. In the case of a fine-grained environment, this implies that organisms are sessile. If we assume that the population dynamics within each habitat can be described by the Ricker equation (Ricker 1952), then population growth is given by

$$N_{t+1} = N_t\left\{P_1 \exp\left[r_1\left(1 - \frac{P_1 N_t}{K_1}\right)\right]\right.$$
$$\left. + P_2 \exp\left[r_2\left(1 - \frac{P_2 N_t}{K_2}\right)\right]\right\}. \quad (7)$$

Only in case of symmetric parameter values $r_1 = r = r_2$, $K_1 = K = K_2$, and $P_1 = 0.5 = P_2$ can we calculate the equilibrium population size analytically as $\hat{N} = 2K$. The population dynamics of this case are well understood. The equilibrium $\hat{N} = 2K$ is stable for $r < 2$, with larger values of r leading to cycles and eventually chaotic dynamics (May and Oster 1976). Here we restrict ourselves to parameter values that produce stable equilibria.

In order to get an individual-level interpretation of equation (7), we again follow Royama (1992, pp. 144). Royama assumes that the number of offspring produced by an individual, R_n, decreases exponentially with the number of conspecifics n within a competition neighborhood of size a: $R_n = R_0 k^n$. The sensitivity parameter k is a positive constant smaller than 1. For the case when individuals are Poisson distributed over the habitat, Royama shows that

$$N_{t+1} = N_t \exp\left\{\log R_0\left[1 - \frac{a(1 - k)}{\log R_0}N_t\right]\right\}. \quad (8)$$

This is the Ricker equation, where $r = \log R_0$ and $K = \log R_0/[a(1 - k)]$. By combining equation (8) with equation (7), we get a two-habitat version of the Ricker equation:

$$N_{t+1} = N_t \left(P_1 \exp\left\{ \log R_{01}\left[1 - \frac{a_1(1 - k_1)}{\log R_{01}} P_1 N_t \right] \right\} \right.$$

$$\left. + P_2 \exp\left\{ \log R_{02}\left[1 - \frac{a_2(1 - k_2)}{\log R_{02}} P_2 N_t \right] \right\} \right) \quad (9)$$

The Mapping of Trade-Offs

The preceding section provides us with an individual-based interpretation of the population-level parameters K_i and r_i:

$$K_i = \frac{b_i - m_i}{a_i l_i},$$

$$r_i = b_i - m_i, \quad (10)$$

for the logistic equation, and

$$K_i = \frac{\log R_{0i}}{a_i(1 - k_i)},$$

$$r_i = \log R_{0i}, \quad (11)$$

for the Ricker equation. We now investigate how a trade-off between the habitat-specific carrying capacities can be derived from a trade-off in traits at the level of the individual. Here we assume that mutational change occurs for the size of the competition neighborhoods a_1 and a_2 and that these traits are coupled by a trade-off, which can be written as a function $a_2(a_1)$ with $da_2/da_1 < 0$. All other traits are assumed to be fixed parameters. We choose a_1 and a_2 because they can, at least in principle, be measured at the level of the individual and because they influence the carrying capacities in the logistic and Ricker equations in the same way, which facilitates a comparison between these models. From here on we refer to a trade-off between a_1 and a_2 as a trade-off in $\boldsymbol{a}$ and, similarly, to a trade-off between K_1 and K_2 as a trade-off in $\boldsymbol{K}$.

Next we introduce specific trade-off parameterizations for $a_2(a_1)$ and $K_2(K_1)$. This allows us to visualize how a trade-off in $\boldsymbol{a}$ maps onto a trade-off in $\boldsymbol{K}$ or, vice versa, what trade-off in $\boldsymbol{a}$ is implicitly assumed when a specific trade-off in $\boldsymbol{K}$ is chosen. Our parameterizations generalize the trade-off function used by Egas et al. (2004) and Parvinen and Egas (2004):

$$\boldsymbol{a} = (a_1, a_2)$$
$$= [a_{1\max} - a_{1\text{var}}(1 - \theta)^{1/z}, a_{2\max} - a_{2\text{var}}\theta^{1/z}], \quad (12)$$

$$\boldsymbol{K} = (K_1, K_2)$$
$$= [K_{1\min} + K_{1\text{var}}(1 - \theta)^{1/z}, K_{2\min} + K_{2\text{var}}\theta^{1/z}]. \quad (13)$$

Here $a_{1\max}$, $a_{1\text{var}}$, $a_{2\max}$, $a_{2\text{var}}$, $K_{1\min}$, $K_{1\text{var}}$, $K_{2\min}$, and $K_{2\text{var}}$ are positive constants determining the range of possible parameter values, while the positive parameter z determines the curvature of the trade-off curve.

Note the following difference between the two trade-off parameterizations. In equation (12), $\theta = 0$ corresponds to a low value of a_1 and a high value of a_2. In equation (13), the opposite holds true: $\theta = 0$ corresponds to a high value of K_1 and a low value of K_2. Since population growth is decreasing in a_i (eqq. [6], [9]) but increasing in K_i (eqq. [3], [7]), this means that in both cases, $\theta = 0$ corresponds to a specialist for habitat 1 while $\theta = 1$ corresponds to a specialist for habitat 2. A similar pattern applies to the curvature of the trade-off and the corresponding curvature parameter z (fig. 2). Values of $z < 1$ correspond to a concave trade-off in $\boldsymbol{a}$ ($d^2a_2/da_1^2 < 0$) and to a convex trade-off in $\boldsymbol{K}$ ($d^2K_2/dK_1^2 > 0$). The opposite pattern holds for $z > 1$. Hence, these parameterizations are such that $z < 1$ corresponds to a strong trade-off and $z > 1$ corresponds to a weak trade-off in both $\boldsymbol{a}$ and $\boldsymbol{K}$. This terminology is motivated by the following observation. In case of symmetric values for $a_{i\max}$, $a_{i\text{var}}$, $K_{i\min}$, and $K_{i\text{var}}$, all phenotypes that lie on a linear trade-off ($z = 1$) have exactly the same value for a and K, respectively, when averaged over both habitats. In comparison with a linear trade-off, generalists on a convex trade-off have a lower competition neighborhood size (eq. [12]) and a lower carrying capacity (eq. [13]) when averaged over both habitats. Such generalists are superior over specialists in terms of their average competition neighborhood size but inferior in terms of its average carrying capacity. The opposite pattern holds for concave trade-offs.

