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Limits to species richness in a continuum of habitat heterogeneity: An ESS approach

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ABSTRACT

I use a co-evolutionary model to investigate the co-existence of species in ecological and evolutionary time in an environment that comprises a continuum of habitat heterogeneity. The model considers the ecology and evolution of communities organized by a trade-off in foraging costs over the environmental continuum. I assume that foragers use an optimal patch departure rule for depleting environments, where the rule itself depends on both the habitat and the forager's phenotype, which is a heritable evolutionary strategy. I consider the effects of three variables on co-evolutionarily stable co-existence: (1) travel cost, (2) maintenance and replacement cost, and (3) the range of habitat heterogeneity. When travel cost is positive, it, as well as the other two variables, affects species richness. Increasing either travel cost or maintenance cost results in a decrease in richness. Increasing habitat heterogeneity can increase species richness.

Keywords: co-evolution, evolutionarily stable strategy, habitat selection, species richness, travel cost.

INTRODUCTION

Species richness results from a combination of processes occurring at different spatial scales. At the provincial scale, immigration, dispersal and source–sink dynamics influence richness (Holt, 1985, 1993; Ricklefs, 1987, Pulliam, 1988). At the local scale, species interactions such as competition may be important (Rosenzweig, 1981; Tilman, 1982). To predict species richness and how it is expected to change with environmental conditions requires an understanding of the importance and relative contributions of both types of processes (Holt, 1993). To this end, we can ask if local population interactions can ever set an upper limit, or a 'hard ceiling', on the number of species that can co-exist locally. If not, then species richness must be set predominantly by provincial processes (Cornell and Lawton, 1992; Rosenzweig, 1992; Cornell, 1993).

For an upper limit to be effective over the long term, the community would have to be resistant to invasion at an evolutionary time-scale, that is, it must be co-evolutionarily stable. A co-evolutionarily stable community is one that comprises a set of species that not

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only co-exist with one another, but also prevent the successful invasion of alternative evolutionary strategies representing other species or mutations of resident species. The question of whether a community is co-evolutionarily stable goes beyond the question of whether it is ecologically stable, a common and important question addressed in many studies of community ecology. The basis of ecological co-existence is becoming better understood for a variety of taxa, and the understanding suggests common principles of community organization (Rosenzweig, 1987). For taxa as different as mammals (Kotler and Brown, 1988) and plants (Tilman and Pacala, 1993), species co-existence often results from the combination of two factors: (1) an axis of environmental heterogeneity and (2) a trade-off in species efficiencies on different parts of the environmental axis. Co-existence depends on each species having a range of the axis of environmental heterogeneity over which it is competitively superior. If the environment were homogeneous, the specialist for that environment could exclude all others. If there were no trade-off, then a single species could be superior throughout the environment. In this model, species co-exist by subdividing the axis of environmental heterogeneity, which may extend over space (e.g. habitat) or time (e.g. season). But how many species can co-exist by doing this?

If the environmental heterogeneity came packaged as a finite number of discrete types, the answer would be straightforward. The number of species could not exceed the number of discrete environmental types at an ecological equilibrium (e.g. habitats; MacArthur and Levins, 1964, 1967; Lawlor and Maynard Smith, 1976).

But heterogeneity is often continuous, not discrete and finite. Structural features of environments that separate co-existing species include continuous variables such as percent vegetation cover (Abramsky, 1988), temperature (Tilman and Pacala, 1993), moisture (Mclay, 1978), light levels (Mulkey, 1986; Tilman, 1986), and tree branch spacing and distribution (Moermond, 1979).

If habitat heterogeneity is continuous, then there is no apparent limit to the number of ways that species could divide it up, allowing each species to be superior over some range of habitat. As Rosenzweig and Abramsky (1993) remarked, 'Physical environmental heterogeneity is continuous and, in principle it should be infinitely sub-divisible by life'. Tilman and Pacala (1993) illustrate this point with a hypothetical graph depicting equilibrium density of a limiting resource (nitrogen) plotted over a range of environmental temperatures. At any temperature, the equilibrium resource density is set by the most efficient species in the community. Because species experience trade-offs in their efficiencies at different temperatures, each species will always have some range of temperatures over which it will deplete resource density to a level that excludes other species. Tilman and Pacala (1993) suggest that such an environmental continuum 'could allow an almost unlimited number of species to coexist on a single resource'. Abrams (1988) also noted that, with no theoretical limit to the number of habitats, there is 'no obvious limit to the number of species that can coexist globally in a system by having competitive advantages in different types of habitats'.

Trade-offs that permit co-existence do not even require that each species prefer or do its best at different parts of the environmental axis. Indeed, many communities appear to reflect a shared-preference organization, meaning that all species would, in a density-free world, experience their highest fitness in the same habitat (Rosenzweig, 1974, 1991). In this type of community, the trade-off occurs with respect to species' tolerances for the less preferred habitats, versus their abilities to exploit or defend the more preferred habitats. In other words, a species that is relatively superior at contending with an environmental

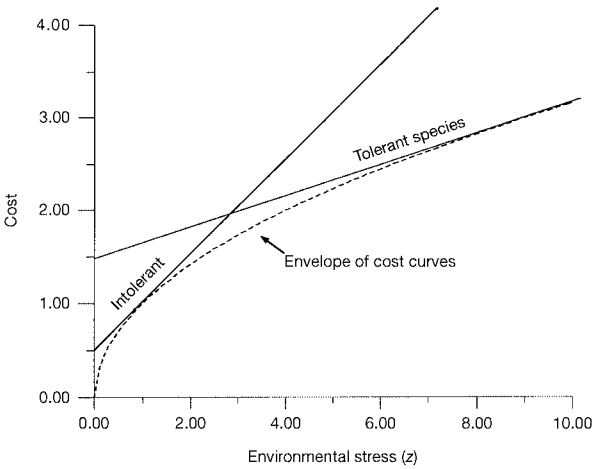

Fig. 1. The solid lines illustrate how the cost of exploiting a habitat increases with environmental stress for each of two different species that differ in their tolerance to the environmental stress. The intolerant species pays a high cost in high-stress environments, but a relatively lower cost in low-stress environments. The tolerant species still prefers low-stress environments (the cost curve has positive slope) but this species finds its relative advantage in high-stress environments. Resource density in each habitat z will be set by the species that pays the lowest cost in that habitat. So the intolerant species will be able to reduce resource density in low-stress habitats to a level that is unprofitable for the tolerant species. Similarly, tolerant species can exclude intolerant species from high-stress habitats. The dashed line represents the 'envelope' of cost curves generated by a range of tolerant-to-intolerant species. Each point on the envelope is the point of tangency of a cost curve, and indicates the habitat at which that species is competitively superior.

stress, such as predation risk, pays a premium in habitats that are less risky. Many communities appear to have this type of organization (Rosenzweig, 1991). Figure 1 illustrates the distribution of equilibrium resource levels over a continuum of habitat type in a shared-preference community. The abscissa represents the environmental heterogeneity as a range of environmental stress; the ordinate represents the cost that an individual pays to exploit a given habitat (indexed by stress). The ordinate plays a dual role because it also represents the relative equilibrium levels of the resource, because at population equilibrium the resource is maintained at a density where the rate of resource consumption just equals consumers' cost (Tilman, 1982).

I have drawn examples of the cost curves for two species. These curves differ in their slopes and intercepts. The steep slope belongs to the intolerant species, because cost rises quickly with environmental stress. The flatter curve of the tolerant species indicates that stress has less effect on individuals of this species. But there is a trade-off. The tolerant species pays a premium to mitigate the effects of stress. This shows up in the higher intercept of the tolerant species' cost curve. Because of the trade-off, each species is guaranteed a range of habitats over which it pays the lowest cost and can reduce resource density to a level below that which can be exploited by competing species. The intersection of the two cost curves separates the range of habitats in which each is relatively superior as indicated by its lower cost curve.

