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Foraging games and species diversity

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We analyze a game theory model in which individuals foraging on a habitat continuum choose behaviors that are the “best responses” to the behaviors and densities of competitors. These behaviors determine community invasibility and coexistence. By making fitness an explicit function of maintenance metabolic cost, we can show that changes in maintenance cost have an indirect but important effect on the best response behaviors, and hence, on community dynamics. In particular, decreasing maintenance cost has the effect of decreasing habitat resource levels by increasing the efficiency with which individuals convert resources into offspring. The resulting decrease in habitat resource levels increases each phenotype’s relative foraging advantage in whatever habitat(s) it holds an absolute advantage. As a result, more phenotypes can successfully invade the community. Indeed, low enough maintenance costs results in species inhabiting evolutionary minima in the adaptive landscape, which promotes disruptive selection and provides the potential for an evolutionary bifurcation.

Introduction

Density-dependent habitat selection influences community structure through the interplay of habitat heterogeneity, competition, and behavior (Rosenzweig 1987, Werner 1992, Fryxell & Lundberg 1998). Habitat heterogeneity provides a basis for species coexistence if there exists a trade-off among species in their abilities to exploit different habitats (Kotler & Brown 1988). Competition influences fitness consequences of using different habitats (Fretwell & Lucas 1970). And behavior allows individuals to respond adaptively to the fitness differentials among habitats (Abramsky *et al*. 1990). Because the adaptive behavior of an individual depends on the behavior and densities of its competitors, density-dependent habitat selection follows the logic of an evolutionary game (Maynard Smith 1982, Brown 1998).

The evolutionary game of habitat selection can also be used to study how behavior influences the coevolution and diversification of physical phenotypes in evolutionary time (Brown 1990, 1996, Fryxell 1997). We can ask, for example, whether habitat heterogeneity limits the number of species in an ESS. If habitat variety is finite and discrete, then the number of species may be limited in evolutionary time by the number of habitats. But if habitat heterogeneity is continuous and infinite, it is hard to see how diversity could be limited in evolutionary time, since a habitat continuum would appear to be infinitely subdivisible (Tilman & Pacala 1993, Rosenzweig & Abramsky 1993). But using an ESS approach, Mitchell (2000) showed that habitat selectors subject to maintenance and travel costs cannot infinitely subdivide a habitat continuum. Instead, the community evolves to an evolutionarily stable state that comprises a finite diversity. Furthermore, an increase in either the travel or maintenance cost results in reduced diversity. And, as travel cost or maintenance cost becomes smaller, not only does diversity increase, but species may evolve to stable minima in the adaptive landscape. From this minimum, a species will not change by directional selection, but it is subject to disruptive selection and possible sympatric speciation (Geritz *et al.* 1998).

The major goal of the analysis in Mitchell (2000) was to demonstrate that diversity is finite when travel costs and maintenance costs are nonzero. While the analysis also showed how diversity varies with maintenance and travel cost, there was not space in that work to explore in depth the causal links tying maintenance cost to changes in population densities, resource levels, behavior, fitness and diversity. We examine these links here to show how lower maintenance cost allows each species greater relative advantage over competitors in its favored habitats. By increasing each species' advantage in its favored habitat, lower maintenance cost allows species to more finely subdivide the habitat continuum.

Linking species diversity in an ESS community to maintenance cost allows us to make testable predictions since maintenance cost likely depends on measurable climatic variables such as temperature (Porter *et al.* 1994). Warmer climates should result in lower maintenance cost due to less need for thermoregulation (Porter *et al.* 1994). Thus, the model provides a mechanistic basis for increased diversity in warmer climates (Currie 1991, Wright *et al.* 1993).

Model

Before describing the model in detail, we give a brief overview of it. In our model of habitat selection, we use the familiar paradigm of foragers that encounter habitats at random, and then choose the amount of time they devote to foraging each habitat (Rosenzweig 1987, Brown 1990, Mitchell 2000). The adaptive choice of foraging time depends on the combination of resource levels and foraging costs, both of which may vary among habitats. The sum of foraging in all available habitats is an individual's total foraging profit. Individuals must use their total foraging profit to pay off their maintenance metabolic costs. Any remaining energy can be put towards reproduction. We assume that in a population of foragers at equilibrium the per capita total foraging profit equals the maintenance metabolic cost plus replacement cost, where replacement is defined as the energy cost of producing an individual in the next generation.

