

Evolution Restricts the Coexistence of Specialists and Generalists: The Role of Trade-off Structure

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ABSTRACT: Environmental variability and adaptive foraging behavior have been shown to favor coexistence of specialists and generalists on an ecological timescale. This leaves unaddressed the question of whether such coexistence can also be expected on an evolutionary timescale. In this article, we study the attainability, through gradual evolution, of specialist-generalist coexistence, as well as the evolutionary stability of such communities when allowing for immigration. Our analysis shows that the potential for specialist-generalist coexistence is much more restricted than originally thought and strongly depends on the trade-off structure assumed. We establish that ecological coexistence is less likely for species facing a trade-off between per capita reproduction in different habitats than when the trade-off acts on carrying capacities alone. We also demonstrate that coexistence is evolutionarily stable whenever it is ecologically stable but that in most cases, such coexistence cannot be reached through gradual evolution. We conclude that an evolutionarily stable community of specialists and generalists may be created only through immigration from elsewhere or through mutations of large effect. Our results highlight that trade-offs in fitness-determining traits can have counterintuitive effects on the evolution of specialization.

Keywords: coexistence, evolution, foraging behavior, specialization, temporal heterogeneity, trade-off structure.

One of the major challenges in ecology and evolutionary biology is to achieve a better link between evolutionary and ecological dynamics. Do fast selection responses add

new properties to ecosystem dynamics? And, perhaps more important, does ecological feedback affect selection pressures in unexpected ways? The various ways through which evolutionary and ecological dynamics interact are only beginning to be explored. For example, including natural selection in metapopulation models can lead to predictions of selection-driven metapopulation extinction (Gyllenberg et al. 2002; Parvinen 2002; Parvinen et al. 2003). Also, ecological feedback is increasingly viewed as a widespread source of frequency-dependent selection that may favor sympatric speciation through selection for assortative mating (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000, 2003; Geritz and Kisdi 2000).

A topic where such questions are particularly pertinent is species coexistence. Here, the aim is to pinpoint conditions under which n species can live together on less than n resources, violating the principle of competitive exclusion (Hardin 1960). On the one hand, the ecological dynamics are well explored (e.g., Hutchinson 1961; Stewart and Levin 1973; Koch 1974; Armstrong and McGehee 1976a; Levins 1979; Chesson and Warner 1981; Abrams 1984; Chesson 1985; Brown 1989; Huisman and Weissing 1999; Anderies and Beisner 2000; Richards et al. 2000; Wilson and Richards 2000; review in Chesson 2000), and the evolutionary dynamics of coexisting species have been well studied in the context of ecological character displacement (e.g., MacArthur and Levins 1967; May and MacArthur 1972; Roughgarden 1972; Slatkin 1980; Case 1981; Taper and Case 1985, 1992a, 1992b; Drossel and McKane 1999, 2000; Abrams and Chen 2002). On the other hand, we do not know whether natural selection with ecological feedback will restrict or broaden conditions for species coexistence.

Questions concerning species coexistence have been related to specialization in resource utilization (e.g., Kotler and Brown 1988; Wilson and Yoshimura 1994; McPeck 1996; Morris 1996). Wilson and Yoshimura (1994) studied the ecological coexistence of one generalist and two specialists on two resources. They concluded that such coexistence is likely, assuming some degree of optimal foraging and environmental variability. However, evo-

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lutionary change in the strategies of specialists and generalists was not considered, leaving open the question of whether such coexistence may occur or persist at an evolutionary timescale. Specifically, evolution may restrict conditions for coexistence of specialists and generalists for two reasons. First, the coexistence of two specialists and a generalist may not be evolutionarily stable, implying that evolution would change their degree of specialization, which may even lead to extinction of one or more species. Second, such coexistence may not be evolutionarily attainable, implying that the trimorphic state cannot be reached through gradual evolution. To what extent these factors restrict species coexistence is the topic of this article.

Model Description

This section extends the model by Wilson and Yoshimura (1994) and explains how to analyze the evolutionary attainability and stability of community states involving both generalists and specialists.

Population Dynamics

We consider the population dynamics of up to three species in two habitats, described by the following discrete-time Ricker equations,

$$N_{i,t+1} = \sum_{j=1}^2 N_{ij,t} \exp \left[r \left(1 - \frac{N_{1j,t} + N_{2j,t} + N_{3j,t}}{e_{ij} K_j} \right) \right]. \quad (1)$$

Here, the basic reproduction ratios of populations in each habitat are described by an exponential function, where r is the intrinsic growth rate (assumed to be equal for all species), $N_{ij,t}$ is the abundance of species i in habitat j at time t , K_j is the carrying capacity of a species in habitat j when maximally specialized on that habitat, and e_{ij} is the level of specialization, or relative efficiency, of species i in habitat j . Throughout this article, we focus on symmetric habitats, $K_1 = K_2$.

Temporal variability among generations is introduced by randomly varying the values of K_1 and K_2 symmetrically around their mean, according to a uniform distribution. The relative variation v_j for habitat j is defined by $(K_{j,\max} - K_{j,\min})/K_j$. Both carrying capacities are varied independently among generations.

Foraging Rules

Complementing the dynamics described by equation (1), at the start of each generation, individuals are redistributed over the two habitats on the basis of their ideal free dis-

tribution (IFD; Fretwell and Lucas 1970). For the three species studied here, the IFD cannot be obtained analytically and thus has to be derived numerically. Departures from the IFD, which itself is biologically unrealistic, are considered as follows. Wilson and Yoshimura (1994) distributed a fraction g according to the IFD, while the remaining fraction $1 - g$ was distributed randomly, that is, with a probability $K_i/(K_1 + K_2)$ of entering habitat i . The fraction g allowed for the distribution of a consumer population over the two habitats to be continuously varied between fully optimal ($g = 1$) and completely random ($g = 0$). This rule, however, results in discontinuous foraging behavior; the proportion of foragers in a habitat exhibits large jumps even if efficiencies are being varied only gradually. To avoid such unrealistic foraging behavior, we consider an alternative continuous foraging rule, assuming that foragers necessarily make some foraging errors relative to the IFD. In reality, such errors will be more pronounced when the foragers experience a smaller fitness difference $f_2 - f_1$ between the two habitats. According to this rule, the probability p_1 of using habitat 1 is

$$p_1 = \frac{1}{1 + \exp [a(f_2 - f_1)]}, \quad (2)$$

where the parameter a determines the foraging accuracy. By varying a in the range $[0, +\infty)$, we can vary the distribution of consumers from random to IFD (fig. 1a). When there is no fitness difference, foragers are randomly distributed over the two habitats. For $a > 0$, an increasing fitness difference results in an increasing proportion of foragers entering the habitat to which they are best adapted.