The two cost curves in this graph are only two of an infinite number of possible curves spanning the range from extremely intolerant to extremely tolerant. If we were to draw all possible cost curves that satisfy the trade-off, we would generate a cost envelope (the dashed line in Fig. 1). This envelope illustrates the minimum cost incurred from all possible strategies that are evolutionarily feasible in the sense that they satisfy the trade-off. For each and every value of environmental stress there is an evolutionary strategy from this set that minimizes cost. And, for each and every strategy there is a value of environmental stress for which that strategy minimizes cost. This means that, no matter how many strategies are present in this community, there is always room for another strategy to invade – the invader will always possess a range of the habitat heterogeneity over which it can make a profit because its cost there is lower than the resource level maintained by resident species.

The best way to illustrate how easily the community can be invaded is to show the adaptive landscape. An adaptive landscape plots fitness against strategy for all strategies, residents as well as potential invaders. Resident species that persist at equilibrium population levels have zero fitness, because, in the habitats they exploit, they reduce resources to levels that just cover the cost of exploitation. An invading species has negative fitness if resident species can maintain resources too low for the invader to make a net foraging profit in any habitat. On the other hand, an invading species that can profitably exploit at least some habitat will have positive fitness. The cost envelope discussed in the previous paragraphs ensures that any invader can make a net foraging profit, and so would have a positive fitness. So, an inspection of an adaptive landscape (or Wrightian surface) at ecological equilibrium shows that each species sits in a valley (Fig. 2). Thus any deviation from a resident species' strategy possesses a fitness higher than zero and should be able to increase in population size after invading. And, given the opportunity for reproductive isolation, the situation is ripe for rampant speciation. What prevents a trend towards ever increasing species richness?

One possible explanation relies on the relationship between small population sizes and extinction rates. At higher species richness, more species share the same resource productivity, which means that some species' population sizes must become quite small. Small populations are more likely to go extinct as a result of random fluctuations (MacArthur and Wilson, 1967). In this case, species richness equilibrates at the number where the rate of immigration and origination equals the rate of extinction resulting from small populations. In this view of species richness, there is no 'hard' upper limit to the number of co-existing species. The constraint imposed by small population sizes can be relaxed by increasing resource productivity. Greater productivity will allow more species to escape from low population size. Thus we expect to see increased species richness at higher productivities. But this is not the empirical pattern observed. For many animal taxa, there is a maximum species richness at intermediate levels of productivity. Rosenzweig and Abramsky (1993) reviewed the evidence and hypotheses for this unimodal relationship. None of the hypotheses appear to be completely satisfactory, but some do possess a testable ecological mechanism and corroborating evidence.

One of those is the resource-ratio hypothesis of Tilman (1982), which does predict that the addition of a limiting resource can result in the loss of species from a community. The mechanism here is that the effective variance in resource ratios that provided the basis of co-existence is reduced by augmenting one of the resources. Experimental evidence corroborates Tilman's model (Tilman, 1986). But this is not really a model that predicts

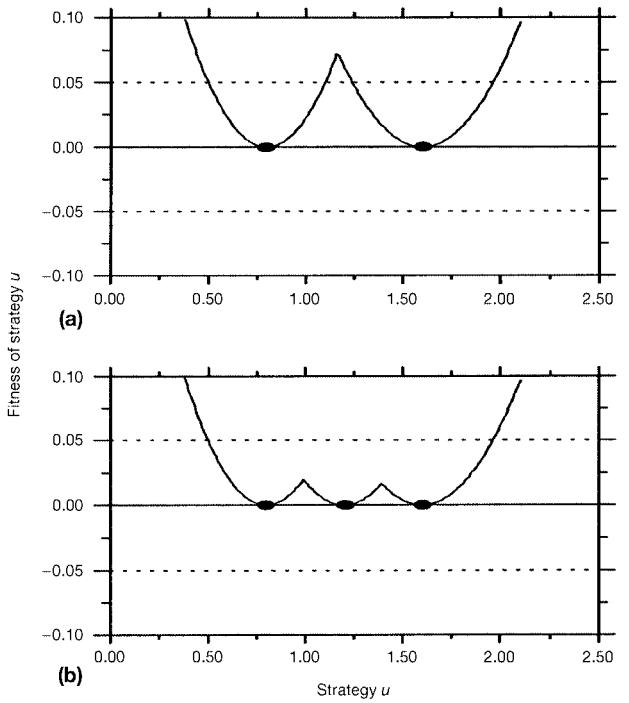

Fig. 2. This adaptive landscape represents the fitnesses of a range of strategies if the community comprises two species at ecological equilibrium, and species pay no travel cost. (a) The two species at equilibrium possess strategies indicated by the solid ellipses. Because these species are at equilibrium, their fitnesses are each equal to zero. The line in the graph indicates the fitnesses of invading mutants or propagules of other strategies, where all strategies are subject to trade-offs illustrated in Fig. 1. In this case of no travel cost, any non-resident strategy has positive fitness and can invade. The reason for this is that each strategy always has a range of habitats in which it is superior. (b) This adaptive landscape results if a third strategy is added as a resident to the community, and there is no travel cost. As in the case with two resident strategies, any non-resident strategy has positive fitness and can invade.

a limit to species richness. It predicts only that when species co-exist by dividing up a given range of heterogeneity, a reduction of that heterogeneity may cause some of those particular species to be lost. It does not provide a mechanism that prevents the successful invasion of the remaining heterogeneity by other species. There still exists a continuum of heterogeneity and no apparent upper limit to the number of potentially co-existing species set by the local interactions. As Rosenzweig and Abramsky (1993) state, 'We know no *a priori* reason to expect that life will subdivide any particular variance into more niches than it will a smaller variance'.

A critical element missing from the discussion so far is the effect of travel cost on habitat use and species co-existence. Travel cost is paid when an individual must spend some time or effort, or incur some risk to travel over habitat that it rejects, to reach habitat that it exploits. Theory in behavioural ecology predicts that increased travel cost expands the optimal range of acceptable choices, whether the alternatives are among prey, habitats, mates, etc. Experimental studies provide strong support for these predictions (Stephens and Krebs, 1986;

Mitchell, 1990; Morris, 1992). Density-dependent habitat selection theory predicts that the pattern of exploitation resulting from competition depends on travel cost (Rosenzweig, 1974, 1981). But this theory deals with habitat choice over a finite number of habitat types. We need a theory that addresses density-dependent habitat use when environmental heterogeneity is continuous and organisms pay travel costs. Furthermore, we need to understand how the habitat choice on an environmental continuum would affect the long-term evolutionary dynamics where evolutionary strategies may be drawn from a continuous set such as that generating the cost envelope in Fig. 1. We should address these questions with the intent of understanding whether these hypotheses can lead to a hard upper limit on local species richness.

Joel Brown (1990, 1996) has analysed the evolution of habitat selection for the cases of two and three discrete habitat types. He approached the problem using the theory of continuous evolutionary games (Vincent and Brown, 1988). These games are called 'continuous' because they deal with continuous strategy sets like the one illustrated by the cost envelope in Fig. 1. Although Brown assumed a finite number of habitat types, he let the criterion of co-evolutionary stability indicate the (finite) number and type of species that would resist invasion in evolutionary time. An important feature of Brown's approach is that he studied phenotypic evolution under the assumption that phenotypes would employ optimal behaviours of habitat selection, including how the behaviour depended on travel cost.

The subject of my study is the effect of travel cost on species co-existence and co-evolution on a continuum of habitat types. I shall demonstrate that the importance of this cost goes beyond its capacity to reduce population sizes. By changing optimal behaviours, travel cost can limit species richness.