We want to model the foraging environment as a continuum of habitat types, so we denote habitat type by the continuous variable, $z \in (z_{\min}, z_{\max})$. Individual foragers pay a habitat specific foraging cost, defined as the additional energy expended in the act of foraging beyond what would be spent anyway in maintenance metabolism. An energy foraging cost may result from activities such as locomotion, digging and climbing in search of food (Brown 1988). Although we treat only an energy foraging cost here, the basic results of our model do not change if foragers are instead subject to additional predation risk (W. A. Mitchell unpubl.).

In general, the foraging cost paid by an individual depends not only on the habitat in which it forages but also on its phenotype. We assume that a trade-off among different phenotypes in their abilities to exploit different habitats prevents the evolution of a "jack-of-all-trades" capable of outcompeting all other phenotypes across the range of habitats. A variety of such trade-off functions are feasible and realistic. Mitchell (2000) analyzed a trade-off function that yielded a "shared preference" community organization. In shared preference communities all species rank habitats similarly, but differ in their tolerance of poorer quality habitats (Rosenzweig 1987). Here, we use a trade-off function that generates a "distinct preference" organization (Rosenzweig 1987). In this type of community, different species rank habitats differently. To model a distinct preference community we let the foraging cost of a phenotype u in a habitat z be defined by the quadratic function:

$$\mathrm{Cost}(u,z) = c_0 + c_1(u - z)^2 \qquad (1)$$

The constant, c_0, represents "base" foraging cost, while c_1 is the coefficient of the quadratic penalty of deviating from the phenotype best suited for the habitat. Hence, for each phenotype there is a best habitat, and for each habitat there is a feasible phenotype that is best for that habitat. And, different phenotypes pay their respective lowest costs in different habitats (Fig. 1).

The regulation and importance of habitat resource levels

We assume that a forager experiences diminishing returns in a patch due to resource depletion. Letting $R_0(z)$ be the initial resource level encountered by a forager upon entering the patch, and a be a parameter that converts resource level to the resource encounter rate, then, the amount of resources remaining after $t_f(z)$ time spent foraging is,

$$R(z, t_f(z)) = R_0(z)\exp(-at_f(z)) \qquad (2)$$

After a forager leaves a patch the resources build up due to renewal. The next forager that encounters the patch will encounter the renewed level of resources. This renewed level depends on the resource level left by the previous forager, the rate of renewal, and the time over which renewal has occurred. For simplicity, we assume that the rate of resource renewal is constant. So, the expected resource level encountered by a forager in a patch of habitat z is,

$$R_0(z) = (\text{Expected resources left by previous forager}) + (\text{renewal rate})(\text{Expected renewal time}) \qquad (3)$$

Because Eq. 3 gives the resource level that will be encountered by the next forager we use the zero subscript for R.

According to Eq. 3, factors that decrease expected renewal time decrease $R_0(z)$. We assume that expected renewal time decreases as a function of forager densities, because more foragers mean a higher frequency of patch visits. So, higher forager densities should translate into lower patch resource levels. Consequently, factors that reduce forager densities will concomitantly increase resource levels (at least in those habitats the foragers exploit). This is not surprising, but it is important for our model, because we consider the role of maintenance cost, and decreasing maintenance cost will tend to increase forager density, resulting in decreased resource levels. As we will show below, reduced resource levels change foraging behavior in a manner makes species invasion and coexistence more likely.