Trade-off Structure

Specialization on one habitat is assumed to go at the expense of specialization on another. Extreme specialists have efficiency 1 in one habitat and efficiency 0 in the other habitat, whereas generalists have intermediate efficiencies in both habitats. The trade-off constraining the levels of specialization on the two habitats is given by

$$(e_{i1})^{1/s} + (e_{i2})^{1/s} = 1. \quad (3)$$

The strength of the trade-off is determined by the parameter s (fig. 1b); the trade-off is called weak when $s < 1$ (convex relation between e_{i1} and e_{i2}) and strong when $s > 1$ (concave relation between e_{i1} and e_{i2}).

In addition to varying the trade-off's strength, different impacts of the trade-off can be considered. Individual-based derivations of the (population-level) Ricker model show how r and K depend on more mechanistic param-

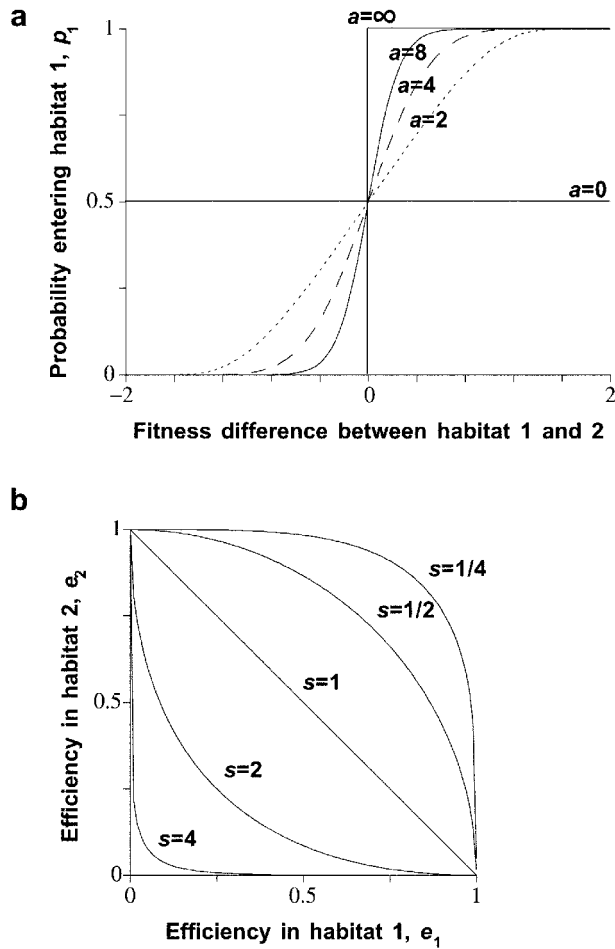


Figure 1: Functions used for specifying foraging behavior and trade-offs. *a*, Continuous foraging rule (eq. [2]) for various values of foraging accuracy *a*. The case *a* = 0 corresponds to random foraging. *b*, Trade-off function (eq. [3]) for different values of the trade-off strength *s*. Trade-offs are called strong for *s* > 1 and weak for *s* < 1.

eters. All these derivations agree in three conclusions: *r* and *K* are not independent, *r* and *K* are linearly related, and *K* depends on mechanistic parameters not affecting *r* (Royama 1992; Dieckmann and Law 2000; Van Dooren 2000; Sumpter and Broomhead 2001). Two examples are $r = \ln \{ \rho / [1 - (1/n)] \}$, $K = \ln \{ \rho / [1 - (1/n)] \} / \{ - \ln [1 - (1/n)] \}$, where ρ is the density-independent per capita reproduction and *n* is the population's maximal size (Sumpter and Broomhead 2001), and $r = \gamma$, $K = \gamma / s(1 - k)$, where γ is again density-independent per capita reproduction, *s* is the neighborhood area of one individual, and *k* measures competition intensity (Royama 1992).

These dependences of the population-level parameters *r* and *K* on individual-based traits have implications for the trade-off structures considered in our model. When

individual traits determining density-independent reproduction (i.e., ρ or γ) in the two habitats trade off, this results—at the population level—in a trade-off affecting both *r* and *K* equally. A trade-off in *K* alone (i.e., a trade-off between *K*₁ and *K*₂ for habitats 1 and 2, respectively) is also possible because *K* depends on parameters that do not affect *r*. This trade-off structure occurs when individual traits that determine the maximum population size in the two habitats trade off (see eq. [1]). By contrast, assuming a trade-off in *r* alone (i.e., a trade-off between *r*₁ and *r*₂ for habitats 1 and 2, respectively) is impossible because any parameter affecting *r* will likewise affect *K*.

Thus, we analyze two alternative trade-off structures: a trade-off in *K* as described by equation (1) and a trade-off in both *K* and *r* as described in the following equation,

$$N_{i,t+1} = \sum_{j=1}^2 N_{ij,t} \exp \left[r \left(e_{ij} - \frac{N_{1j,t} + N_{2j,t} + N_{3j,t}}{K_j} \right) \right]. \tag{4}$$

Notice that in equation (4), both *r* and *K*_{*j*} are multiplied with *e*_{*ij*}, whereas in equation (1), this multiplication is applied to *K*_{*j*} only.

Evolutionary Analysis

For the evolutionary analysis, we use the framework of adaptive dynamics (Dieckmann and Law 1996; Metz et al. 1996; Dieckmann 1997; Geritz et al. 1998). One of the advantages of this approach is that it provides tools for analyzing conditions for the buildup of polymorphisms through gradual evolution.