MODEL AND METHODS

In the following sections, I describe the equations that I used to model: (1) the evolutionary trade-off that generates a continuous (infinite) set of evolutionary strategies that are all candidates for invading the community; (2) the general foraging scenario and resulting fitness representation; and (3) habitat-dependent foraging profit and resource dynamics, including renewal and depletion.

The evolutionary trade-off function

I assume that there is a habitat-specific cost of foraging. The habitat-specific foraging cost also depends on the forager's phenotype, which I let be a heritable evolutionary strategy. As an evolutionary strategy, its dynamics depend on the selection pressure imposed by a combination of the environment, population densities and strategy frequencies. Let u represent the evolutionary strategy. This variable is continuous and defined on some appropriate interval $(u_{\min}, u_{\max})$.

I assume that the habitat variable, z, imposes an environmental stress of some kind (e.g. desiccation, risk of predation), such that larger z implies greater stress. The evolutionary strategy, u, is a means of mitigating the effect of z. In particular, the effect of increasing environmental stress is less when an organism possesses a higher value of u. In comparing two species, I refer to the one with the higher value of u as the *tolerant* species (or strategy). Lower values of u indicate relatively *intolerant* species (or strategies).

The ability to mitigate the environmental stress is not free, and will itself impose a cost – that is, there is a trade-off. To perform the numerical analyses, I chose a simple cost function that embodies such a trade-off. The cost paid by an individual of strategy u per unit time while exploiting a habitat patch characterized by the environmental stress, z, is

$$c(u, z) = c_0 + uc_1 + \frac{zk}{1 + u} \tag{1}$$

The first term, c_0, is just a base cost that must be paid in any environment. The second term represents the energy cost of u, where the constant, c_1, is the unit energy cost. The third term represents the effect of environmental stress, z. Here, k is a constant that transforms the environmental stress into energy cost per unit time. The strategy u enters in the denominator so that it mitigates the effect of z. The function $c(u,z)$ increases with z. But increasing u may increase or decrease cost. That depends on the values of u and z. For any given z, there is a value of u that minimizes cost. For equation (1) this minimizing value of u is a continuous function of z:

$$u^* = \sqrt{\frac{zk}{c_1}} - 1$$

This function describes a cost envelope, like the one illustrated in Fig. 1. For the numerical analyses that I report on below, I set $c_0 = 0.1$, $c_1 = 1$, $k = 1$. Additional numerical analyses with different values for these coefficients did not change the qualitative results. Nor did the qualitative results differ when I used a completely different functional form for the cost function representing trade-offs for tolerant to intolerant strategies.

The foraging scenario and fitness

Consider an environment that comprises a continuum of habitat types. Habitats may differ in some climatic variable such as temperature or humidity, or perhaps in some structural feature such as percent vegetation cover, bush size or substrate type. Let the variable z represent habitat type, and assume that it is continuous on some interval $(z_{\min}, z_{\max})$. And let $p(z)$ be the probability density function for its occurrence in the environment. For the numerical analyses I discuss below, I assumed the probability distribution of the habitat variable was uniform, that is, $p(z) = 1/(z_{\max} - z_{\min})$. Actively foraging animals search this heterogeneous environment, encountering habitats characterized by z, at random. Upon encountering a habitat, the animal must decide whether to forage or continue searching. If the habitat is too poor to exploit, the animal rejects it and continues searching. If the animal forages, it experiences diminishing returns due to resource depletion, and it must pay a cost of foraging that is a function of habitat type z. An optimal forager will exploit a habitat patch only as long as the benefit from spending another increment of time foraging is greater than the cost.

This foraging scenario is typical of patch depletion models from behavioural ecology in which a forager encounters discrete patch types (Charnov, 1976; Stephens and Krebs, 1986). In these models, the forager attempts to maximize its average rate of energy harvest, which is represented by

$$\frac{E(\text{energy})}{E(\text{time})} = \frac{\sum(\lambda_i)(\text{net rate of energy gain at } i)}{1 + \sum(\lambda_i)(\text{handling time of } i)}$$

where λ_i is the encounter rate with habitat patches (or prey) of type i. Charnov (1976) showed that the optimal foraging behaviour is to leave a patch i when the marginal rate of return from i equals the average rate of return over the whole environment (see Brown, 1988, for extensions and modifications of this rule).

To model the foraging over a continuum of habitat types, I replace the summation operator with an integral operator. I also rearrange the equation so as to emphasize the effect of travel cost. Encounter rate with a given habitat type i is the frequency (or probability density) of that habitat multiplied by the total (or unconditional) encounter rate with all habitat types. Let $\hat{\lambda}$ be the total encounter rate with all habitats, and recall that $p(z)$ is the probability density of habitat type z. Then, the encounter rate with type z is $\lambda(z) = \hat{\lambda}p(z)$. The inverse of total encounter rate (i.e. $1/\hat{\lambda}$) is the time required to travel through the environment to have the option of exploiting a patch. The critical feature of travel time is that it must be spent whether or not the forager exploits the habitat. I shall denote the travel time by T, where $T = 1/\hat{\lambda}$. Replacing the summation operators in the expression for fitness with integral operators and dividing the numerator and denominator by travel cost yields

$$\frac{E(\text{energy})}{E(\text{time})} = \frac{\int_{z_{\min}}^{z_{\max}} p(z)(\text{net gain at } z)\mathrm{d}z}{T + \int_{z_{\min}}^{z_{\max}} p(z)(\text{harvesting time at } z)\mathrm{d}z} \tag{2}$$

As in the case modelled by Charnov, an optimal forager in a continuous environment will leave a habitat of type z when the marginal rate of return equals $E(\text{energy})/E(\text{time})$. I assume that fitness is equal to the average rate of energy acquired minus the energy cost of maintenance and replacement (including reproduction):

$$\text{fitness} = \frac{E(\text{energy})}{E(\text{time})} - \mu \tag{3}$$

I assume that μ does not depend on foraging behaviour (at least not directly). It may be a function of other limiting factors, such as the availability of roosting sites or nest predation.

Foraging profit and resource dynamics in a habitat

In this section, I describe how I obtain the equations for net energy gain and harvesting time in a habitat characterized by environmental stress z. These are the equations that I integrate over habitat type to arrive at the average rate of energy gain (equation 2).

When an animal forages in a habitat, its per unit time benefit (i.e. marginal benefit) equals the assimilable energy per unit resource, v, multiplied by the rate of resource harvest. The rate of resource harvest equals resource density, R, multiplied by an 'area of search' parameter, a, in dimensions of $(\text{area})(\text{time})^{-1}$ (Royama, 1971). Assuming that handling time for a resource item is negligible compared with search time, then resource density changes over foraging time, t_f, according to the equation:

$$\frac{\mathrm{d}R(t_f)}{\mathrm{d}t_f} = -aR(t_f) \tag{4}$$

Thus, cumulative benefit acquired after t_f time units spent foraging is

$$F(R_{\text{initial}}, t_f) = vR_{\text{initial}}(1 - e^{-at_f}) \tag{5}$$

In this foraging scenario, an animal incurs two costs of foraging. One is the energy cost given above in equation (1). The second is the missed opportunity cost. This is what the forager misses by not spending its time on other fitness-enhancing activities, including searching for and exploiting other parts of the environment. The missed opportunity cost (MOC) in this foraging scenario is simply the average net rate of energy intake while foraging (Charnov, 1976). An optimal forager will deplete resources in a habitat until the rate of return (avR) equals the sum of these two costs, $c(u,z)$ + MOC.