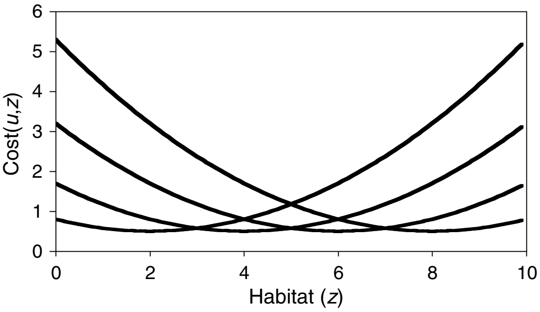

Fig. 1. Foraging cost as a function of habitat and phenotype. There exists a continuum of habitat types, as well as a corresponding continuum of feasible phenotypes. Each phenotype possesses a cost curve in which cost is lowest in the habitat index equal to the phenotype. So, the four foraging cost curves shown here are for the phenotypes u = 2, 4, 6, 8. These are only four curves from the continuum of possible phenotypes.

Calculating the energy profit and fitness

We let foraging time in a patch be modeled as a behavioral ESS. In order to determine the ESS we describe functions that relate energy profit to foraging time, and then show how the foraging ESS changes with resource level.

If we let v be the unit value of the resource, and Eq. 2 represent patch depletion by a forager, then the energy harvested from the habitat after $t_f(z)$ time spent foraging is:

$$\text{Energy consumed in habitat } z = vR_0(z)[1 - \exp(-at_f(z)))] \qquad (4)$$

Recalling the cost function from Eq. 1, we represent the total cost of harvesting this energy as

$$\text{Total cost of exploiting habitat } z = t_f(z)\text{Cost}(u,z) \qquad (5)$$

The difference between Eq. 4 and Eq. 5 is the profit from a patch of habitat z. To find the total profit from foraging at the end of the day, we integrate the energy profit over all habitats, z. Letting $f(z)$ be the probability density function for habitats, and 'npatches' be the number of habitat patches encountered per day, the total foraging profit for a day is,

$$\text{Profit} = (\text{npatches}) \times \int_{z_{\min}}^{z_{\max}} \left\{vR_0(z)\left(1 - e^{-at_f}\right) - \text{Cost}(u,z)t_f(z)\right\} \times f(z)dz \qquad (6)$$

For simplicity we let $f(z)$ represent a uniform distribution, meaning that all habitat types are equally abundant.

We use Eq. 6 for the total foraging profit in a simple fitness function:

$$\text{Fitness} = b \times (\text{Profit} - \text{MC}) \times \text{ndays} \qquad (7a)$$

Here, b is the conversion rate of energy into offspring, 'Profit' is from Eq. 6, MC is the daily maintenance cost, and 'ndays' is the number of days per generation. We define maintenance cost as the unavoidable daily metabolic expenditure that is not attributable to the activity of foraging. When we analyze the model, we allow MC to represent the effect of the climate on the organisms, under the assumption that cooler climates result in increased MC.

For a population at ecological equilibrium Fitness equals 1. At equilibrium individuals are harvesting just enough energy profit to cover their maintenance and replacement costs. We determine this Profit level by setting Fitness equal to 1 and rearranging Eq. 7a.

$$\text{Profit}_{\text{eq}} = \text{MC} + 1/(\text{ndays} \times b) \qquad (7b)$$

Eq. 7b 'Profit' must equal the maintenance plus a term that represents the energy cost of replacement which accounts for the conversion of energy to offspring.

Characterizing the behavioral ESS

The behavioral ESS is a set of foraging times, $t_f^*(z)(\forall z \in (z_{\min}, z_{\max}))$, that will maximize fitness given the distribution of resource levels, $R_0(z)$, generated by the foraging of competitors. This amounts to finding the fitness maximizing value of $t_f(z)$ as a function of $R_0(z)$ for each z. Hence, the behavioral ESS, $t_f^*(z)$ will satisfy,