Such buildup is related to processes of evolutionary branching, through which a population under frequency-dependent selection evolves toward a fitness minimum. Under the resulting regime of disruptive selection, phenotypically similar species straddling the fitness minimum, when they occur, are predicted to diverge. Applying such analysis of frequency-dependent selection regimes sequentially yields the conditions for evolutionarily attainable coexistence. In a population with only a single species, evolution may initially converge on the generalist strategy (fig. 2*a*) even though this strategy may not be evolutionarily stable under all conditions. If evolutionary branching can occur in that situation, two very similar generalist species will be able to coexist around the branching point; these generalists will gradually diverge by specializing on one of the two habitats (fig. 2*b*). Subsequently, these two species may end up at an evolutionary attractor that allows for secondary evolutionary branching, potentially resulting in two extreme specialists and two more generalist species (fig. 2*c*). The two generalist species may then converge

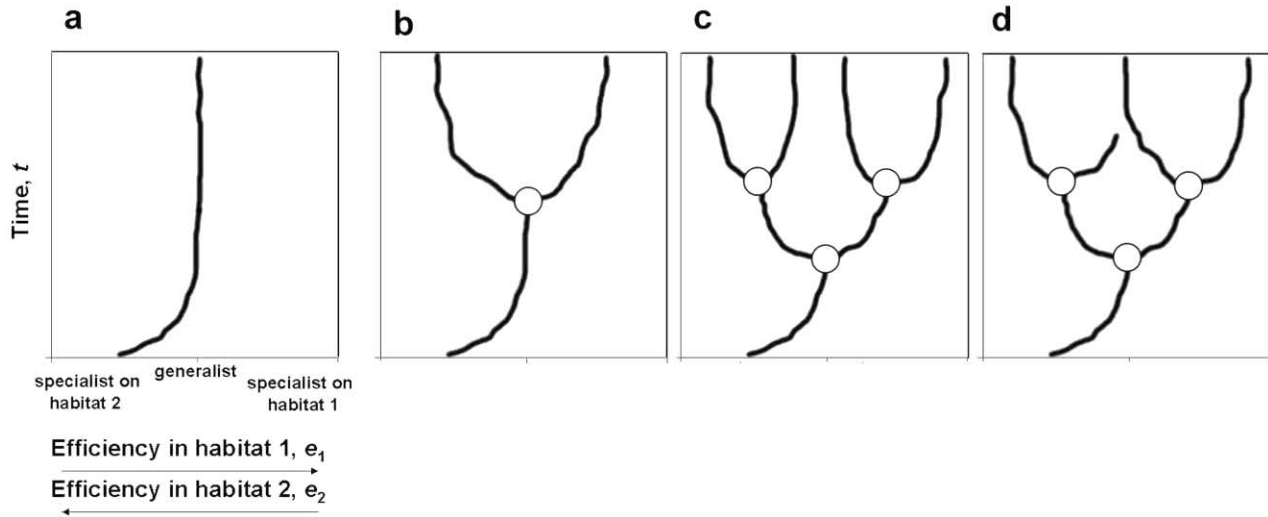


Figure 2: Sketch of the potential pathway by which coexistence of two specialists and one generalist species may be established through gradual evolution. *a*, Evolution converges to the generalist strategy. *b*, Primary evolutionary branching may allow for the coexistence of two similar generalist species that subsequently diverge. The white circle atop the branching point indicates that we explicitly do not deal with the detailed genetic processes through which the two species might emerge. Secondary evolutionary branching may produce four species, all of which may coexist (*c*) or two of which may converge to the generalist strategy whereby one becomes extinct (*d*). Our results ascertain the specific ecological settings for which outcomes *a*, *b*, and *d* occur in our model, whereas option *c*, coexistence of four species, is shown to occur in our model only as a transient phenomenon.

toward each other to the extent that one of them may become extinct, leaving the other generalist in a state of evolutionarily stable coexistence with the two specialist species (fig. 2*d*). Whereas evolutionary branching points will lead to the adaptive radiation of asexual morphs, the evolutionary processes that allow sexual species to differentiate have been investigated elsewhere (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000, 2003; Geritz and Kisdi 2000; Matessi et al. 2001). Such extension to sexual species is beyond the scope of this article.

Complementing the analysis of evolutionary attainability, we analyze the evolutionary stability of specialist-generalist coexistence in two steps: first, we delineate the conditions required for the generalist to invade a community of two extreme specialists (e.g., through immigration), and second, we check whether the ensuing gradual evolutionary change results in the extinction of one or more of the three species.

The evolutionary analyses are based on evaluating the invasion fitness of rare phenotypes, defined as their long-term per capita growth rate in a population dominated by a given resident strategy (Metz et al. 1992). In this way, the residents determine the environment in which the rare phenotype under consideration either succeeds or fails. If the rare phenotype can grow in the resident population, its invasion fitness is positive, whereas mutants that are deleterious in the resident's environment have negative

invasion fitness. To calculate invasion fitness in this model, we numerically analyze the population dynamics of rare phenotypes; after sampling for 50,000 generations, a rare phenotype's invasion fitness is calculated as the logarithm of the geometric average of its reproduction ratio over all generations.

We use pairwise invasibility plots (PIPs) to show the sign structure of invasion fitness for different combinations of common and rare phenotypes (Matsuda 1985; Van Tienderen and de Jong 1986; Geritz et al. 1998; see also fig. 3 for examples). In such plots, each point represents a combination (pair) of considered rare and common trait values (commonly called mutant and resident trait values, respectively) and gives the sign of the rare phenotype's invasion fitness. Hence, a PIP shows areas of positive and negative invasion fitness. Along the plot's main diagonal (where the two considered trait values equal each other), invasion fitness is necessarily zero; usually, there is at least one other contour line of zero invasion fitness. Where this line intersects the main diagonal, an evolutionarily singular point is located, corresponding to an equilibrium of the considered evolutionary dynamics. Whether gradual evolution leads toward such a point or away from it is easily determined from the PIP (Geritz et al. 1998); for instance, if we start left of the singular point and invasion fitness above the diagonal is positive, phenotypes with a value closer to that of the singular point can invade and replace