Brown (1988) defined the density of resources left by an optimal forager as the giving-up density (GUD). I will use the function GUD (u,z) to indicate the giving-up density of an individual of strategy u in a habitat type z. At the giving-up density of resources the forager's rate of return, avGUD (u,z). So, an optimal forager with strategy u will leave a patch characterized by z when the density of resources, R = GUD (u,z), satisfies

$$\text{GUD}\,(u,z) = (av)^{-1}\,(c(u,z) + \text{MOC}) \tag{6}$$

The number of resources taken from the habitat characterized by z is then the initial R minus the GUD. Multiplying this number by the per item energy value of resources, v, yields the gross benefit of using the patch:

$$\text{benefit} = v(R_{\text{initial}} - \text{GUD}\,(u, z)) \tag{7}$$

The net benefit is the benefit (equation 7) minus the cost of exploiting the habitat. The cost of exploiting the habitat is the per unit time cost, $c(u,z)$ (equation 1), multiplied by the time actually spent depleting the resources. Using equation (4) to calculate the foraging time required to deplete R_{initial} to GUD (u,z) gives

$$t_f = \frac{1}{a} \ln\left(\frac{R_{\text{initial}}}{\text{GUD}(u,z)}\right) \tag{8}$$

Of course, if GUD > R_{initial}, then $t_f = 0$: an optimal forager would not exploit a patch in which the initial resource density is less that the giving-up density. The total net gain from exploiting the patch is, assuming GUD < R_{initial},

$$\begin{aligned} \text{net gain}\,(u,z) &= v(R_{\text{initial}} - \text{GUD}\,(u,z)) - t_f\, c(u,z) \\ &= v(R_{\text{initial}} - \text{GUD}(u,z)) - \frac{1}{a}\ln\left(\frac{R_{\text{initial}}}{\text{GUD}(u,z)}\right)\left(c_0 + uc_1 + \frac{zk}{1+u}\right) \end{aligned} \tag{9}$$

I entered equation (9) for net gain in habitat z and equation (8) for foraging time in habitat z as the integrands in equation (2) for the average rate of energy gain in the environment.

To solve for R_{initial}, I had to account for resource dynamics within a patch due to resource depletion by foraging and renewal. I assumed that a forager knows the expected number of resources in each habitat type (indexed by z), but not the actual number of resources in a particular habitat. This is a reasonable assumption when the sampling effort required to estimate actual resource density in each habitat encountered is more costly than whatever

benefit would result from the more refined resource estimate (Stephens, 1989; Kotler and Mitchell, 1995). Despite this constraint, the foragers can choose an optimal foraging time. Because the number of resources harvested is a linear function of the initial number (equation 5), the optimal foraging time is simply the time required to deplete the *expected* value of R_{initial} to that strategy's giving-up density. R_{initial} is the sum of two variables: the giving-up density of the last strategy to visit the habitat and the number of resources renewed, which is a product of the renewal rate and the time available for renewal since the last visit to the habitat. Both the giving-up density and the time available for renewal are random variables depending on the densities and frequencies of foraging strategies. So, expected R_{initial} is equal to the expected giving-up density plus the product of the renewal rate and the expected renewal time. If foragers encounter patches at random, then the distribution of waiting times between patch encounters is distributed as a negative exponential. This similarly implies that the renewal time is distributed as a negative exponential (Possingham, 1988). The parameter of this waiting time distribution is proportional to the number of foragers that are searching (as opposed to exploiting) and would actually exploit the habitat once encountered. And, because giving-up densities depend on the environmental stress, so will the expected initial resource densities. I will denote the expected initial resource density in a habitat patch type z as simply $\bar{R}(z)$. When only one strategy, u, is consuming resources, then

$$\bar{R}(z) = E(\text{GUD}(u,z)) + \frac{b}{N_S q} \tag{10}$$

where b is the renewal rate, N_S is the number of searching foragers, and q is the 'area of search' for patches. When two or more strategies exploit the resources, $\bar{n}(z)$ is a function of the expected GUD calculated from the giving-up densities of each strategy weighted by its relative population abundance.

Numerically generating adaptive landscapes

To assess the evolutionary stability of communities, I used the equations described above to generate adaptive landscapes (Wrightian surfaces). An adaptive landscape plots fitness against strategy for all strategies, residents as well as potential invaders. The shape of the adaptive landscape depends on the resident strategies, because these dictate equilibrium resource distributions across habitat types. I assumed that resident species or strategies were at ecological (not necessarily evolutionary) equilibrium, so their fitnesses equalled zero. I assumed that invading species or strategies were rare enough that their initial densities could be ignored in calculating fitnesses – their fitnesses depended solely on the resource levels due to resident foraging. If an invading species or strategy had negative fitness, then I assumed that invading propagule would go extinct. On the other hand, if the invader's fitness was positive, then I assumed that it would grow until its fitness was reduced to zero by resource depression at a new ecological equilibrium. I defined a community as invasible if any part of the adaptive landscape was higher than zero, because then some non-resident strategies' population could grow after invading.

Because my analysis of community structure considers foraging behaviour, I had to find the ESS *behaviours* of all resident and invader strategies. The behavioural ESS in my model is the patch-leaving rule that is uninvadable once adopted by all members of that strategy.

The reason why the rule must be calculated as an ESS is that the fitness resulting from it depends on how the patch-leaving rules of other individuals affect habitat resource levels. The habitat specific patch-leaving rule is the function GUD(u,z). But the easiest way to characterize this rule is by the rate of energy profit at the GUD(u,z), because for optimal foragers this will be the same across all habitats. (If the rate of energy profit were lower at the GUD in some patches than others, the forager would have spent too much time there, and too little time in the other patch.)

I solved for the behavioural ESS by an iterative method that compared in each iteration the fitness of a candidate for the patch-leaving rule with fitnesses of rare alternatives. A bisection routine updated the candidate at each iteration. This routine always converged quickly to the behavioural ESS, that is, the patch-leaving rule generating higher fitness than any alternatives. To calculate fitnesses, I integrated the net rate of energy return across habitat types, including the travel cost of moving among habitats (equation 2) and subtracting from this the maintenance and replacement cost (equation 3). These integrals for fitness are too complicated to solve analytically, so I used Romberg integration to solve them numerically (Press *et al*., 1992).

To generate an adaptive landscape, I first solved for the behavioural ESSs and equilibrium densities of residents. Because the equilibrium densities of residents are defined by where their fitnesses equal zero, I used an iterative routine that find roots of non-linear equations. Due to the complexity of the non-linear equations for fitness, I used the secant root finding method, which works when derivatives of the equations are not available (Press *et al.*, 1992). I started the iterative routine with an initial guess for density, and then solved for the behavioural ESS at that density. This behavioural ESS yielded a fitness for the residents at the intially guessed density. Based upon whether the fitness was positive or negative, the routine adjusted resident density downward or upward, respectively, for the next iteration, stopping when the value of fitness converged to within a tolerably small distance from zero. Although this routine adjusts density to where resident fitness equals zero, it is in fact the effect of resident densities on habitat resource levels that determines fitness. That is, the foraging of a resident species imposes an equilibrium level of resources across habitats which then determines the fitnesses of invader species.

Once I had established the equilibrium densities of resident species and the concomitant resource levels, I calculated the fitnesses of a range of potential invader strategies. Because I assumed that invader strategies were too rare to influence resource levels, I found their patch-leaving rule that maximized fitness given the habitat resources generated by resident foragers. I calculated fitnesses of equally spaced invader strategies to fill in the rest of the adaptive landscape between the residents.