$$\frac{\partial \text{Fitness}(R_0(z))}{\partial t_f(z)} = 0 \qquad (8)$$

where Eq. 8 is evaluated at $t_f(z) = t_f^*(z)$, for all habitats z. In Eq. 7a for Fitness, only the Profit term is a function of foraging time, $t_f(z)$. So, the best response foraging time is the one that maximizes Eq. 6 subject to the distribution of resource levels, $R_0(z)$, generated by the foraging of all individuals. Inspection of Eq. 6 reveals that the partial derivative of Profit with respect to the foraging time in one habitat is independent of foraging times in other habitats. This is because our model allows a variable amount of foraging time within a day, and so the sum of foraging time is not forced to equal a constant. Hence time spent in one habitat does not effectively reduce time spent in other habitats. This assumption is not necessary to the results (*see* Mitchell 2000 for a case with an explicit missed opportunity cost), but it does simplify the analysis and it may represent reality for many foragers (e.g., Mitchell *et al.* 1990). In this case, the best response behavior in habitat z is the foraging time that maximizes foraging profit from habitat z, given the encountered resource level that is determined by the foraging of competitors. This is simply the $t_f(z)$ that maximizes the difference between the total energy gain Eq. 4 and total foraging cost Eq. 5 of using habitat z. For the functions described in Eq. 4 and Eq. 5, the best response, $t_f^*(z)$, satisfies the equation,

$$R_0(z)\exp(-at_f^*(z)) = \mathrm{Cost}(u,z)/av \qquad (9)$$

The term on the left-hand side of Eq. 9 is the "quitting" resource level to which the forager depletes the habitat z (Brown 1988). The right hand side shows that this quitting level is proportional the foraging cost in the habitat. For the model discussed here, the foraging time in one habitat is independent of time foraging in other habitats. This is not true of more complicated fitness functions involving predation risk in which foraging cost is a function of overall energy state (W. A. Mitchell unpubl.).

When there is only one phenotype, u, then $t_f^*(z)$ will be the best response of that phenotype to itself. If a rare phenotype invades the community, then the invader will pick a best response foraging time to the resource level generated by the residents. But the invader's behavioral ESS will differ from the resident's because it pays a different activity cost.

Community invasibility and maintenance cost

An adaptive landscape provides a visual representation of the fitnesses of resident phenotypes, as well as non-residents that would attempt to invade the community. We constructed adaptive landscapes to show how community invasibility depends on maintenance cost.

We first introduced a resident phenotype, u, and then solved for its equilibrium density and behavioral ESS. The resident's density and behavior generated a distribution of resource levels across habitats. Next we solved for the ESS behaviors and fitnesses for all nonresidents, given the resource levels generated by the resident. This tells us which nonresidents could successfully invade. If the nonresident's fitness is larger than 1 then it can increase in numbers and invade. Conversely, the nonresident cannot invade if its fitness is less than 1.

In our analysis, the functions linking phenotypes, behaviors and fitness were complicated, so we solved for the resident's equilibrium density by numerical methods using a root-solving algorithm. Because we were analyzing a foraging game, each iteration of the routine had to include a subroutine that determined the behavioral ESS. The behavioral ESS had to be determined anew for each iteration because it depended on $R_0(z)$ which changed with each new iteration's population density. Below, we outline the procedures for finding the resident's density and the nonresident's fitness.

Finding the resident's equilibrium density:

1. Start with a candidate for the equilibrium density.
2. Find the behavioral ESS for each habitat:
   a. Use Eq. 9 to find the quitting resource level.
   b. Use the quitting resource level and the candidate density to calculate $R_0(z)$ according to Eq. 3.
   c. Go back to Eq. 9 and substitute the value of $R_0(z)$ obtained in step b to find $t_f(z)$.
3. Calculate Profit and Fitness using Eqs. 6 and 7.
4. If fitness is sufficiently close to the equilibrium value of 1, then we are done; the candidate density is the resident's equilibrium density. Otherwise, adjust density using the bisection routine and return to step 2.

To generate the fitness values for nonresidents, we calculated their behavioral ESS's under the assumption that the resident determined the distribution of resources over habitats.

Finding the fitness of nonresidents:

1. Find the behavioral ESS for each habitat
   a. Use Eq. 9 to find the quitting resource level.
   b. Calculate $t_f(z)$ using the initial resource level, $R_0(z)$, generated by the resident and the quitting resource level (Eq. 9).
2. Calculate Profit and Fitness using Eq. 6 and Eq. 7.