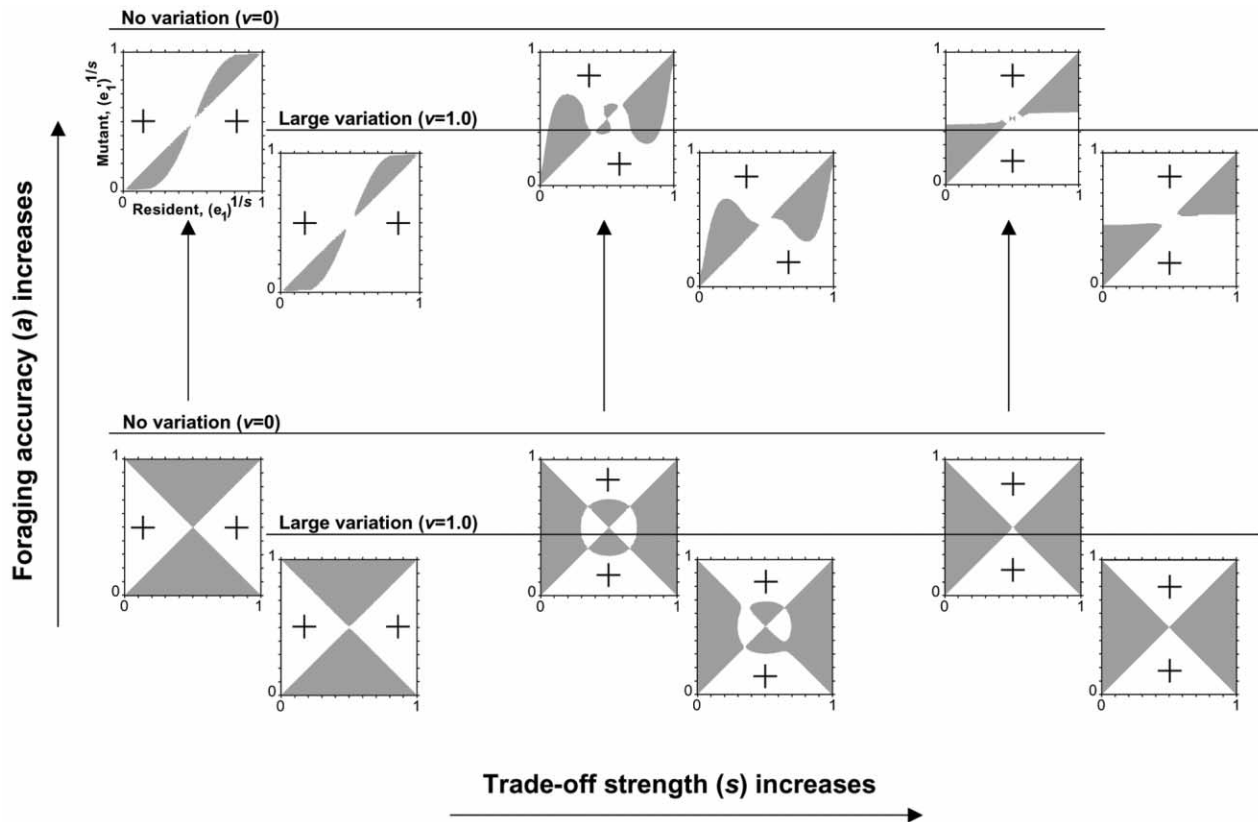


Figure 3: Representative gallery of pairwise invasibility plots for the case when the trade-off acts on K only. The effects of varying trade-off strength s (horizontal), foraging accuracy a (vertical), and temporal variability ν (stacked) thus become visible. White areas indicate positive invasion fitness; gray areas indicate negative invasion fitness. Other parameters are as follows: $r = 1.3$ and $K_1 = K_2 = 100$.

the resident phenotype. Also, the evolutionary stability of singular points is readily established from the PIP (Geritz et al. 1998) by checking whether the vertical line through the singular point lies within an area of negative invasion fitness (no phenotypes can invade the singular one) or positive invasion fitness (phenotypes on both sides can invade a resident population with the singular phenotype). In the latter case, the singular phenotype is an evolutionary branching point; phenotypes narrowly straddling this point can then invade each other, allowing them to coexist (Geritz et al. 1998).

Coexistence in the Absence of Evolution

In this section, we analyze the potential for coexistence of specialists and generalists on an ecological timescale on the basis of the continuous foraging rule and considering the two alternative trade-off structures. That is, we chart the parameter ranges for foraging accuracy a and trade-off strength s in which the extreme specialists can invade a population of generalists and, vice versa, the generalist

can invade the community of two extreme specialists. The overlap between these two ranges characterizes the conditions for the ecological coexistence of specialists and generalists in a protected polymorphism.

It turns out that the potential for ecological coexistence strongly depends on the assumed trade-off structure. With the trade-off in K only, such coexistence is possible under a wide range of conditions (fig. 4a). The extreme specialists are always able to invade a population of generalists, and, at least under weak trade-offs, the generalist can also invade the community of specialists, provided the temporal variability in the environment is sufficiently high ($\nu_1 = \nu_2 \geq 0.2$). In contrast, with the trade-off in both K and r , the potential for coexistence is much more restricted (fig. 4b). Specifically, there are many settings (roughly, whenever foraging accuracy is below 1) in which the specialists cannot invade a population of generalists.

The reason for this difference lies in the way trade-offs involving carrying capacities and growth rates translate into trade-offs in fitness. With the trade-off in K only, fitness approaches negative infinity for an extreme spe-

cialist in the habitat to which it is not adapted because a carrying capacity approaching zero means instant death. Accordingly, K appears in the denominator of fitness (see appendix). Hence, for any degree of foraging accuracy, an extreme specialist will always choose to live in the habitat to which it is adapted. Because the generalist has a lower carrying capacity for that habitat, the invading extreme specialist will always attain a positive growth rate. With the trade-off in both K and r (i.e., between reproduction ratios in the two habitats), fitness does not reduce so drastically for an extreme specialist in the unfavorable habitat (see appendix). This results in a wide range of settings in which an extreme specialist cannot invade a population of generalists because (given the strength of the trade-off) the specialist cannot forage accurately enough for the habitat on which it is specialized. This large difference in coexistence between the two trade-off structures remains when we consider less extreme specialists, which never experience a fitness of negative infinity; even with an efficiency of 0.1 in one habitat (instead of 0), a specialist still has such a low fitness in that habitat that through its foraging behavior, it concentrates completely on the habitat to which it is adapted.

In their analysis, Wilson and Yoshimura (1994) considered a trade-off in K only. They found coexistence of specialists and generalists even for moderately low variation in carrying capacities, for a wide range of efficiency of the generalist (between 0.99 and 0.4 when variability is high), and for moderate departures from optimal foraging ($g \geq 0.75$, i.e., up to a quarter of the individuals distributed randomly across habitats). Our findings for a trade-off in K only (fig. 4a) agree with these earlier results. We can thus conclude that while the choice of foraging rule (discontinuous or continuous) is immaterial for the ecological coexistence of specialists and generalists, the assumed trade-off structure has a dramatic impact on the potential for ecological coexistence.

Coexistence under Gradual Evolution

In this section, we analyze the effects of temporal variability and foraging accuracy on the evolution of specialization, thus establishing how the coexistence of specialists and generalists can come about through gradual evolution. We start by examining the baseline case with random foraging and without temporal variation. Taking advantage of the resulting overview regarding the impact of the trade-off structure, we then explore the effects of nonrandom foraging and temporal variability.

The discontinuous foraging rule suggested by Wilson and Yoshimura (1994) involves an unrealistic jump in foraging behavior; phenotypes arbitrarily close to the resident phenotype are assumed to detect the diminutive differ-

entials in their relative fitness unfailingly and to select their habitat accordingly. As long as the considered phenotypes are kept sufficiently apart, this shortcoming is not critical. Gradual evolution, however, is driven by competition between similar phenotypes and thus turns out to be structurally unstable when the discontinuous foraging rule is applied (results not shown). Because biologically meaningful conclusions must never be based on structurally unstable models, we use only the continuous foraging rule for the evolutionary analyses.