The adaptive landscapes allowed me to determine whether strategies could co-exist in ecological time and, if so, whether they were resistant to invasion. Occupied global peaks in the adaptive landscape indicate the presence of ESSs. The mere presence of peaks in an adaptive landscape predicated on a continuous array of habitat types distributed uniformly would answer in the affirmative the fundamental question of this paper: 'Can there be a hard upper limit to the number of species in a continuous environment?' This is because when resident species occur on peaks in the adaptive landscape, all other strategies are unable to invade successfully.

I investigated the effects on adaptive landscapes of three variables which I have discussed above: (1) travel cost, (2) maintenance and replacement cost, and (3) the range of habitat heterogeneity.

RESULTS

Effect of travel cost

Changing travel cost had a dramatic and qualitative effect on the adaptive landscapes, co-evolution and species co-existence. The simplest way to view these results is by categorizing three qualitatively different outcomes according to the relative magnitude of travel cost that generated them. I give the numerical values in the figure legends that accompany the adaptive landscapes.

High travel cost

When travel time, T, is high, the evolutionarily stable community may comprise just one strategy. This evolutionarily stable strategy (ESS) resides at a global maximum in the adaptive landscape (Fig. 3). And, because this strategy is assumed to be at an ecological equilibrium, the summit of the global maximum is at a fitness value of zero. Any other strategy that attempts to invade would have negative fitness and therefore fail. These non-ESS strategies fail despite the fact that each one would be superior to the ESS over some range of the environment variable z. The problem for these strategies is that travelling costs are too high to allow them to restrict themselves to their superior habitats, and yet they receive little or no benefit while travelling across habitat that has been made unexploitable by the ESS in order to arrive at that range of habitat in which they have the advantage. So, their net profit is negative.

A resident species not at the ESS is subject to directional selection that sends it toward the ESS value (Fig. 4a,b). So, given enough time, the resident species will either evolve to the ESS or it will be replaced by an invading species which is closer to the ESS.

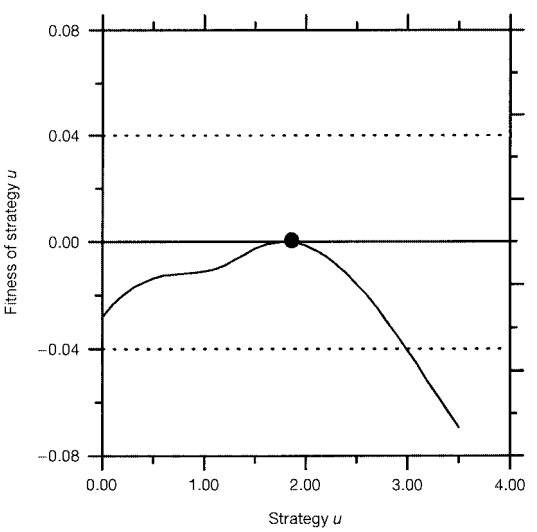

Fig. 3. The solid circle indicates the ESS for the case of high travel cost ($T = 1$, $\mu = 0.2$). The solid line is the adaptive landscape when the ESS species is present. The ESS represents a global maximum in this landscape. As such, it can prevent the successful invasion of any alternative strategy.

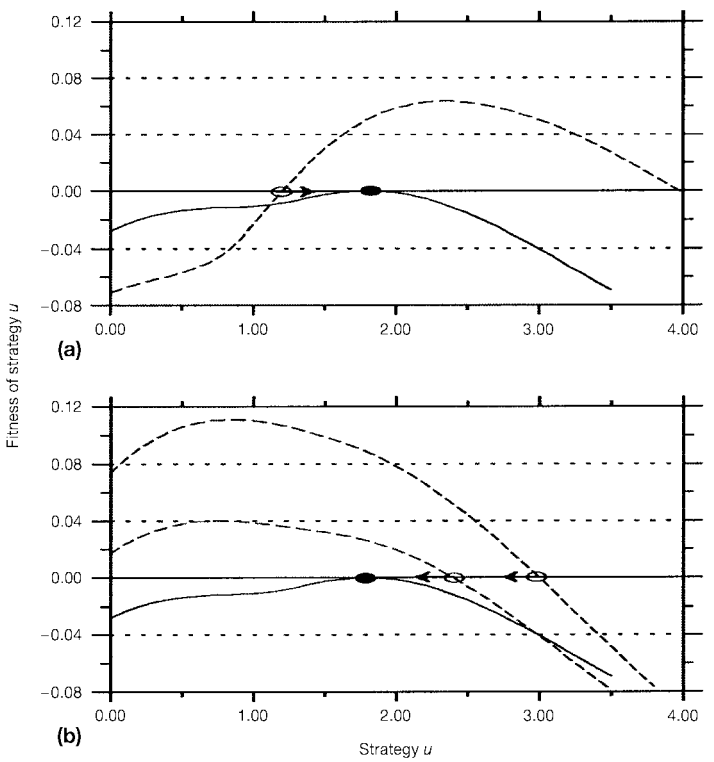

Fig. 4. The adaptive landscape changes its shape as strategies replace one another in the approach to the ESS. Here, an open ellipse represents a non-ESS strategy at ecological equilibrium by itself. The dashed line indicates the adaptive landscape generated by the presence of that non-ESS. The arrow indicates the direction of evolution by a resident species that produces small variations of its strategy allowing it to climb uphill in the landscape. As the ESS is approached, the steepness and height of the hill are reduced and strategies that could have invaded earlier in the evolutionary progression find their fitnesses sinking due to competition.

In the absence of the ESS, the community may comprise two species, each of which occurs on opposite sides of a hill in the adaptive landscape (Fig. 5a). Although these two species can co-exist in ecological time, they are not resistant to invasion. Any intermediate strategy will have positive fitness upon invasion, and displace at least one of the previous residents. Another evolutionary possibility exists. The invading strategies may not belong to other species, but be small, mutant variations on the resident strategies. In this case, we would expect to see adaptive 'hill-climbing'. Eventually, convergent evolution will yield the one-species ESS (Fig. 5b).

Intermediate travel cost

Now consider an environment that is identical to the one discussed above with the single exception that travel cost is lower. If the community were somehow restricted to contain only one species, that species would climb a hillside in the adaptive landscape changing the topography as it evolves (Fig. 6a,b). Evolution stops when the species has attained

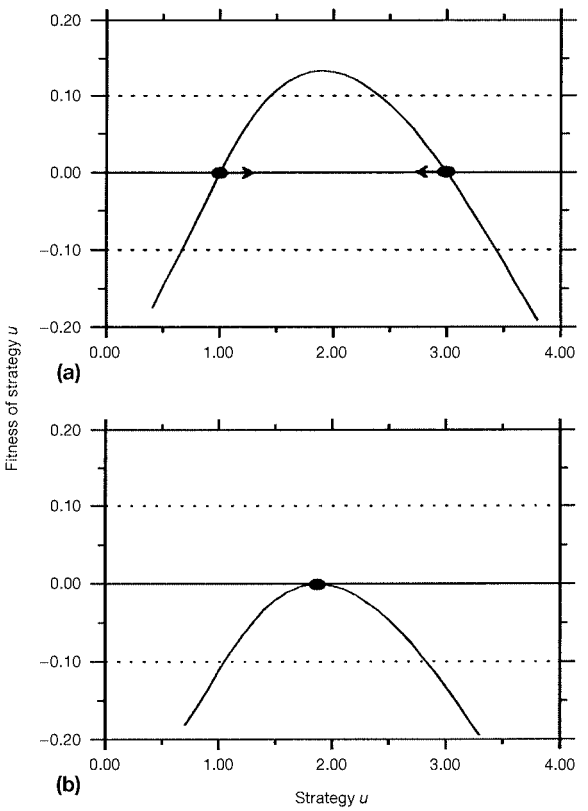

Fig. 5. In the absence of the ESS, two species may co-exist, even when travel cost is high. But the two-species community is subject to invasion by intermediate strategies. Convergent evolution will eventually produce a one-species community that exists at a global maximum, the ESS.