We used the procedure described above to generate adaptive landscapes for communities of habitat selectors at different values of mainte-

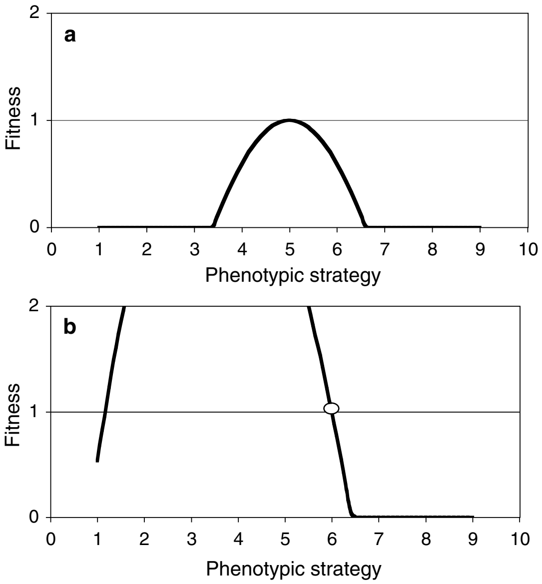

Fig. 2. — **a**: A single-species ESS resides on a maximal hilltop in the adaptive landscape. From this vantage point, no nonresident has fitness > 1, and thus the system cannot be invaded. — **b**: The ESS is dynamically stable. If a resident is not at the ESS, directional selection will evolve the system to the ESS.

nance cost, MC, in Eq. 7). For these analyses we let npatches = 50, ndays = 100, and the area of encounter, $a = 1$.

Results

The ESS comprises a finite number of species on a habitat continuum

For our first adaptive landscape we assigned the maintenance cost of 40 KJ day^{-1}. The resulting ESS contained a single phenotype, or species (Fig. 2a). No other nonresident phenotype was able to invade, even though each nonresident could forage more efficiently than the resident over some range of habitats (recall Fig. 1).

This ESS is an attractor. A resident that is not at the ESS resides on a slope in the adaptive landscape (Fig. 2b). From its position on the slope the resident may evolve by directional selection, or it may be replaced by the invasion by a different species, as long as the species comes from the upslope direction. In either case, the new resident phenotype will replace the original, and the adaptive landscape will shift to represent the new distribution of $R_0(z)$. After successive invasions or directional selection the resident will come to the dynamic equilibrium represented in Fig. 2a. In this case, the equilibrium is on a global maximum in the adaptive landscape, which means that no other feasible strategy can invade. This phenotypic ESS occurs at $u = 5$.

Decreasing maintenance cost increases invasibility

For our second adaptive landscape we reduced the maintenance cost to 20 KJ day^{-1}. Reducing maintenance cost dramatically changed the adaptive landscape. The fitnesses of nonresidents increased (Fig. 3). In fact, reducing the maintenance cost to 20 KJ day^{-1} resulted in the resident sitting in a valley of the adaptive landscape (Fig. 3a). This valley, or minimum, is dynamically stable. If the resident phenotype varies even slightly the adaptive landscape shifts, resulting in directional selection to return to the original equilibrium phenotype, just as in the case of the ESS. Although a species will not evolve out of a stable minimum, the system is open to invasion by any small variation of the resident phenotype that is reproductively isolated from the resident (Mitchell 2000). After invasion, divergent selection ensues and the newly coevolved community consists of a two-species evolutionarily stable state (Fig. 3b and c).

Examining the mechanism with a simple case

We illustrate why lower MC permits invasion and coexistence with a case much simpler than the ones described above. In this case, we restrict the number of habitats to two, and the number of species to three. Two of the species are specialists on different habitats. The third species is a generalist. Each specialist pays a low foraging cost in one habitat, and because of the assumed trade-off, a much higher foraging cost in the other habitat. The generalist pays the same foraging cost in each habitat, which cost is intermediate between the maximum and minimum costs paid by the two specialists. In this simple case, three types of communities are possible — (1) two specialists, (2) a specialist and a generalist, and (3) the generalist alone. How does MC influence which of these community types occurs?