How does the function $a_2(a_1)$ mediate the trade-off in $\boldsymbol{K}$? To see this, we have to combine the expression for K_i from equation (10) with equation (12). The result is shown in figure 2a, 2b. Note that the curvature of the derived trade-off in $\boldsymbol{K}$ can change from convex to concave along a single trade-off curve (see fig. 2b, right panel). In the following, we refer to the curvature around the generalist's trait with $\theta = 0.5$. In figure 2a, the trait space encompasses values of a_i between 0.1 and 0.2 ($a_{i\max} = 0.2$, $a_{i\text{var}} = 0.1$), while in figure 2b, the trait space encompasses values between 0.1 and 1 ($a_{i\max} = 1$, $a_{i\text{var}} = 0.9$). In the first case, all trade-offs in $\boldsymbol{a}$ corresponding to $z < 2$ are mapped into a strong trade-off in $\boldsymbol{K}$. In other words, for trade-offs in $\boldsymbol{a}$ with $1 < z < 2$, that is, for moderately weak trade-offs,

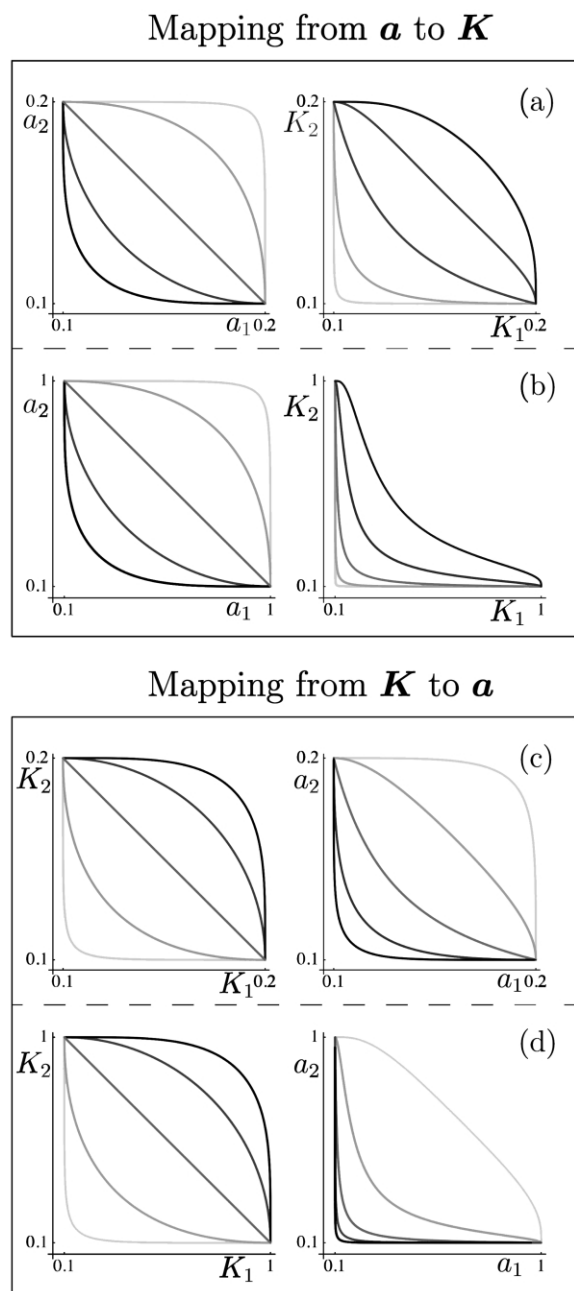## Mapping from *a* to *K*

Mapping from *K* to *a*

Figure 2: Mapping of five different trade-off curves for the habitat-specific size of competition neighborhoods a_i onto trade-off in carrying capacities K_i through function given by equation (10) (*a*, *b*) and vice versa through the inverse function (*c*, *d*). The left graph in each pair shows trade-offs for five values of the curvature parameter z before the application of the mapping, while the right graph shows trade-offs as a result of the mapping. Curves with the same gray scale correspond to the same value of $z \in \{4, 2, 1, 0.5, 0.25\}$, with z decreasing with lighter coloration. Other parameters: $b = (0.3, 0.3)$, $m = (0.1, 0.1)$, $P = (0.5, 0.5)$; *a*, $a_{max} = (0.2, 0.2)$, $a_{var} = (0.1, 0.1)$, $l = (10, 10)$; *b*, $a_{max} = (1, 1)$, $a_{var} = (0.9, 0.9)$, $l = (2, 2)$; *c*, $K_{min} = (0.1, 0.1)$, $K_{var} = (0.1, 0.1)$, $l = (10, 10)$; *d*, $K_{min} = (0.1, 0.1)$, $K_{var} = (0.9, 0.9)$, $l = (2, 2)$.

their weakness is not inherited. In the second case, only extremely weak trade-offs in *a* corresponding to $z > \approx 12$ are mapped onto weak trade-offs in *K*. For trade-offs with $1 < z < 12$, the weakness is not inherited. Hence, weak trade-offs in *a* are mapped to strong trade-offs in *K* for z values below some threshold. In appendix B, we show that this threshold increases with increasing values of a_{ivar}. In the limit of $a_{ivar} = 0$, the threshold becomes 1 and the curvature property is always inherited. In the limit of $a_{ivar} = \infty$, the threshold becomes infinity; hence, any trade-off in *a*, weak or strong, is mapped to a strong trade-off in *K*.

Models assuming a trade-off directly at the level of the carrying capacities make an implicit assumption about the shape of the trade-off in an individual-level trait. This implicit assumption can be shown by applying the inverse mapping, from the trade-off in the carrying capacities *K* to the trade-off in *a*. The result of this exercise is shown in figure 2*c*, 2*d*.