a strategy which sits on a local maximum or hilltop (Fig. 6c). From this point, slight variations from the resident strategy experience negative fitnesses and cannot invade successfully. Consequently, if the only likely invasions were from nearby or similar strategies, then, for all intents and purposes, this strategy would resist invasion. But it is not globally stable. A very different strategy can invade. Another hill rises in the adaptive landscape distant to the hilltop which the resident occupies. This hill represents the potential for successful invasion for any one of a set of distinctly different strategies. In my example, those strategies are distinctly less tolerant of the environmental stress. If one of these strategies does invade, population growth to its carrying capacity changes the shape of the adaptive landscape. The hilltop on which the original species had resided shifts out from underneath that species, leaving it on a hillside sloped away from the invader strategy, which is still separated from the original species by a valley. Natural selection on the original species will cause it to chase the hilltop. The invading species may evolve either towards or away from the original resident, depending on its original strategy and its eventual ESS value. Any time during the evolution of the two species towards their ESS values, the community is subject to invasion by a restricted set of strategies represented by other species. But once two species reach their respective ESS values, they are globally resistant to

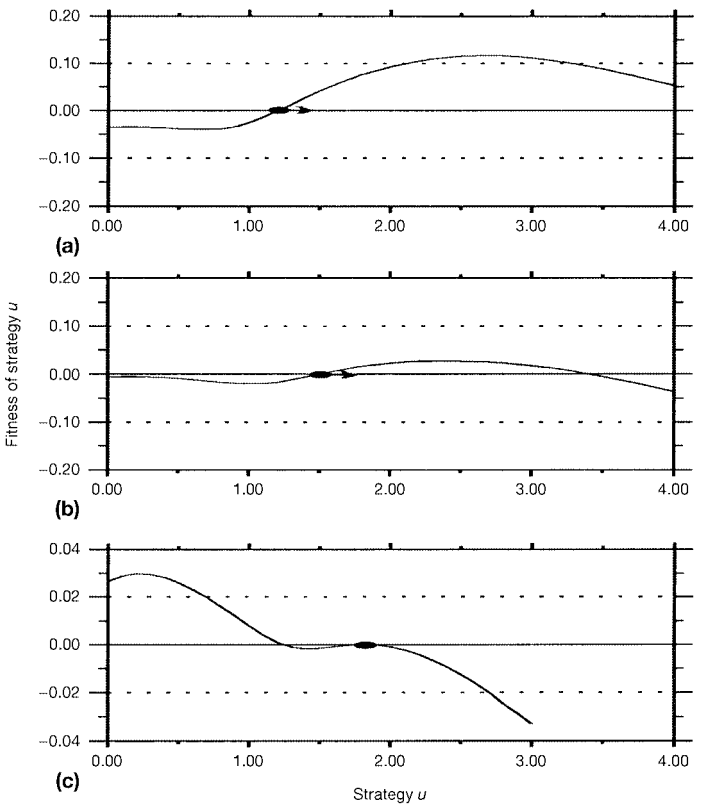

Fig. 6. At intermediate travel cost, a single species will evolve by hill climbing (a, b) to a local maximum in the adaptive landscape (c). At this local maximum, small variations in the resident strategy have negative fitness. But large deviations from this strategy have positive fitness and can invade ($T = 0.5$, $\mu = 0.2$).

invasion by any other strategies – that is, they sit on two equal hilltops in the adaptive landscape (Fig. 7).

As in the case of the single-species ESS, strategies that attempt to invade the two-species ESS will still be superior over a range of habitats. But the cost they must pay to have the chance of exploiting that range is prohibitively high. Thus their fitness is negative, and they go extinct.

Low travel cost

When travel cost is very low, there is a qualitative change in the adaptive landscape. Once again, consider the evolution of a single species. In the previous examples, a single species evolved to an equilibrium represented by a hilltop in the adaptive landscape. The equilibrium was stable because alternative strategies suffered negative fitness. But a somewhat different situation holds when travel cost is low. In this case, a single species will evolve to reside at the bottom of a valley in the adaptive landscape (Fig. 8a). From this perspective, any direction is uphill and any variation on the resident strategy would seem to be superior. But if the species under consideration is sexual and interbreeds, and speciation does

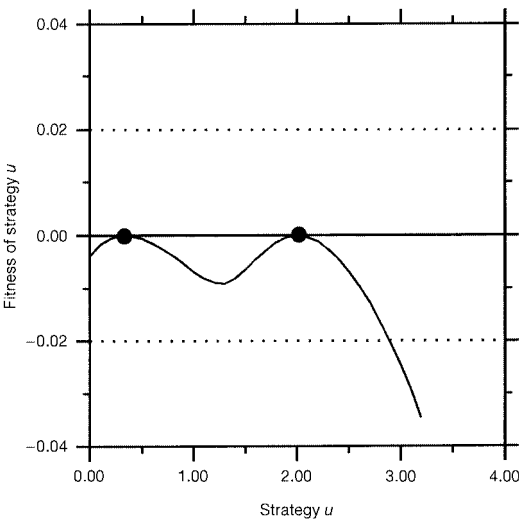

Fig. 7. At intermediate travel cost, the ESS comprises two species. They sit at equal-valued global maxima, and prevent the successful invasion of any alternative strategy ($T = 0.5$, $\mu = 0.2$).

not occur, the variant strategy cannot drag the species up either slope. The presence of the valley and the slopes of the valley walls depend on the presence of a population at ecological equilibrium there. If the species shifts strategy *en masse* to one side or the other, the valley walls deform and slope upward so as to send the species' evolution back to the valley (Fig. 8b–c). Thus if the species is sexual, it may not escape from this position.

Although one species will stay in a valley, a second can invade. In fact, any distinct species utilizing a strategy on either side of, and arbitrarily close to, the resident can invade. The invader will have positive fitness and, as it grows to carrying capacity, it will deform the adaptive landscape. At the two-species ecological equilibrium, each species sits on either side of a valley, so that natural selection produces divergent evolution (Fig. 9a). (An alternative scenario to the invasion of a distinct species would be the *in situ* occurrence of a reproductive isolating mechanism allowing the evolution of ecologically distinct species.) The new two-species equilibrium occurs with one species residing on a local maximum (hilltop) and the other species in a local minimum (valley) (Fig. 9b). The strategy sitting at the local maximum precludes invasion from nearby strategies. But the strategy at the minimum will, as in the single-species case, allow invasion by a local variant of this resident strategy. I have not yet generated the adaptive landscape resulting from the successful invasion of a third species and subsequent evolution of the three-species community.