Recall that lower MC results in increased forager density, which in turn results in lower resource levels. We will use our simplified community to examine how the lowered resource levels make invasion easier.

For any combination of habitat and species, we can graph three curves as a function of patch resource density. One curve is the energy consumed (Eq. 4), another is the energy expended (Eq. 5), and the third curve is the patch profit, which is simply the difference between the first two curves (Fig. 4a). All three curves intersect the resource axis at a positive (i.e., non-zero) level, reflecting the fact that there is a threshold resource level set by the foraging cost below which an individual will not feed. This threshold resource level can be found from Eq. 9 by setting $t_f^* = 0$. Above this threshold, the three curves increase monotonically.

Assume that Fig. 4a represents the results of the generalist foraging in a habitat patch. Which type of habitat does not matter since the generalist pays the same cost in both. The patch profit obtained by the generalist depends on the resource level. If only generalists inhabit the community then the resource level is entirely under the control of the behavior and density of generalists (Eq. 3). In this case the resource levels in habitats are driven to the levels at which a generalist individual can obtain just enough total foraging profit to cover its maintenance and replacement cost. If the resource renewal rate does not differ among patch types then the resource level depends only on the population density of generalists.

Similar curves for a specialist in its preferred patch would differ from the generalist in two ways. The threshold resource would be lower, indicating that the specialist could forage on scarcer resources than the generalist. Also, the specialist would pay a lower total patch foraging cost and reap a higher patch profit than would the generalist at all resource levels. We can use these profit curves to determine whether a specialist can invade a community comprising only the generalist, under the assumption that the generalist as resident determines the patch resource levels.

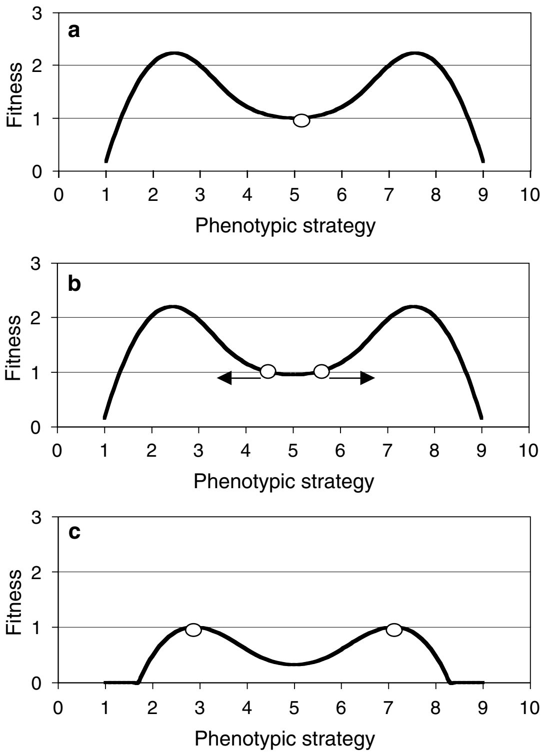

Fig. 3. — **a**: When MC = 20, a single resident resides at a stable minimum. This minimum is stable in the sense that if the resident were not at the equilibrium, directional selection would send it there, just as in the case of the ESS in Fig. 2. However, the minimum is susceptible to invasion from a reproductively isolated population, or species. — **b**: After invasion, there is directional selection for divergence of the two phenotypes. — **c**: The ESS at MC = 20 comprises two species.