Evolutionary Dynamics

Analyses of long-term evolution should be based on an invasion argument: can a rare mutant type increase in frequency, or is it doomed to extinction? This is determined by its invasion fitness *s*, its long-term average growth rate when rare in an environment dominated by a given resident type (e.g., Metz et al. 1992). If $s > 0$, then such a mutant has a positive probability of invading the resident population, and if $s < 0$, such a mutant will disappear. Under certain conditions, an invasion analysis is equivalent to solving an optimization criterion (Metz et al. 1996). The quantity that is maximized by evolution cannot be chosen a priori but has to be derived from an invasion argument (Mylius and Diekmann 1995). For our examples, we are able to show that equilibrium population size $\hat{N}$ serves as an optimization criterion. Populations with trait values that correspond to a higher equilibrium population size $\hat{N}$ replace populations with lower equilibrium population size, and trait values that maximize population size are potential endpoints of evolution. Such trait values are attractors of the evolutionary dynamics and are uninvadable by nearby mutants. Eshel (1983) coined the term continuously stable strategies (CSSs) for such trait values. Trait values that correspond to minima of $\hat{N}$ are evolutionary repellors from which the evolutionary dynamics move away. The existence of an optimization criterion allows us to visualize the evolutionary process using Levins's fitness set approach (Levins 1962; Rueffler et al. 2004). In this graphical method, the trade-off curve is plotted on top of the contour lines of the fitness landscape given by $\hat{N}$ (fig. 3). Evolutionary endpoints are those phenotypes
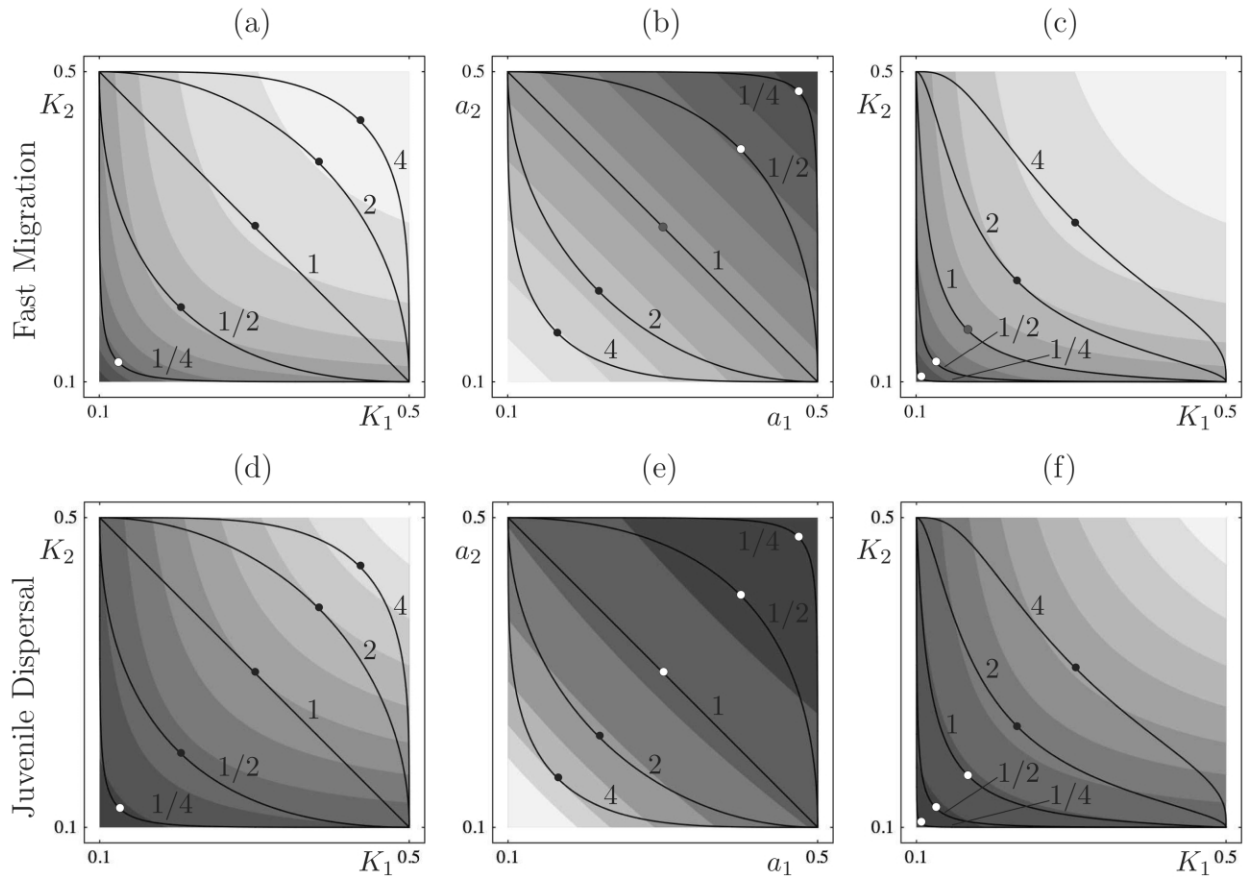
Figure 3: Fitness contour plots for model with fast migration between habitats (logistic equation; *a–c*) and juvenile dispersal (Ricker equation; *d–f*). Fitness contours represent values of optimization criteria as functions of K_1 and K_2 (*a, c, d, f*) or a_1 and a_2 (*b, e*). Lighter coloration indicates higher values of the optimization criterion and therefore higher fitness. Trade-offs with different values of the curvature parameter *z* are plotted on top of the fitness landscape. For a given trade-off curve, the optimal phenotype is given by the point on the trade-off curve lying on the highest contour. The color of the circles at the position of the habitat generalist indicates evolutionary properties: *black* = continuously stable strategy, *white* = repellor, *gray* = selectively neutral with respect to all other traits on the trade-off. *a, d*, Trade-off is assumed directly in **K**. *b, e*, Trade-off is assumed in **a**. *c, f*, Trade-off in **K** is derived from the underlying trade-off in **a**. The latter two representations necessarily give the same result. Parameter values: **P** = $(0.5, 0.5)$; *a, c*, $\mathbf{K}_{min} = (0.1, 0.1)$, $\mathbf{K}_{var} = (0.4, 0.4)$, **r** = $(0.2, 0.2)$; *b, d*, $\mathbf{a}_{max} = (0.5, 0.5)$, $\mathbf{a}_{var} = (0.4, 0.4)$, **l** = $(4, 4)$; *b*, **l** = $(4, 4)$, **b** = $(0.3, 0.3)$, **m** = $(0.1, 0.1)$; *d*, **k** = $(0.1, 0.1)$, $\log \mathbf{R}_0 = (0.2, 0.2)$.

on the trade-off curve that lie on the highest fitness contour line.