Crucial Importance of Trade-off Structures for the Evolution of Specialization

As a starting point for the evolutionary analysis, we consider the baseline case without temporal variability ($\nu_1 = \nu_2 = 0$) and with random foraging ($a = 0$). Under these conditions, the model has a one-dimensional feedback loop (through total population size), which implies that evolution is optimizing (Mylius and Diekmann 1995; Meszena et al. 2001; Meszena and Metz 2004).

When the trade-off acts on K only, even the baseline case offers some surprises. For rather weak trade-offs ($s < s_1 < 1$), evolution converges to the generalist strategy (fig. 3, *bottom left*). This is just what would be expected from classical theory (e.g., Levins 1962, 1968; Lawlor and Maynard Smith 1976). However, for moderately weak or moderately strong trade-offs ($s_1 < s < s_2$), the system becomes evolutionarily tristable (fig. 3, *bottom middle*); depending on the initial phenotype, the population evolves either to full specialization on either habitat or to full generalization. When the trade-off is strengthened well beyond the linear case ($1 < s_2 < s$), the tristability disappears, giving way to the traditionally expected bistability; there is now always selection for increased specialization on the habitat to which the initial phenotype is best adapted (fig. 3, *bottom right*), which is in line with classical theory again.

This pattern is based on a pitchfork bifurcation occurring at $s = s_2$; when the trade-off strength is lowered beyond that threshold, the generalist repeller (fig. 3, *bottom right*) is replaced by a generalist attractor surrounded by two repellers (fig. 3, *bottom middle*). As s is further decreased, these new repellers move apart until they collide at $s = s_1$ with the boundaries of trait space. For trade-offs weaker than the latter threshold, only the generalist attractor remains (fig. 3, *bottom left*). (When habitats are asymmetric, $K_1 \neq K_2$, the pitchfork bifurcation at $s = s_2$ is replaced by a fold bifurcation, and the two evolutionary repellers collide with the boundaries of trait space at two different trade-off strengths, $s = s_{10}, s_{11}$.) In a further departure from classical theory, the thresholds for the strength of the trade-off at which the described transitions

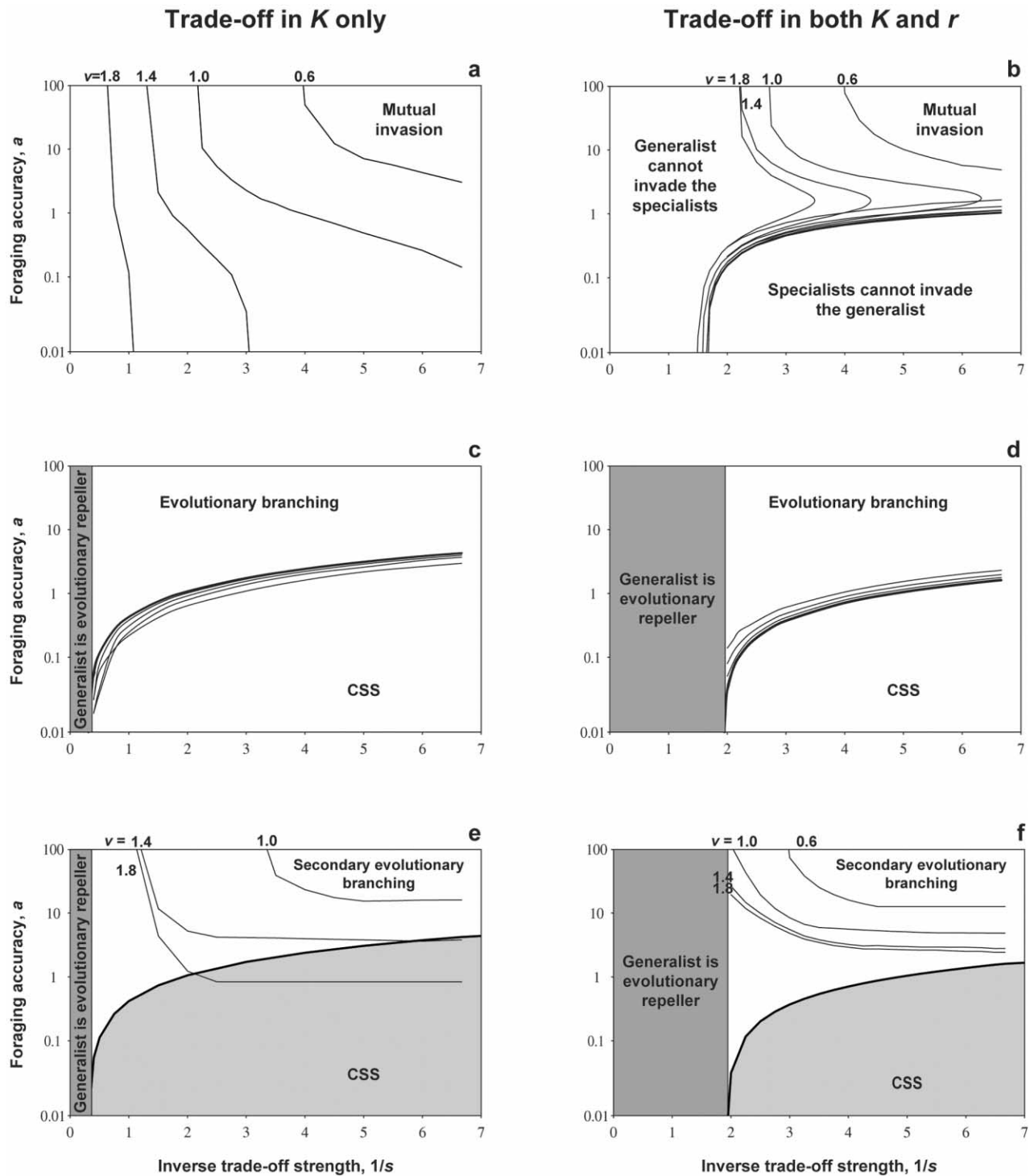


Figure 4: Conditions for ecological and evolutionary coexistence of specialists and generalists, with the trade-off in K only (left column) or in both K and r (right column). *a, b*, Critical combinations of foraging accuracy a and trade-off strength s for the generalist to invade the community of two extreme specialists and vice versa. Coexistence of specialists and generalists is possible in the mutual invisibility areas (to the right and above the curves indicating various levels of temporal variability: $\nu = 0.6, \nu = 1.0, \nu = 1.4, \nu = 1.8$). Note that the extreme specialists can always invade the generalist population in *a, c, d*, Critical combinations of foraging accuracy a and trade-off strength s to result in specialization through evolutionary branching or, alternatively, in a continuously stable generalist strategy (CSS). *c*, Thick curve, no variability ($\nu = 0$); curves below, from top to bottom,

occur depend on the value of the intrinsic growth rate r . In particular, the generalist strategy is always selected against and, hence, tristability gives way to bistability when $s > s_2 = 1/(r - 1)$ (see appendix).