Effect of habitat variation

When travel cost is non-zero, community composition and co-evolution depend on the range of (continuous) habitat variation. In general, the greater the range of habitat variation, the greater the species richness at the ESS. For example, starting with the parameters that generated a single-species ESS (high travel cost), I increased the range of z by increasing the maximum value of stress by 25%. The effect of this was to promote evolution of a more tolerant species (higher value of u) and produce a second hill in the

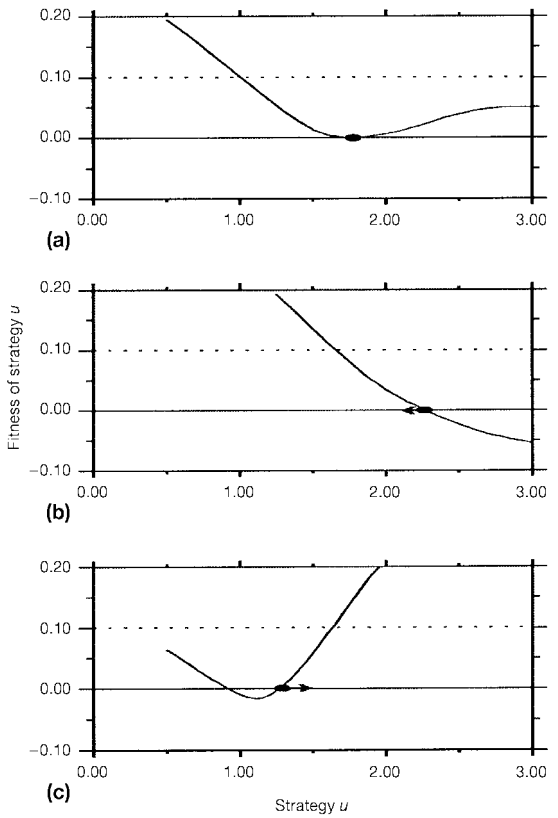

Fig. 8. At low travel cost ($T = 0.2$, $\mu = 0.2$), a single-species community will evolve to a local minimum (a). This minimum is stable to deviations in the single species' position. Although either direction from the minimum is uphill, the species cannot evolve in either direction because once it leaves the valley bottom, the landscape shifts, providing selection to return to the original position (b) and (c). This is different than the case illustrated in Fig. 2, where there was no such stabilizing force on local deviations on the species' evolution.

adaptive landscape (Fig. 10a,b). This second peak allows for the successful invasion of another species. Interestingly, the co-evolutionary effect of increasing the upper limit of environmental stress was to allow the successful invasion of a second species less tolerant to environmental stress than the original resident.

Effect of maintenance cost

Recall that maintenance cost is the expected rate of energy profit that a strategy must generate at equilibrium. Increasing maintenance cost tends to reduce the number of species that can co-exist at a co-evolutionarily stable equilibrium. For example, the two-species community whose adaptive landscape is depicted in Fig. 7 collapses to a single-species ESS community if the maintenance cost is increased sufficiently (Fig. 11).

Maintenance cost has no effect unless search cost exceeds zero. If search cost is zero, then increasing maintenance cost simply increases equilibrium resources. It does not

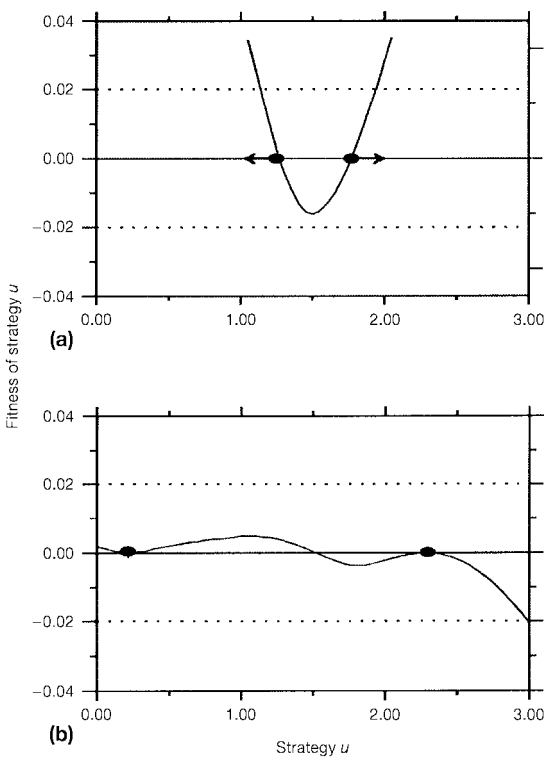

Fig. 9. If a second species, reproductively isolated from the first, invades, then a valley opens up between the two species that sit on opposing hillsides (a). Selection causes divergent evolution. Eventually, one species resides at a local maximum and the other at a local minimum (b).

change optimal behaviour regarding the acceptance of habitats. Species still show complete separation of habitat use and each strategy can still invade any combination of strategies at equilibrium.

DISCUSSION

Recent theories of species diversity have emphasized processes that work on the regional and provincial, rather than local, scale. But my results suggest that competition at the local scale can limit species richness, even when there is a continuous distribution of habitat quality generating an infinite variety of habitat types. Moreover, these results hold in evolutionary time, because the model predicts a finite number of ESSs. And these are globally resistant to invasion by an infinite variety of species and evolutionary strategies. The critical component that limits species richness in my model is travel cost, which is the time required to travel across a unit area of habitat, whether or not that habitat is exploited.

Why does travel cost make such a difference to community composition and co-evolution? Travel cost prevents strategies from being too selective on habitats where they enjoy a comparative advantage. The more selective a strategy, the more time it must spend travelling to find its selected habitat, and the more profit it has to make foraging there. To make a large profit, the level of resources must be high in the selected habitat. But

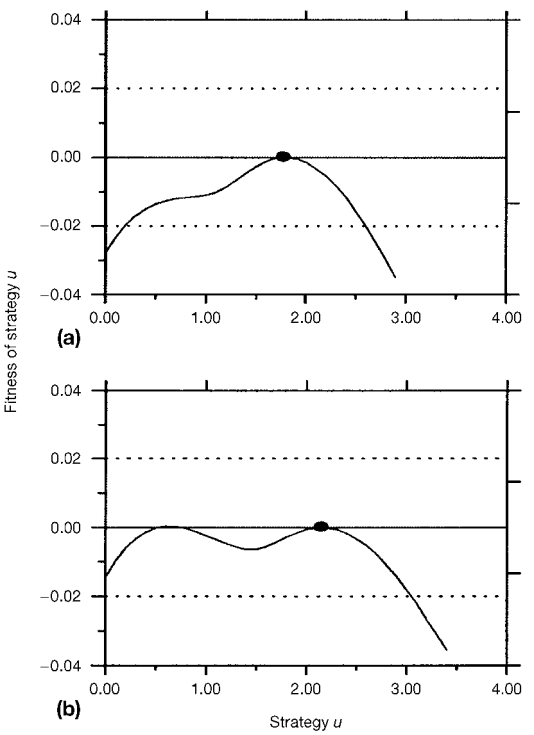

Fig. 10. Increasing habitat variance can change the adaptive landscape to allow the successful invasion of an additional species. (a) The adaptive landscape dominated by a single ESS when z ranges over the interval (0, 20). (b) The adaptive landscape when the range of z is increased by 25% (0, 25), and the resident strategy has responded by evolving to a higher value of u, indicating a greater degree of tolerance to z. This new strategy is at a local equilibrium and would allow the successful invasion of a second, less tolerant strategy.

other strategies, even those that hold a comparative disadvantage in the selected habitat, can still profitably forage there if the resources are high enough. In fact, foraging by other, more opportunistic strategies can maintain resources in the selected habitat at a low enough level to prevent the selective strategy from making a profit sufficient to cover its travel cost.

When communities are not globally resistant to invasion because they do not include the ESS(s), travel cost is still important in determining the limited range of strategies that can invade successfully (e.g. Figs 4, 5 and 6). Thus, while the regional and provincial processes may dictate the rate of immigration, local competition will establish the probability of successful colonization, at least when there is a travel cost.