Fast Migration between Habitats

First we consider the case where evolutionary change is assumed to directly affect K_1 and K_2. Invasion fitness of a mutant type $\mathbf{K}' = (K_1', K_2')$ in a resident population with carrying capacities $\mathbf{K} = (K_1, K_2)$ can be derived from equation (3) as

$$s(\mathbf{K}', \mathbf{K}) = P_1 r_1 + P_2 r_2 - \hat{N}(\mathbf{K}) \left(\frac{P_1^2 r_1}{K_1'} + \frac{P_2^2 r_2}{K_2'} \right). \quad (14)$$

Equation (14) is obviously monotonically decreasing in $\hat{N}$ (eq. [4]). As mentioned above, this is a sufficient condition for the equilibrium population size to be an optimization criterion (Mylius and Diekmann 1995). Figure 4*a* shows the numerically calculated locations of the minima and maxima of the optimization criterion as a function of the curvature parameter *z* for one specific set of symmetric parameter values. For weak trade-offs, the habitat generalist with $K_1 = K_2$ maximizes equilibrium population size $\hat{N}$ and therefore displays a CSS. The habitat generalist maintains a CSS for moderately strong trade-offs, and it is only for very strong trade-offs with $z < 0.35$ that the generalist turns into an evolutionary repellor.
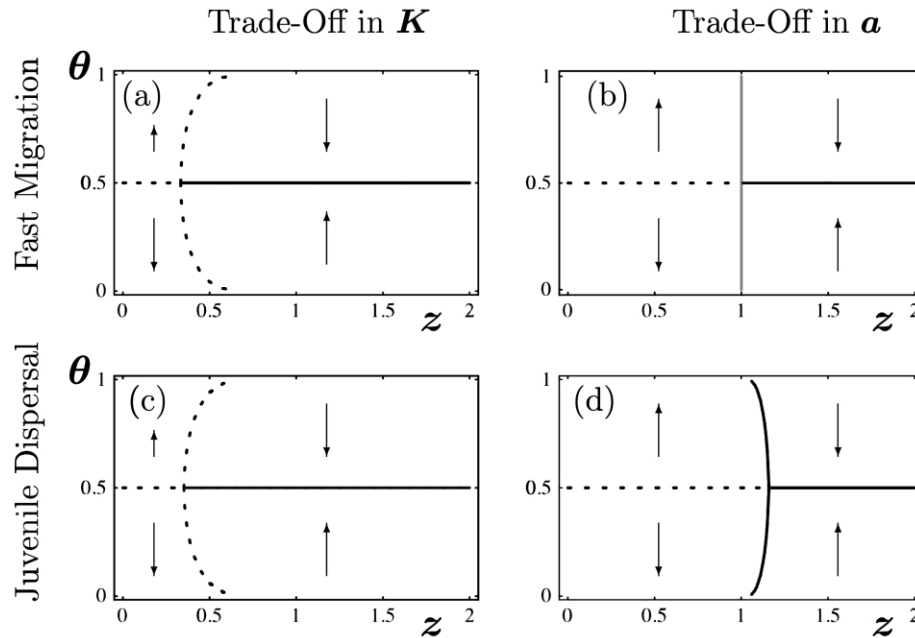
In appendix C, we show that whether the habitat gen-

Trade-Off in **K**

Trade-Off in **a**

Figure 4: Bifurcation diagram of extrema of optimization criterion as a function of curvature parameter z for model with fast migration between habitats (logistic equation; a, b) and juvenile dispersal (Ricker equation; c, d). Ordinate shows value of the specialization coefficient θ. a, c, Trade-off directly in **K**. b, d, Trade-off in **a**. Solid lines indicate maxima of the optimization criterion and correspond to continuously stable strategies, while dashed lines indicate minima of the optimization criterion and correspond to evolutionary repellors. The gray vertical line in b indicates that for $\theta = 1$, all trait combinations are selectively neutral. Arrows indicate the direction of evolutionary change. Parameter values as in figure 3.

eralist with $K_1 = K_2$ constitutes a minimum or a maximum of $\hat{N}$ also depends on the parameters $K_{i\min}$ and $K_{i\text{var}}$, that is, on the range of possible parameter values for K_i. Small values of $K_{i\min}$ favor the generalist even for $z < 1$ (strong trade-offs), while with small values of $K_{i\text{var}}$, a situation is approached where weak trade-offs select for a generalist while strong trade-offs select for specialists.

Do the evolutionary dynamics change when we implement evolutionary change in individual-level traits? Invasion fitness of a rare mutant type with competition neighborhood size $\boldsymbol{a}' = (a_1', a_2')$ in a population with $\boldsymbol{a} = (a_1, a_2)$ can be derived from equation (6) as

$$s(\boldsymbol{a}', \boldsymbol{a}) = P_1 r_1 + P_2 r_2 - \hat{N}(\boldsymbol{a})(P_1^2 a_1' l_1 + P_2^2 a_2' l_2), \quad (15)$$

where $r_i = b_i - m_i$. As in the previous version, fitness is a monotonically decreasing function of $\hat{N}$, which therefore qualifies as an optimization criterion. From equation (4) we can derive that $\hat{N} = (P_1 r_1 + P_2 r_2)/(P_1^2 a_1 l_1 + P_2^2 a_2 l_2)$. Differentiation of $\hat{N}$ reveals that critical points are given by $da_2/da_1 = -P_1^2 l_1/(P_2^2 l_2)$ and that the sign of the second derivative equals the sign of $-d^2 a_2/da_1^2$. Hence, critical points of $\hat{N}$ are maxima for $z > 1$ (weak trade-offs) and minima for $z < 1$ (strong trade-offs). For $z = 1$, all trait combinations are selectively neutral. Figure 4b depicts this

result for the case of symmetric parameter values. A comparison of figure 4a and 4b shows that the range of z values that favor habitat generalists over specialists is considerably smaller when the trade-off is implemented between a_1 and a_2. This indicates that, in this case, the shortcut of directly implementing a trade-off in demographic parameters overestimates the likelihood of finding generalists.