Say that, in the course of a day, a typical individual can visit 20 habitat patches, or 10 of each type. For simplicity, assume that the cost to a specialist in it non-preferred habitat is prohibitively high, so that it will only exploit the ten patches of its preferred type. The generalist, on the other hand, can exploit all 20 patches, 10 of each type, with equal efficiency. A generalist individual then acquires a total profit (comparable to Eq. 6) that is 20 times the profit for a

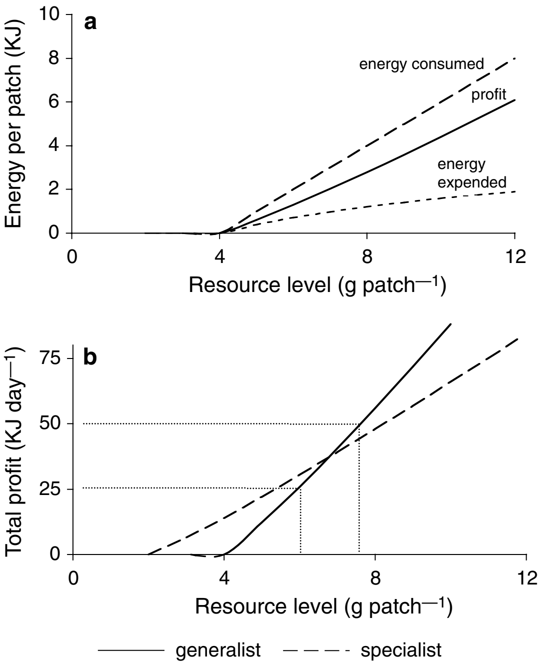

Fig. 4. — **a**: Curves representing energy consumption, expenditure and profit as functions of encountered resource density in a habitat patch. All three curves intersect the resource axis at point (threshold density), below which the individual cannot profitably forage. The positions of the curves depend on the foraging cost. A lower foraging cost would result in a lower threshold resource density, a lower energy expenditure curve and a higher profit curve. — **b**: Total profit curves for a generalist and a specialist where the generalist can forage all 20 habitat patches it encounters, but the specialist can profitably forage only 10. Total profit of the generalist is 20 times its patch profit, as represented in panel **a**. The specialist only forages the 10 patches where it has a lower cost. Its lower foraging cost results in a lower threshold density. But because it can only forage 10 patches, the slope of its total profit curve is less than that of the generalist. These curves indicate the levels of maintenance and replacement cost at which the specialist can invade a resident generalist, whose foraging determines equilibrium resource levels. The total foraging profit of the resident generalist will match the maintenance and replacement cost at equilibrium. So at high maintenance and replacement, the generalist holds the resource level too low for the specialist to invade. But as maintenance and replacement decreases, the specialist can cover these costs and have surplus energy for reproduction and invasion.

single patch as shown in Fig 4a. The specialist, however, will obtain a total profit of 10 times the patch profit it would harvest in a single preferred patch. In Fig 4b we graph total profit for the (resident) generalist and the (invading) specialist as a function of the resource level in a typical patch. The specialist profit curve has a lower intercept on the resource axis, reflecting the advantage of being a specialist — lower foraging cost in its preferred habitat. But the specialist curve also has a lower slope, reflecting the disadvantage of being a specialist, which is that it can feed profitably in only half the patches.

Since the generalist is the resident, its total foraging profit must equal the sum of its maintenance and replacement costs. And, since the resident foraging determines resource level, we can use Fig. 4b to find the patch resource level resulting from any maintenance and replacement cost. For example, when the maintenance and replacement cost is 50 KJ day^{-1}, the foraging and population density of the generalist will result in patch resource levels of 7.8 g patch^{-1}. If the resource level were higher (lower) than this, the generalist population would increase (decrease), resulting in a decrease (increase) of the resource level.

The resource level determined by the generalist also determines the profit of the invading specialist. In the case where the maintenance and replacement cost is 50 KJ day^{-1}, the specialist is unable to cover its cost, because the generalist determines a resource level of 7.8 g patch^{-1}, at which the specialist can only make a profit of 47 KJ day^{-1}. Hence the specialist cannot invade when maintenance and replacement costs sum to 50 KJ day^{-1}, even though it holds a foraging advantage in half of the habitat patches.