The results of my model suggest that travel cost will affect the distribution of co-existing species in phenotypic space. When travel cost is zero, competition cannot exclude species from a community or impose directional selection on resident species to become less similar. So species can be randomly arrayed in phenotypic space. But when travel cost is positive, co-existing species that are too similar will be subject to divergent selection, or the invasion of dissimilar species. Travel cost, by punishing habitat selectors, predicts the overdispersion of species in phenotypic space. Real communities show such

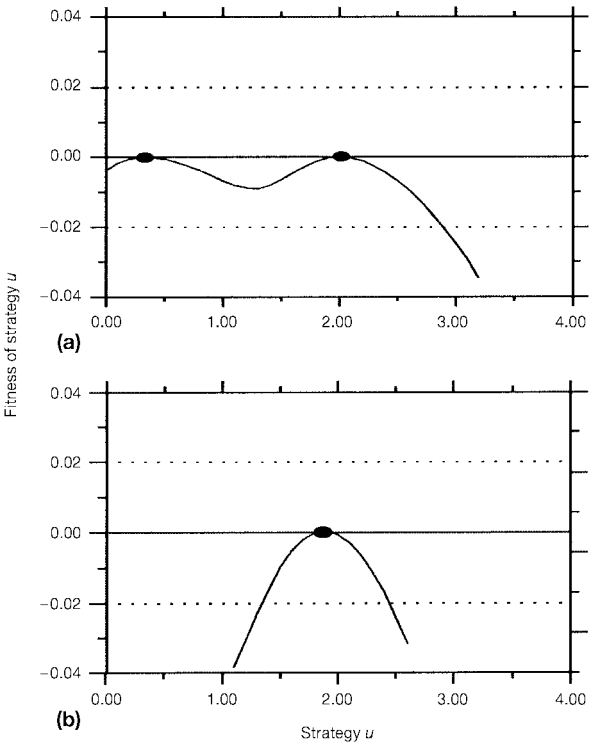

Fig. 11. Increasing the maintenance and replacement cost, μ, can reduce the number of species in the ESS, in a manner similar to the effect of increasing the travel cost: (a) $\mu = 0.2$, (b) $\mu = 0.5$.

overdispersion. For example, studies of bird introductions on Pacific islands have shown that successful invaders are significantly overdispersed in a phenotypic space reflecting body size and beak shape (Moulton and Pimm, 1987; Lockwood *et al.*, 1993; Lockwood and Moulton, 1994).

Other studies have suggested that, in the absence of frequency-dependent selection, a single phenotype should reign supreme. For example, J. H. Brown *et al.* (1994) hypothesized that body size represents a trade-off between more efficient energy harvest by larger species and more efficient energy conversion for reproduction by smaller species. Based on this trade-off (derived from allometric equations), they calculated an optimal body size for mammals. The predicted size (~100 g) closely approximated the mode of the frequency distribution of actual mammalian body sizes. But of course all mammals are not the same size, so what accounts for size diversity? Brown *et al.* suggested that body size diversification is the result of competition for limited resources generating frequency-dependent fitnesses.

One of the counterintuitive results of my analysis is that increased immigration rates may actually reduce species richness in a community that does not comprise the ESS. As indicated in Fig. 5, the absence of the ESS may allow the persistence of more species at ecological (but not evolutionary) equilibrium. At high immigration rates, it is more likely that one of the potential invaders would possess a strategy very close to the ESS. Thus, immigration could be responsible for the collapse of a two-species community to a single-species (ESS) community.

Evolutionarily stable minima and sympatric speciation

In my analysis, low travel cost or low maintenance and replacement costs caused species in isolation to evolve to a strategy that resided at a stable minimum in the adaptive landscape (Fig. 8). This strategy was stable to perturbations in the strategy used by the species as a whole, but not to reproductively isolated individuals (i.e. another species) employing a different strategy (Fig. 9). Such evolutionary minima have been discovered in other theoretical analyses of continuous traits subject to frequency-dependent selection (Eshel and Motro, 1981; Eshel, 1983; Taylor, 1989; Abrams *et al.*, 1993). Eshel and Motro (1981) referred to this type of stability as *m-stable* because it represents stability to deviations in the mean population strategy, as opposed to deviations by rare mutants, which they term *δ-stable*. ESS conditions generally refer to *δ*-stable strategies. Taylor (1989) acknowledged their theoretical possibility, but doubted whether biologically reasonable models would produce them. Abrams *et al.* (1993) produced a stable minimum from a biologically reasonable model, but suggested that they might be rare because they would be especially prone to competitive exclusion. In my model, a strategy that gave rise to a stable minimum was invasible, but it was not competitively excluded by the successful invader species. Instead, it (as well as the invader) simply became subject to directional selection.

In the absence of invasion by a different species, a stable minimum is ripe for sympatric speciation. Whereas the classic paradigm of allopatric speciation requires some kind of geographic separation of sub-populations, the hypothesis of sympatric speciation does not, and builds upon disruptive selection within a continuous population (Thoday and Gibson, 1962; Bush, 1969, 1975; Rice, 1987; Wilson and Turelli, 1986). The subject has been contentious, but evidence has been accumulated that some multi-species communities are the result of a single colonization followed by adaptive radiation and sympatric speciation (e.g. Schliewen *et al.*, 1994). Theories of sympatric speciation typically involve two steps. The first is disruptive selection that leaves intermediate phenotypes (and genotypes) at a selective disadvantage. The inferiority of intermediates gives a selective advantage to those individuals that mate with similar phenotypes. The second step is evolution of homogamy (i.e. positive assortative mating), which leads to the reproductive isolation and speciation of the extreme phenotypes. Rosenzweig (1978) and Pimm (1979) hypothesized that competition for habitat could provide the necessary disruptive selection. In their models, a homozygous population of habitat specialists can be invaded by a mutant that is superior in a different habitat even in its initial heterozygous form. But the initial success of the heterozygotes leads to an increase in homozygotes that are even more specialized for the second habitat. As the homozygous specialists for the second habitat become common enough, the heterozygotes suffer a severe fitness disadvantage relative to the two homozygous habitat specialists. As a result of this disruptive selection, positive assortative mating within homozygous habitat specialists becomes selectively advantageous. But a nagging question remains. Does the mechanism of competitive speciation require that habitats be discrete?

My model indicates that sympatric speciation by a competitive mechanism could occur even when habitats are continuous rather than discrete. When travel cost is low enough, species may evolve to occupy a minimum in the adaptive landscape. In this case, there are two ways that the community could add a species: first, any second species can invade; second, sympatric speciation could occur. Competitive speciation appears possible because, as the mutants become more prevalent in the population, a valley similar to the

one in Fig. 9a should form between the wild type and the homozygous mutants. If heterozygotes are intermediate in strategy between these two homozygous types, then selective pressure exists for assortative mating. And Rice (1987) has shown that possible genetic constraints that may prevent the evolution of reproductive isolation in sympatry may be circumvented when different strategies bias their activity towards different habitats, as they do in my model.

Resource productivity and species richness

Species richness often declines as a function of resource productivity (Rosenzweig and Abramsky, 1993). In the model I have analysed, increasing resource productivity would have no direct effect on equilibrium resources and, consequently, no effect on co-existence. It would only increase the population sizes of consumers. But resource productivity may have an indirect effect if μ, the maintenance and replacement cost, is density-dependent. Imagine a density-dependent factor other than the resource modelled above – nest predation or disease, for example. Then, an increase in resource productivity will increase μ by increasing population density. As shown above and in Fig. 11, increasing μ has an effect similar to that of increasing travel cost. It decreases the number of ESS species. So, if μ is density-dependent, then the number of species in an ESS community decreases with resource productivity (at least for the model presented here).

Temporal niche diversification

Although the model analysed here assumes that individuals select habitat, similar results should hold when individuals select times (e.g. seasons) of activity. That is, travel cost should also be important for species that 'travel' through time to select profitable periods for activity, germination, flowering, and so on. An individual organism or seed does not generally get to pass over unprofitable periods cost-free. Resting metabolic costs, seed predation and desiccation are all costs that resting or dormant individuals must pay to get to to travel through time to reach the period at which germination, foraging, and so on occur. The more restrictive an organism's activity period, the higher its average rate of gain must be over that period. Thus when the community appears to be organized by temporal heterogeneity, travel costs may still constrain the number of species that can co-exist.

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