It is illuminating to plot these results in terms of fitness sets (Levins 1962). The fitness landscape, that is, the optimization criterion, can be plotted as a function of either the demographic parameters K_1 and K_2 (fig. 3a, 3c) or the underlying individual-level traits a_1 and a_2 (fig. 3b). In the first case, the contours of the fitness landscape are given by those values of K_1 and K_2 that result in equal values c of the optimization criterion $\hat{N}$. These K_i values lie on convex hyperbolas given by $K_2 = c P_2^2 r_2 K_1/(K_1 - c P_1^2 r_1)$. In the second case, the contours of the fitness landscape are straight lines with a negative slope given by $a_2 = (1 - c P_1^2 a_1 l_1)/(c P_2^2 l_2)$. In the next step, we plot different trade-off curves on top of the contour plot of the fitness landscape. This is done in figure 3a for trade-offs in **K** and in figure 3b for trade-offs in **a**. In figure 3c, this is done again for a trade-off in **K**, but now the trade-off is derived from the underlying trade-off in **a**. From figure 3a, we see that fitness landscapes with convex fitness contours favor gen-

eralists, and it is only for very strong trade-offs (e.g., $z = 1/4$) that specialists do better (cf. fig. 4*a*). In the presence of a fitness landscape with linear contours (fig. 3*b*), weak trade-offs favor generalists and strong trade-offs favor specialists (cf. fig. 4*b*). Figure 3*c* shows that optimizations in terms of *K* and *a* are equivalent approaches as long as the trade-off in **K** is derived from an underlying trade-off in **a**. In both cases, the trade-off curve given by $z = 1$ exactly follows a contour line of the fitness landscape, which accounts for the evolutionary neutrality of all traits.

Juvenile Dispersal

Fitness in discrete-time models can be expressed more easily as $w = \exp(s)$. If $w > 1$, a mutant is able to invade, while a mutant with $w < 1$ cannot invade. As in the previous section, we first perform an evolutionary analysis under the assumption that K_1 and K_2 are traded off directly, followed by an analysis where evolutionary change is implemented in the size of the two competition neighborhoods a_1 and a_2. In both cases, the fitness function is monotonically decreasing in $\hat{N}$, which therefore again qualifies as an optimization criterion (Mylius and Diekmann 1995). Unfortunately, we can calculate $\hat{N}$ analytically only for the case of symmetric parameter values and a consumer that is equally specialized for both habitats. Hence, the maximization of $\hat{N}$ has to be done numerically.

For the first case, where the trade-off is directly assumed in **K**, we find the following fitness function:

$$w(\boldsymbol{K}', \boldsymbol{K}) = P_1 \exp\left[r_1\left(1 - \frac{P_1\hat{N}(\boldsymbol{K})}{K_1'}\right)\right]$$
$$+ P_2 \exp\left[r_2\left(1 - \frac{P_2\hat{N}(\boldsymbol{K})}{K_2'}\right)\right]. \quad (16)$$

Numerical analysis of the optimization criterion $\hat{N}$ reveals a pitchfork bifurcation of θ values that correspond to extrema in $\hat{N}$ (fig. 4*c*). For small values of z (strong trade-offs), the generalist is an evolutionary repellor. The generalist adopts a CSS when some threshold value of z is passed. For $r < 2$, that is, for stable population dynamical equilibria, we prove in appendix C that this threshold always has a value smaller than 1.

In the second case, where the trade-off is assumed between the underlying traits a_1 and a_2, invasion fitness is given by

$$w(\boldsymbol{a}', \boldsymbol{a}) = P_1 \exp\left\{r_1\left[1 - \frac{P_1\hat{N}(\boldsymbol{a})a_1'(1 - k_1)}{r_1}\right]\right\}$$
$$+ P_2 \exp\left\{r_2\left[1 - \frac{P_2\hat{N}(\boldsymbol{a})a_2'(1 - k_2)}{r_2}\right]\right\}. \quad (17)$$

By numerical calculations, we again find a pitchfork bifurcation (fig. 4*d*). For this case, we can prove (app. C) that the change from a repelling generalist to an attracting generalist takes place for some z value larger than 1 (for a weak trade-off). In appendix C, we also show that the bifurcation point moves toward higher z values with increasing population growth rate r. This means that fast growth favors habitat specialization. Figure 3*d*–3*f* illustrates these results with the use of fitness sets.

Discussion

Genetic variation is the fuel for evolutionary change. This variation occurs at the level of DNA sequences. The direction of evolutionary change depends on the available genetic variation and on the per capita growth rate of the different genotypes in the environment where selection takes place. A complete understanding of the evolutionary process would require knowledge of how variation at the level of the DNA sequence is mapped through the process of development to variation in demographic parameters. In most cases, we are far from such a detailed knowledge, and in order to deal with this difficulty, theoretical biologists have followed either of two different paths. Theoretical population geneticists study variation in allele space and assume an extremely simplified genotype-phenotype map by assigning fixed fitness values to alleles. The other approach neglects the genotype-phenotype map altogether and studies the effect of variation directly at the level of phenotypes (optimization models, quantitative genetics, game theory, and adaptive dynamics). Both approaches are shortcuts, and it is important to develop an understanding of the possible consequences of such shortcuts. In this article, we show how patterns of variation and covariation at one level are mapped to a higher level, and we pinpoint two pitfalls that can occur when variation at a higher level is not derived from variation in underlying traits.

Our article is motivated by a recent series of models where habitat specific population growth is described by either the logistic equation (de Mazancourt and Dieckmann 2004; Parvinen and Egas 2004) or the Ricker equation (Wilson and Yoshimura 1994; Egas et al. 2004). In these models, variation is implemented in habitat-specific growth rates or carrying capacities. Assuming evolutionary change in these population-level parameters might not be

acceptable for at least two reasons. First, population-level parameters that appear as independent variables in a population dynamical equation might not be independent when derived from processes at the individual level. Such is the case with r and K in both the logistic and Ricker equations. In these growth models, K appears to be linearly dependent on r. Consequently, variation in r alone cannot be derived from variation in an underlying trait. Independence of r and K should be assumed only based on a derivation showing how different independent traits at the individual level can affect the different demographic parameters separately. Kuno (1991), Olson (1992), and Berryman (1992) all discuss why the logistic equation is likely to be a bad candidate to find such a derivation. Second, trade-offs between population-level parameters originate from correlations in underlying individual-level traits. If the mapping from these traits to higher-level parameters is nonlinear, then specific trade-off curvatures are not inherited from one level to the next. By implementing a certain trade-off curvature between population-level parameters, the modeler makes an implicit assumption about the nature of the trade-off at the individual level. Because of the involved nonlinearity, this assumption might often be rather unrealistic, and as we have shown in some cases, a certain curvature cannot be derived from an underlying trade-off at all.