But invasibility becomes easier when maintenance and replacement costs are reduced. For example, when these costs are 25 KJ day^{-1}, the generalist sets the resource levels at 6 g patch^{-1}. At 6 g patch^{-1}, the specialist's profit is 30 KJ day^{-1}, which exceeds it maintenance and replacement cost of 25 KJ day^{-1}, and allows it to invade (Fig. 4b.). After successfully invading, the specialist population size will increase, and it will control the resource density in its preferred habitat at the level at which it just covers its maintenance and replacement cost of 25 KJ day^{-1}. The generalist may still profitably forage in this patch if this level is not below the threshold level of the generalist. If it is below the generalist's threshold, then the generalist is forced to obtain all of its profit from the alternate patch. In either case the resource levels in the patches used exclusively by the generalist would have to increase to allow the generalist to cover its maintenance and replacement cost. But the generalist could coexist with the specialist, it would just do so at reduced population density.

Of course, the second specialist may invade this community because its lower foraging cost in the habitat used by the generalist would give it a competitive advantage. The second specialist would reduce resources to the level at which it could cover maintenance and replacement cost, and a level too low for the generalist to do so and persist. In this case, the community would comprise the two specialist species, but not the generalist. This situation is comparable to that illustrated in Fig. 2c for case in which there is a continuum of habitat types, as well as a continuum of feasible strategies.

Discussion

Habitat selection modeled as a foraging game allows us to make several predictions about competition communities. First, even when there exists a continuum of habitat types and a continuum of feasible phenotypes a community may not be infinitely invasible (*see also* Mitchell 2000). While each phenotype can forage more efficiently than other phenotypes in one or more habitats, a successful invader needs a finite foraging profit at least equivalent to its maintenance and replacement cost. When resource levels are high the one phenotype with the lowest average foraging cost will be able to meet its maintenance and replacement cost while preventing other phenotypes from doing the same. To see why this is so, imagine a case of extremely high resource levels. In this case all foragers acquire about the same amount of resources, because their differences in quitting levels are small relative to the total resources consumed. Hence, the only significant difference among phenotypes is the cost they pay to harvest similar amounts of resource. The phenotype with the lowest average cost will then have the highest foraging profit. This is the ESS. In our model, the phenotype $u = 5$ has the lowest average cost because the cost function is a quadratic over the interval 0 to 10, and 5 is the midpoint. But there is nothing special about the quadratic cost function in generating the result of a finite species diversity. Other cost functions yield similar results (e.g., Mitchell 2000).

A second prediction of the model is that lowering maintenance cost in a system with a resident ESS increases the fitness of non-residents. Reducing maintenance cost enough leaves the resident in a minimum of the adaptive landscape. This minimum is stable, in the sense that a perturbation in the resident phenotype is followed by directional selection that returns to the original resident phenotype (Eshel 1983, Taylor 1989, Christiansen 1991, Abrams *et al.* 1993, Mitchell 2000). The minimum allows the invasion of phenotypes infinitely near to the resident, a situation that may promote competitive speciation (e.g., Rosenzweig 1979).

To see why lowering the MC increases invasibility, we can reverse the thought experiment described above. Assume that MC is negligible (~0). In this case the resident at equilibrium will crop the resource level until it is essentially "on top" of the curve representing the its quitting level in each habitat. A nonresident (with a different quitting level curve) will forage profitably where it pays a lower foraging cost than the resident. In this case a nonresident can invade as long as it makes any foraging profit, which means as long as its cost curve is less than the resident's in at least some habitat. For cost function described in Eq. 1, this means that virtually any non-resident could invade. Of course, a major point of the model has been to show that when MC > 0, the number of species in the ESS is finite. But at least we can use the case of MC = 0 to gain insight into the case where MC is lower rather than higher.

The basic results of our model do not change when features other than activity costs distinguish habitats. For example, we obtain similar results when habitats differ with respect to encounter rates rather than foraging cost, or when the foraging cost is in terms of predation risk (W. A. Mitchell unpubl.).

The model we present here complements Brown's (1990, 1998) work on the evolutionary game of habitat selection in the context of a finite number of habitats. His work investigates the influence of habitat frequencies, handling times and productivities on competition and species coexistence. We do not consider these questions for the habitat continuum in this chapter (but *see* Mitchell in review, for the effect of productivity). But the effect of habitat frequencies could be easily considered by changing the probability density function for the habitat types.

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