When the trade-off is in both K and r , results are more similar to the classical theory in that there are only two evolutionary regimes; for this trade-off structure, we have not found any tristability. Evolution converges to the generalist when $r < [(1/s) - 1]2^s$ (see appendix). To satisfy this condition for positive r , s must be smaller than 1, $s < s_3 < 1$. Notice, however, that in contrast to classical theory, a moderately weak trade-off, $s_3 < s < 1$, will still select for full specialization. Also, the evolutionary outcome again depends on the growth rate r .

Effects of Temporal Variability and Foraging Behavior on the Evolution of Specialization

We now move to the general case, first considering foraging behavior and then temporal variability as well. The analysis follows the outline in figure 2.

Our investigations show that the only attracting singular point of single-species evolution is the generalist strategy. It is therefore only at this point that gradual evolution can transform the single-species community into a two-species community. If a resident population of generalists cannot be invaded by nearby strategies, the generalist strategy is continuously stable (a CSS; Eshel 1983; see fig. 3, *bottom left*); if, instead, such invasion is possible, the generalist strategy is an evolutionary branching point (an EBP; see fig. 3, *top row*). Investigating the evolutionary stability of the generalist strategy with foraging behavior but without temporal variability, we find that for both trade-off structures, the generalist strategy changes from a CSS to an EBP when foraging accuracy is increased beyond a threshold (fig. 4c, 4d; note that each point in these panels corresponds to a PIP as shown in fig. 3). When the trade-off acts only on K , there is—for each value of the intrinsic growth rate r —a linear relationship between the foraging accuracy and the strength of the trade-off for which the CSS-EBP transition takes place (see appendix). Also, when the trade-off acts on both K and r , such a relationship exists, but for this trade-off structure, the relation is non-linear (see appendix).

Our numerical results show that the boundary of gen-

eralist evolutionary stability is only slightly affected by considering different levels of temporal variability in the carrying capacities ($\nu_1 = \nu_2$ ranging from 0.2 to 1.8). Therefore, up to this stage in the analysis, temporal variability hardly affects the evolutionary outcome (see, e.g., fig. 3). However, again there is a remarkable difference between the two trade-off structures (fig. 4c, 4d). When the trade-off is in both K and r , higher temporal variability slightly increases the critical foraging accuracy (fig. 4d). This is what we expected on the basis of the traditional notion that higher variability favors the generalist. By contrast, with the trade-off in K only, the reverse is true; higher temporal variability causes the generalist's evolutionary stability to be lost already at a lower foraging accuracy (fig. 4c).

For the parameter values that allow for evolutionary branching in a single-species community, we numerically analyzed gradual evolution in the resulting two-species community. For the resulting evolutionary attractors, we again assessed whether evolutionary branching can occur. Such secondary evolutionary branching could transform the two-species community into a four-species community (fig. 2c, 2d). In absence of temporal variability, evolution always leads to two extreme specialists; transitions to higher degrees of polymorphism are then precluded (fig. 4e, 4f). With temporal variability, the outcome of gradual two-species evolution is also often a pair of extreme specialists. Only when temporal variability is high and foraging accuracy is very high, we find singular points of two-species evolution inside the trait space of our model; these points always are secondary branching points (fig. 4e, 4f).

For the parameter values that allow for secondary evolutionary branching, we numerically analyzed gradual evolution in the resulting four-species community. For the parameter space considered in figure 4, these four-species communities always collapsed to three-species communities involving two extreme specialists and one generalist, as sketched in figure 2d. That is to say that two of the four species evolved toward extreme specialization, and the other two species evolved toward the generalist strategy whereby one of the latter went extinct.

In summary, gradual evolution in this model can result in coexistence of specialists and generalists but only for consumers whose foraging accuracy is very high and who live in an environment affected by strong temporal vari-

$\nu = 0.2, \nu = 0.6, \nu = 1.0, \nu = 1.4, \nu = 1.8$. *d*, Thick curve, no variability ($\nu = 0$); other curves, from top to bottom, $\nu = 1.8, \nu = 1.4, \nu = 1.0, \nu = 0.6, \nu = 0.2$. *e, f*, Critical combinations of foraging accuracy a and trade-off strength s for the existence of an interior pair of specialist singular strategies that are branching points (above the curves), leading to secondary branching and hence to the coexistence of specialists and generalists through gradual evolution. The thick curves delineating the gray areas indicate, according to *c* and *d*, where primary evolutionary branching cannot happen in the absence of temporal variability. Other parameter values are as in figure 3.

ability. In this limited parameter range, even when one, or several, species accidentally becomes extinct, evolution is predicted to reconstitute the coexistence of specialists and generalists.

Coexistence under Gradual Evolution after Generalist Immigration

Finally, we investigate the evolutionary stability of ecologically stable three-species communities. Evolutionary stability of the community of specialists and generalists is already ensured in the parameter region where we predict secondary evolutionary branching. However, the region of parameter space where the generalist can invade a community of two extreme specialists is larger. It is quite possible that the generalist, after invading, is also able to coexist stably with the two extreme specialists on an evolutionary timescale. One possibility for such an invasion scenario is that a generalist phenotype is created through a mutation with large effect. However, genes of large effect leading to viable phenotypes do not commonly occur (for an exception, see de Jong et al. 2000). A more likely possibility therefore is invasion of a generalist into the two-specialist community by immigration from another geographic location.

For the parameter region where the generalist can invade a community of two extreme specialists (fig. 4*a*, 4*b*), we numerically assessed whether this invasion leads to selection on the specialists to become generalist. We find that over the entire parameter space considered, invasion of the generalist always results in stronger divergent selection on the specialists (which must remain inconsequential because the specialists are already maximally specialized). Hence, the three-species community is indeed always evolutionarily stable once created through invasion of the generalist.