Based on all derivations of the logistic equation and the Ricker equation that are known to us, the observation that the carrying capacity increases linearly with intrinsic growth rate has important consequences for the theory of r and K selection. In the classical sense, as popularized by MacArthur and Wilson (1967), Roughgarden (1971), and Charlesworth (1971), this theory states that variable environments, in which population densities are regularly set back to low values, select genotypes with high intrinsic growth rates, while more stable environments select genotypes corresponding to high equilibrium population densities. The influential article by Roughgarden (1971) uses the logistic equation to derive these predictions formally. In this model, a trade-off is assumed: genotypes with a high intrinsic growth rate correspond to a low carrying capacity and vice versa. This assumption is clearly at odds with the viewpoint championed in this article suggesting that r and K are positively rather than negatively correlated. Thus, in models that are based on the logistic equation but where the demographic parameters are derived from processes at the level of the individual, selection for high growth rates results in a concomitant increase of the carrying capacity. This point has also been made by Kuno (1991). That the theory of r and K selection in its narrow sense is flawed for other reasons has been known at least since the important article by Matessi and Gatto (1984). They showed that stable environments need not

select the genotype corresponding to the highest carrying capacity but rather select the genotype that can live on the fewest resources. These authors suggest using the terms r and K selection to refer to the conditions of selection (density independent vs. density dependent) rather than to the outcome of selection (r maximization vs. K maximization).

Application to the Recent Literature

The ideas presented in this article affect the results of a recent series of articles that study the evolution of habitat specialization. In these models, mutational change is assumed for habitat-specific carrying capacities or intrinsic growth rates.

Wilson and Yoshimura (1994) have explored the scope for coexistence of two habitat specialists and a habitat generalist, as determined by their habitat-specific carrying capacities in a model where habitat-specific growth is described by the Ricker equation. In their basic model version, the carrying capacity for a specialist is 10 times higher in the habitat it is adapted to than in the habitat it is not adapted to. This situation corresponds to our figure 2b, 2d, where the two specialists are characterized by $K = (1, 0.1)$ and $K = (0.1, 1)$. The shape of the trade-off is determined by the carrying capacities of the generalist. To cover trade-off relations from strong to weak, Wilson and Yoshimura varied the carrying capacity of the generalist between 0.3 and 0.99. Wilson and Yoshimura (1994) find that coexistence is possible for generalists ranging from $K = (0.99, 0.99)$ to $K = (0.4, 0.4)$. According to our parameterization (see eq. [13]), these generalists correspond to trade-offs in a that are parameterized by z values between 617 (for $K = [0.99, 0.99]$) and 3.8 (for $K = [0.4, 0.4]$). Hence, all of these trade-offs correspond to very weak or extremely weak trade-offs in a (cf. fig. 2d). Moderately weak, linear, and strong trade-offs in a all correspond to strong trade-offs in K (cf. fig. 2b) and do not allow for the coexistence of two specialists and a generalist. From this viewpoint, the scope for coexistence seems to be far more restricted than suggested by Wilson and Yoshimura.

Egas et al. (2004) present a reanalysis of the model of Wilson and Yoshimura. In one version of their model, they assume that the habitat-specific carrying capacities can vary continuously between 0 and 100. A carrying capacity of 0 corresponds to an infinitely large competition neighborhood size with $a_{i_{\max}} = \infty = a_{i\text{var}}$. In appendix B, we prove that in this case any trade-off in a is mapped into a strong trade-off in K. However, from the analysis in Egas et al. (2004), it becomes clear that coexistence of two specialists and a generalist requires a weak trade-off in K in all cases where environmental variability is not extremely

high. This perspective therefore suggests again that co-existence is far more restricted than it appears from the analysis of the authors.

Parvinen and Egas (2004) studied the evolution of habitat specialization in a metapopulation model with two types of habitat and logistic growth within patches. Evolutionary change is assumed in either habitat-specific intrinsic growth rates or carrying capacities. Currently, no derivation of the logistic equation known to us provides a mechanism that would allow variation of the intrinsic growth rate while leaving the carrying capacities constant; in all published mechanisms known to us, the latter is linearly dependent on the former. Hence, we lack an individual-based interpretation of habitat specialization in terms of intrinsic growth rates.

The main purpose of an article by de Mazancourt and Dieckmann (2004) is to extend Levins's (1962) graphical fitness set approach to accommodate frequency-dependent selection. In order to illustrate their methodology, they analyze a model of one consumer feeding in two habitats. The consumer grows logistically in each habitat and evolves in a trait that determines habitat-specific carrying capacities. Evolution in the carrying capacities is assumed to be constrained by a trade-off, and in the specific case analyzed by de Mazancourt and Dieckmann (2004), the space of possible carrying capacities ranges from 0 to 10. As mentioned above, no individual-based derivation of the logistic equation is known to us that can produce a weak trade-off in K for this choice of parameters. Since a weak trade-off is a prerequisite for evolutionary branching in their model, this seems, at least from the viewpoint of individual-level traits, contrary to the statement of the authors, a very unlikely outcome. We want to emphasize that our objection against the specific example does not detract from the eminent suitability of their methodology for analyzing situations where little knowledge is available on the mapping from individual-level traits to population-level parameters. An analysis along their lines produces graphical conditions that a trade-off curve has to fulfill for a specific outcome to be realized.

Ultimately, the nature of variation at any given level is an empirical question. It might very well be that in a certain species, a pattern of variation is found that matches the assumed variation in the above. Therefore, theoretical studies of an a priori chosen pattern of variation in population-level parameters without deriving it from an underlying level can still be useful. However, such a match would seem to be a lucky coincidence and should not form the basis of a research program. Instead, we suggest the following approach. Evolutionary predictions should be derived from models that assume evolutionary change at the level of individual-based traits. In order to get a broader picture, one should get a collection of different individual-based derivations. In a second step, one can classify the traits occurring in these derivations with respect to how variation at this level is mapped to the level of demographic traits and therefore result in the same class of evolutionary dynamics.

The Evolution of Resource Specialization

Finally, we want to draw attention to the results of our evolutionary analysis. In the face of trade-offs, theory predicts two qualitatively different evolutionary outcomes. Natural selection can lead either toward an intermediate phenotype where the gain from improving one trait is exactly balanced by the loss through the accompanying change in another trait or to an extreme phenotype at the boundary of the trait space. The evolution of habitat specialization in terms of the size of the interaction neighborhood a shows a marked difference in the continuous- and the discrete-time models. In the continuous-time model, where fast migration between habitats is assumed, the generalist is selected for in the case of weak trade-offs, while specialists are selected for in the case of strong trade-offs. This scenario coincides with the intuition of many evolutionary ecologists about the evolution of resource specialization (e.g., Benkman 1993; Robinson 2000) and with Levins's predictions for evolution in an environment that is stable in time but heterogeneous in space (Levins 1962). By contrast, in the discrete-time model, which assumes juvenile dispersal and no migration, specialists are also selected for in combination with weak trade-offs. This scenario shows that Levins's result does not hold generally but only when fitness is a linear function of the traits considered evolvable.

Acknowledgments

APPENDIX A

Fast Migration between Habitats

The population dynamics of one consumer species exploiting two different habitats can be described by the following system of coupled differential equations:

$$\frac{dN_1}{dt} = h_{12}N_2\frac{A_2}{A_1} - h_{21}N_1 + b_1N_1 - m_1N_1, \tag{A1}$$

$$\frac{dN_2}{dt} = h_{21}N_1\frac{A_1}{A_2} - h_{12}N_2 + b_2N_2 - m_2N_2. \tag{A2}$$

Quantities N_1 and N_2 denote the population density in habitats 1 and 2, respectively. Individuals migrate at rate h_{ij} from habitat j to habitat i. Absolute habitat size is denoted by A_i. In each habitat, individuals reproduce and die at the habitat-specific rates b_i and m_i, respectively. If we assume that migration rates are high in comparison with the birth and death rates, we can calculate the equilibrium distribution of the population over the two habitats as $\hat{N}_1 = \hat{N}_2 A_2 h_{12}/A_1 h_{21}$. Combining this with $n = A_1N_1 + A_2N_2$, where n denotes the total population size, we find that $P_1 = A_1\hat{N}_1/\hat{n} = h_{12}/(h_{21} + h_{12})$ and $P_2 = A_2\hat{N}_2/\hat{n} = h_{21}/(h_{21} + h_{12})$.

In order to write the model purely in terms of individual-level traits, we assume that the habitat-specific death rates increase linearly with the number of competitors and therefore that the realized rate of increase of a consumer with n competitors in its competition neighborhood of size a is given by $r_n = b - (m + ln)$. Here l is a positive constant. It describes the sensitivity to competition such that the sensitivity increases with increasing values of l. If we substitute r_0 for $b - m$, we can rewrite the realized rate of increase as $r_n = r_0 - ln$. The expected rate of increase for any probability distribution $P(n)$ is then given by

$$\mathrm{E}[r] = r_0 - l\sum_n nP(n) = r_0 - l\bar{n} = r_0 - lNa = r_0\left(1 - \frac{laN}{r_0}\right), \tag{A3}$$

that is, $K = r_0/la$.

APPENDIX B

Mapping of the Trade-Off

Consider a trade-off between a_1 and a_2 that can be described by the function $a_2(a_1)$. This trade-off curve is translated into a curve $K_2(K_1)$ by the map $K_2(a_2(a_1(K_1)))$. This map has to be derived from equations (12) and (10) or (11). To study the curvature of the trade-off in $\mathbf{K}$, we have to differentiate $K_2(a_2(a_1(K_1)))$ twice:

$$\frac{d^2K_2(a_2(a_1(K_1)))}{dK_1^2} \propto 2\frac{da_2}{da_1}\left(\frac{da_2}{da_1}\frac{1}{a_2} - \frac{1}{a_1}\right) - \frac{d^2a_2}{da_1^2}. \tag{B1}$$

This gives us an expression for the shape of the trade-off in terms of the first two derivatives of $a_2(a_1)$. Further analytical results can be obtained for specific parameterizations of the trade-off curve. Here we choose equation (12), which can also be written as

$$1 = \left(\frac{a_{1\max} - a_1}{a_{1\mathrm{var}}}\right)^z + \left(\frac{a_{2\max} - a_2}{a_{2\mathrm{var}}}\right)^z. \tag{B2}$$

We can derive the trade-off function $a_2(a_1)$ by solving equation (B2) for a_2. The first two derivatives of this function can be simplified using equations (12) and (B2) to

$$\frac{da_2}{da_1} = -\frac{(1-\theta)\theta^{1/z}a_{2\text{var}}}{(1-\theta)^{1/z}\theta a_{1\text{var}}},$$

$$\frac{d^2a_2}{da_1^2} = \frac{(1-\theta)\theta^{1/z}a_{2\text{var}}(z-1)}{(1-\theta)^{2/z}\theta^2 a_{1\text{var}}^2}. \tag{B3}$$

Now we are able to simplify condition (B1) using equation (B3):

$$\frac{d^2K_2(a_2(a_1(K_1)))}{dK_1^2} \propto 1 - z + 2\left[\theta \frac{a_{1\text{var}}(1-\theta)^{1/z}}{a_{1\max} - a_{1\text{var}}(1-\theta)^{1/z}} + (1-\theta)\frac{a_{2\text{var}}\theta^{1/z}}{a_{2\max} - a_{2\text{var}}\theta^{1/z}}\right]. \tag{B4}$$

This condition depends on the magnitude of z relative to 1 plus two times some complicated expression in brackets. If both instances of $a_{1\text{var}}$ and $a_{2\text{var}}$ are small, then the term in brackets is small as well, and the sign of the second derivative will be determined by the difference between 1 and z. In this case, whether $K_2(a_2(a_1(K_1)))$ is a strong or a weak trade-off is inherited for most values of z from the corresponding property in the underlying trade-off $a_2(a_1)$. By contrast, if both instances of $a_{1\text{var}}$ and $a_{2\text{var}}$ are large, that is, very similar to $a_{i\max}$, then the term in brackets will be large as well and can dominate the whole expression. In this case, moderately weak trade-offs in **a** will be mapped into strong trade-offs in **K**. When $a_{i\text{var}}$ approaches infinity, then $K_2(K_1)$ will be a convex trade-off for any value of z.