We can thus conclude that after immigration, the stable coexistence of specialists and generalists can be attained under a wider range of ecological settings than with gradual evolution alone (cf. fig. 4*a*, 4*b*, 4*e*, 4*f*), and allowing for community construction through migration relaxes the conditions for stable coexistence. Note that the extra parameter region allowing for coexistence is small when the trade-off acts on both K and r (cf. fig. 4*b*, 4*f*) because ecological coexistence is already restricted in this case, but it is much larger when the trade-off acts on K only (cf. fig. 4*a*, 4*e*) because in that case, ecological coexistence is widely possible.

Discussion

In this article, we have shown that the potential for coexistence between specialists and generalists crucially de-

pends on the specific trade-off structure assumed (fig. 4). Ecological coexistence is much more feasible with the trade-off in K only than with the trade-off in K and r . However, under gradual evolution without immigration, conditions for the establishment of specialist-generalist coexistence become equally restricted. Specifically, coexistence of two specialists and one generalist is attainable only through gradual evolution if foraging accuracy is very high and if temporal variability is strong. When the generalist can invade a community of two specialists through immigration (or through a mutation of large effect), conditions for the evolutionarily stable coexistence of specialists and generalists are less restricted when the trade-off acts on K only but not when the trade-off acts on both K and r . Considerable environmental variation still remains necessary. Overall, specialist-generalist coexistence turns out to be less likely than a purely ecological analysis (Wilson and Yoshimura 1994) had previously suggested.

Limitations of Our Study

This article is based on a relatively simple model; three of the simplifications we had to make are scrutinized. First, we have not explicitly modeled the dynamics of resources determining the carrying capacities in the two considered habitats. This is not critical as long as resource dynamics occur on a shorter timescale than consumer dynamics; resources can then be assumed to be in a quasi-steady state depending on consumer abundances. Because the discrete-time population dynamics investigated here would often operate on an annual basis, within-season equilibration of resources may indeed be likely. However, including resource dynamics may sometimes result in nonequilibrium dynamics, creating internally driven temporal variability for the consumer. This could have interesting ecological and evolutionary implications.

Second, one may prefer to investigate trade-offs between ecological parameters that are more mechanistic than the intrinsic growth rates and carrying capacities considered in this study. A wide range of specific studies will then be required. Although the Ricker model can be derived from individual-based descriptions, it will often be difficult to decide on the specific trait(s) traded off between habitats. As shown by Matessi and Gatto (1984), descriptions of r and K can be derived from resource-consumer models using the quasi-steady state assumption. For example, there could be a trade-off between attack rates on one resource and the other (or between conversion efficiencies of resource biomass into consumer biomass); Matessi and Gatto (1984) show that this results in a trade-off acting on both K and r , just as described in equation (4). They also find, for various model formulations, that K is linearly related to r , again as described in equation (4).

Third, we have assumed that consumers can partially attain an ideal free distribution (limited by their foraging accuracy) without modeling the dynamics of foraging behavior in detail. If foraging behavior occurs at the same timescale as population dynamics, complex dynamics may result (Abrams 1999). However, the Ricker model assumes discrete time steps, whereas foraging behavior normally takes place on a much shorter timescale. Alternatively, consumers may use various other foraging strategies, such as fixed preference, and ideal free foragers then do not necessarily perform best (e.g., Fryxell 1997; Richards and De Roos 2001). Specialists and generalists may differ in the foraging strategy they adopt. It is at present unclear how such a suite of different foraging strategies would affect coexistence.

Challenges for Future Study

Our results have revealed surprising effects of the trade-off structure on the evolution of specialization, emphasizing two points. First, theoretical predictions based on a trade-off in fitness (e.g., Levins 1962, 1968) do not easily carry over to models (or, for that matter, experimental systems) where such a trade-off is assumed in a fitness component such as carrying capacity. Recently, Rueffler et al. (2004) have extended Levins's (1962, 1968) fitness set approach to include frequency-dependent selection, presenting a framework that can deal with all possible types of trade-offs. Their results show that the way the trade-offs enter the fitness function (i.e., which components of fitness are really traded off) crucially determines the evolutionary dynamics and predictions—including selection for specialists under a weak trade-off or selection for generalists under a strong trade-off. Second, we have shown that models (or, again, experimental systems) with trade-offs in one or several fitness components that do not linearly translate into a fitness trade-off can yield more complex predictions for the evolution of specialization than previously thought, including evolutionary tristability. Because it is generally very difficult to measure the fitness of individuals in experimental systems, evolutionary biologists usually restrict their experiments to measuring one or several components of fitness. For instance, in insect-plant biology, these are oviposition rate, juvenile mortality rate, juvenile body mass increase or rate of development (i.e., traits affecting per capita reproduction rate; see, e.g., Futuyma and Moreno 1988; Jaenike 1990) but typically never the maximum number of individuals a habitat can sustain (i.e., carrying capacity).

It is an interesting open question to assess which additional assumptions are needed to cause the loss of evolutionary robustness of three-species communities composed of two specialists and one generalist. One such

scenario is that the two specialist species are selected to become less specialized to a degree where they “squeeze out” the generalist species. We suggest that separate trade-offs for both per capita reproduction and maximum population size—and thus more complex trade-offs in r and K than we considered—might be necessary and sufficient. Such trade-offs will translate into more complex fitness gradients that might lead to a situation where invasion of a generalist species may actually result in evolution of the specialists toward generalization and the eventual extinction of the generalist. Another scenario is that the two specialist species are selected to become increasingly specialized to a degree where they are outcompeted by the generalist species. This scenario seems to be more likely because the effect of the generalist species is to dampen the variation in growth rate of the specialists (by occupying a habitat in higher numbers if it is relatively empty and the other habitat is relatively full). This dampening effect favors increased specialization in our model but does not lead to extinction. In a fully stochastic individual-based model, extinction may occur over a wider area of parameter space than in our current model (where population growth is deterministic). For instance, the generalist species may force the two specialist species to forage only in the habitat on which they are specialized. If the density of a specialist species is low and carrying capacity is low for several generations, this species may readily become extinct. When, in addition, coexistence can be restored relatively easily through the immigration of specialist and generalist species, our model predicts continuous change in both the number of species and the degree of specialization in the system over time as a result of a complex interplay of ecological and evolutionary dynamics.