APPENDIX C

Analytical Results for Evolutionary Analysis

First, we present some analytical results for the case of fast migration and mutational change in **K**. These derivations are very similar to those in appendix B and will not be repeated in as much detail. The optimization criterion is given by $\hat{N}$ (eq.[4]). Differentiating $\hat{N}$ with respect to K_1 (where K_2 is considered a function of K_1) reveals that critical points of $\hat{N}$ are given by $dK_2/dK_1 = -(P_1^2 r_1 K_2^2)/(P_2^2 r_2 K_1^2)$. To see whether these critical points are maxima or minima of $\hat{N}$, we need to differentiate $\hat{N}$ twice. It appears that we get a more tractable result if we differentiate $\hat{N}' := -1/\hat{N}$, an expression that has minima and maxima for the same values as $\hat{N}$. Differentiating $\hat{N}'$ twice with respect to K_1 yields

$$\frac{d^2\hat{N}'}{dK_1^2} = \frac{P_2^2 r_2}{K_2^2}\frac{d^2K_2}{dK_1^2} - \frac{2P_1^2 r_1}{K_1^3} - \frac{2P_2^2 r_2}{K_2^3}\left(\frac{dK_2}{dK_1}\right)^2. \tag{C1}$$

When we evaluate this derivative at the critical points of $\hat{N}$, we can replace the middle term with $-(dK_2/dK_1)2r_2 P_2^2/(K_2^2 K_1)$. This allows us factor out $P_2 r_2/K_2^2$ from the right-hand side of equation (C1). After replacing dK_2/dK_1 and d^2K_2/dK_1^2 with their explicit expressions, which can be derived analogous to equation (B3), we get

$$\frac{d^2\hat{N}'}{dK_1^2} \propto 1 - z - 2\left[\theta \frac{K_{1\text{var}}(1-\theta)^{1/z}}{K_{1\min} + K_{1\text{var}}(1-\theta)^{1/z}} + (1-\theta)\frac{K_{2\text{var}}\theta^{1/z}}{K_{2\min} + K_{2\text{var}}\theta^{1/z}}\right]. \tag{C2}$$

For $z > 1$ (weak trade-offs), this expression is always negative, and therefore, critical points are maxima. For $z < 1$, the sign of expression (C2) depends on the term in brackets. When this term is larger than 0.5, then $d^2\hat{N}'/dK_1^2$ will be negative for any value of z and the critical point will be again a maximum. This is the case when $K_{1\min}$ and $K_{2\min}$ are sufficiently small. In case of symmetric parameter values for r_i, P_i, $K_{i\min}$, and $K_{i\text{var}}$, we find a critical point of the optimization criterion at $\theta = 0.5$. A sufficient condition for $d^2\hat{N}'/dK_1^2$ to be negative is then given by $K_{\min} < K_{\text{var}}0.5^{1/z}$. However, when both $K_{1\text{var}}$ and $K_{2\text{var}}$ are sufficiently small, then the term in brackets will be close to 0, and the difference between 1 and z dominates the term in brackets. The optimization criterion then has the same qualitative curvature as the trade-off $K_2(K_1)$. In the limit $K_{i\text{var}} = 0$, the term in brackets becomes 0, and a strong trade-off in **K** corresponds to a minimum in $\hat{N}$ and a weak trade-off in **K** corresponds to a maximum in $\hat{N}$.

  Given symmetric parameter values ($P_1 = 1/2 = P_2$, $r_1 = r = r_2$, $K_{1\min} = K_{2\min}$, $K_{1\text{var}} = K_{2\text{var}}$, $a_{1\max} = a_{2\max}$,

$a_{1var} = a_{2var}$, $R_{01} = R_{02}$, $k_1 = k = k_2$), we can prove for the model with juvenile dispersal and no migration that the bifurcation between a repelling generalist and an attracting generalist occurs for $z < 1$ when the trade-off is directly in $\boldsymbol{K}$ and for $z > 1$ when the trade-off is in $\boldsymbol{a}$. Under the assumption of symmetry, the first derivative of the fitness function (eqq. [16], [17]) equals 0 at the generalist trait where $K_1 = K = K_2$ and $a_1 = a = a_2$, respectively. At these trait values, $dK_2/dK_1 = -1$ and $\hat{N} = 2K$ in the case of a trade-off directly in $\boldsymbol{K}$, and $da_2/da_1 = -1$ and $\hat{N} = 2r/[a(1 - k)]$ in the case of a trade-off in $\boldsymbol{a}$. The bifurcation point is given by the z value where the second derivative of the fitness function (eqq. [16], [17]) equals 0: $d^2 w(K', K)/dK_1'^2 = 0$ and $d^2 w(a', a)/da_1'^2 = 0$, respectively. Under the conditions mentioned above, we can derive that the bifurcation points are characterized by

$$\frac{d^2 K_2}{dK_1^2} = \frac{2(2 - r)}{K} \tag{C3}$$

and

$$\frac{d^2 a_2}{da_1^2} = \frac{2r}{a}, \tag{C4}$$

respectively. The right-hand side of equation (C3) is positive for $r < 2$. Hence, for stable population dynamical equilibria, the bifurcation occurs for a convex trade-off in $\boldsymbol{K}$. As explained in "The Mapping of Trade-Offs," this corresponds to a strong trade-off in $\boldsymbol{K}$ ($z < 1$). The right-hand side of equation (C4) is also a positive number, thus indicating again that the bifurcation occurs for a convex trade-off. However, for this case where the trade-off is assumed in $\boldsymbol{a}$, a convex trade-off corresponds to a weak trade-off ($z > 1$).

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