Temporal variability in model systems can be internally driven (instead of externally imposed) when the dynamics consist of sustained cycles or deterministic chaos (May 1973), which can also promote coexistence (Armstrong and McGehee 1976b, 1980; Adler 1990; Huisman and Weissing 1999). In the Ricker model for one population living on a single resource, unstable population dynamics ensue for high values of the intrinsic growth rate r (cycles for $r > 2$, chaos for $r > 2.692$; May 1975). Choosing r in our model such that the generalist species would have stable population dynamics but a specialist species would undergo cycles (or maybe even show chaotic behavior) promises to yield complex evolutionary dynamics. A generalist species would then create a stable environment that may result in evolutionary branching leading to two specialized species. However, these would create an unstable environment that subsequently allows a generalist species to coexist if it is able to immigrate or arise from the odd major-effect mutation. This leads to the same questions as discussed with regard to the evolutionary robustness of

specialist-generalist coexistence. Hence, studying the evolutionary dynamics of coexistence in systems with internally driven fluctuations promises to give intriguing and potentially counterintuitive new insights.

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APPENDIX

Evolution of Specialization in the Absence of Temporal Variation

Because our model contains sums of exponential functions, analytical expressions for the singular point(s) cannot be obtained (except for the special case when the trade-off is in both r and K and foraging is random, $a = 0$). However, our numerical analysis shows that the generalist ($e_1 = e_2 = e$) always is a singular strategy. When foraging is random and temporal variation is absent, evolution is described by an optimization principle; the generalist is an evolutionary attractor (convergence stable) whenever it is at a fitness maximum (evolutionarily stable) and an evolutionary repeller whenever it is at a fitness minimum (Mesz ena et al. 2001). Our numerical analysis also shows that convergence stability is unaffected by foraging accuracy, whereas evolutionary stability changes with foraging accuracy (see fig. 3 for examples). Hence, we can assess the generalist's convergence stability under random and nonrandom foraging by determining its evolutionary stability under random foraging. To determine the generalist's evolutionary stability under random and nonrandom foraging, we calculate the sign of the second derivative of a rare strategy's invasion fitness with respect to that strategy (Geritz et al. 1998) for each of the two trade-off structures considered. Because the efficiency in habitat 2, e_2 , is traded off against the efficiency in habitat 1, e_1 , we express e_2 in terms of e_1 (given by eq. [3]) and derive all results below in terms of the adaptive trait e_1 .

Trade-off in K Only

Using equation (1), the population dynamics of the generalist are described by

$$N_{t+1} = N_t \exp \left[r \left(1 - \frac{N_t}{2eK} \right) \right].$$

Hence, the generalist equilibrium population size is $\bar{N}(e) = 2eK$.

The invasion fitness of a rare phenotype with strategy e'_1 in a generalist resident population is given by the logarithm of its growth rate in the resident population at equilibrium,

$$f(e'_1, e_1) \Big|_{e_1=e_2=e} = \ln \left\{ p'_1(e'_1, e) \exp \left[r \left(1 - \frac{\bar{N}(e)}{2e'_1K} \right) \right] + [1 - p'_1(e'_1, e)] \exp \left[r \left(1 - \frac{\bar{N}(e)}{2e'_2(e'_1)K} \right) \right] \right\},$$

with $p'_1(e'_1, e)$ denoting, analogous to equation (2), the probability of the rare phenotype with strategy e'_1 to enter habitat 1 when the generalist is resident,

$$p'_1(e'_1, e) = \frac{1}{1 + \exp \{ ar[(e/e'_1) - (e/e'_2)(e'_1)] \}}.$$

The second derivative of the invasion fitness with respect to e'_1 , evaluated at $e'_1 = e_1 = e$, is

$$\begin{aligned} \frac{\partial^2}{\partial e_1^2} f(e'_1, e_1) \Big|_{e'_1=e_1=e} &= \frac{r^2}{e^2} - \frac{2r}{e^2} + 2 \frac{r}{e} \frac{\partial}{\partial e'_1} p'_1(e'_1, e) \Big|_{e'_1=e} \\ &\quad + \frac{1}{2} \frac{d^2 e_2(e_1)}{d e_1^2} \Big|_{e_1=e} \\ &= 2^{2s} r \left[r + ar - 1 - \left(\frac{1}{s} \right) \right]. \end{aligned}$$

Thus, the generalist is situated at a fitness maximum if

$$a < \frac{1}{r} \left[\left(\frac{1}{s} \right) + 1 - r \right].$$

Under this condition, gradual evolution ends at the generalist evolutionary attractor. Otherwise, evolutionary

branching at the generalist attractor can produce two specialist populations.

We thus see that the generalist strategy is at a fitness maximum under random foraging ($a = 0$) if $s < 1/(r - 1)$; this condition also determines when the generalist is an evolutionary attractor under nonrandom foraging ($a > 0$).

Trade-off in Both K and r

Following the same line of reasoning but now using equation (4), the population dynamics of the generalist are described by

$$N_{t+1} = N_t \exp \left[r \left(e - \frac{N_t}{2K} \right) \right]$$

Hence, the generalist equilibrium population size again is $\bar{N}(e) = 2eK$.

The invasion fitness of a rare phenotype with strategy e'_1 in a resident population with the generalist strategy ($e_1 = e_2 = e$) is

$$f(e'_1, e_1) |_{e_1=e_2=e} = \ln \left\{ p'_1(e'_1, e) \exp \left[r \left(e'_1 - \frac{\bar{N}(e)}{2K} \right) \right] + [1 - p'_1(e'_1, e)] \exp \left[r \left(e'_2(e'_1) - \frac{\bar{N}(e)}{2K} \right) \right] \right\}$$

with $p'_1(e'_1, e)$ again denoting the probability of the rare phenotype with strategy e'_1 to enter habitat 1 when the generalist is resident,

$$p'_1(e'_1, e) = \frac{1}{1 + \exp \{ ar[e'_2(e'_1) - e'_1] \}}$$

The second derivative of invasion fitness with respect to e'_1 , evaluated at $e'_1 = e_1 = e$, is

$$\begin{aligned} \frac{\partial^2}{\partial e'^2_1} f(e'_1, e_1) \Big|_{e'_1=e_1=e} &= r^2 + 4r \frac{\partial}{\partial e'_1} p'_1(e'_1, e) \Big|_{e'_1=e} \\ &\quad + \frac{1}{2} r \frac{d^2 e_2(e_1)}{de^2_1} \Big|_{e_1=e} \\ &= r \left[r + 2ar - \left(\frac{1}{s} - 1 \right) 2^s \right]. \end{aligned}$$

Thus, the generalist is situated at a fitness maximum if

$$a < \frac{[(1/s) - 1]2^s - r}{2r}.$$

This means that the generalist strategy is at a fitness maximum under random foraging ($a = 0$) and thus serves as an evolutionary attractor under nonrandom foraging ($a > 0$) if $r < [(1/s) - 1]2^s$.

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