Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches

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Summary

The fundamental niche is a description of the range of environmental conditions in which the mean fitness of a population exceeds or equals unity, and outside of which its mean fitness is less than one. The fundamental niche is a mean phenotype of a population, a trait that can evolve by natural selection. In the analysis of the evolution of adaptations by natural selection one must specify the range of environments within which the relative fitnesses of alternative phenotypes are compared. Population dynamics automatically biases the environments experienced by an evolutionary lineage, simply because more individuals tend to be found within the fundamental niche than outside it (unless the population as a whole is going extinct). We argue that this basic asymmetry biases adaptive evolution toward further improvement to conditions inside the fundamental niche, even at the expense of fitness outside it. This suggests that natural selection may act principally as a conservative force on fundamental niches. We place the particular problem of the evolution of fundamental niches into the general framework of specifying the spatiotemporal scale for the analysis of adaptation in heterogeneous environments and introduce the notion of a 'phylogenetic envelope', a heuristic representation of this scaling. Because all of microevolution necessarily occurs within the constraint of the evolutionary dynamics of the fundamental niche, we conclude that understanding such dynamics should be of central concern to evolutionary ecologists.

Keywords: fundamental niche; adaptation; spatial scale; conservative evolution; stasis

Introduction

A central goal in evolutionary biology is to understand the origin and maintenance of adaptations sculpted by natural selection (Mitchell and Valone, 1990). To claim that a phenotype characterizing a population is an adaptation one must specify (1) the array of phenotypes available for selection in that population or, more precisely, in the evolutionary lineage leading up to the current population, (2) the environments occupied by that lineage, and (3) the mapping of phenotypes onto a fitness function (in many but not all circumstances, a *per capita* growth rate), which also depends on the environment. The claim, then, is that the prevalent phenotype is an adaptation because it is the one that maximizes fitness, compared to relevant alternative phenotypes that can potentially invade the population, in the relevant selective environment (Brandon, 1990).
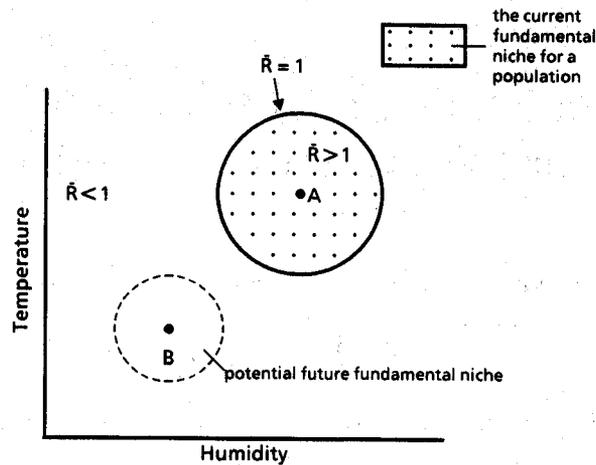
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Figure 1. Hypothetical fundamental niches for a population. The dotted region indicates the combination of temperature and humidity conditions within which a population has a *per capita* finite rate of increase when rare $\bar{R} \geqslant 1$. The environmental conditions in habitat A permit a population to deterministically persist there. By contrast, in the environmental conditions characterizing habitat B, the same population deterministically becomes extinct – unless the fundamental niche itself evolves. The text explores ways in which such an evolutionary shift might occur.

Out of this triad – phenotype space, environmental context, and fitness model – the problem of specifying the appropriate environmental context for the evolutionary analysis of adaptation has received the least attention from evolutionary biologists (Brandon, 1990). In recent years many evolutionists (e.g. Rosenzweig, 1987; Holt, 1987) have discussed how individual habitat selection, by circumscribing the range of habitats experienced by individuals, can thereby channel the direction of adaptive evolution. In this paper we explore the idea that a very similar channelling occurs in the evolution of fundamental niches in spatially heterogeneous environments.

The 'fundamental niche' is usually defined to be that set of environment conditions and resources that permit a population to persist (i.e. *per capita* births exceed deaths over some range of densities) when it is not being limited by interspecific competition or predation (Hutchinson, 1987). Interspecific interactions may at times restrict viable populations to a realized niche within the fundamental niche. For simplicity, in this paper we assume that interspecific competition and predation do not have this effect, so that the fundamental and realized niches are coterminous.

We should emphasize at the outset that the aspect of niche evolution explored below differs sharply from the question traditionally considered in the ecological literature, which is: how do interspecific and intraspecific competition interact over evolutionary time to determine resource and habitat partitioning patterns (e.g. Arthur, 1987)? The evolutionary issue we raise is a general one, regardless of whether or not competition is an important determinant of population dynamics and community structure.

Consider the familiar geometric picture of the fundamental niche shown in Fig. 1. In an environmental space with two axes (e.g. temperature and humidity), we plot the *per capita* growth rate $\bar{R}$ (= mean absolute fitness) of a population as isopleths (the 'niche response surfaces' of Maguire, 1973) on this space. The fundamental niche is described by all points where $\bar{R} \geqslant 1$. Point A specifies the environment currently occupied by the population. Because it is

within the fundamental niche, the population will increase when rare and be bounded away from zero.

Now consider another point, B, outside the fundamental niche (i.e. at B, $\bar{R} < 1$). In the discussion below, we assume a simple 'principle of continuity', which is that fitness declines monotonically with increasing distance in environmental space between point B and the edge of the fundamental niche. Individuals from the focal population could be found in environment B for two quite different reasons. First, there could be a secular environmental change from A to B at the site occupied by the population. Second, individuals could disperse from a population in environment A to a distinct locality with environment B and attempt to found a new population there. In the absence of genetic variation, if a population is closed to immigration, and the environment wanders outside that population's fundamental niche, it is clear that the population will decline toward extinction. In like manner, attempts at colonization into habitats described by point B will surely fail.

But given genetic variation, the fundamental niche can evolve. At any given time in its evolutionary history, a species possesses some evolutionary strategy, which defines its fundamental niche. Moreover, the species also possesses a set of evolutionarily feasible strategies, the union of which represent the evolutionary feasible fundamental niche. In this paper we concentrate on evolution in a species that inhabits two distinct habitats, one like point A in Fig. 1, with $\bar{R} > 1$, and the other akin to point B, with $\bar{R} < 1$; the species persists as a population at point B, if at all, only because of dispersal from point A. In what circumstances will natural selection modify the fundamental niche of the population so that it can persist at point B without immigration? One can imagine that this happens either by an expansion in the fundamental niche (so that the species can persist either at A or B, without immigration), or that it involves a niche shift (as depicted in Fig. 1) such that the species can now persist at B, but can no longer persist at A. We will argue that it often may be difficult for a species to break out of the fundamental niche that it starts with, for reasons that have to do with the interplay of population dynamics, natural selection, and spatial processes in heterogeneous landscapes. In other words, natural selection may be a powerfully conservative force in the evolution of those characters of greatest ecological importance.

There is tantalizing evidence for such conservatism in some phylogenetic lineages. For instance, Huntley *et al.* (1989) observed that the distribution and abundance of beech (*Fagus*) in Europe and in North America can be described by quite similar climate-response surfaces, even though these lineages have been isolated for millions of years. They concluded that the 'physiological characteristics determining the species' distributions are presumably evolutionarily conservative.'

To forestall at the outset one source of confusion for our readers, in our discussion of the evolution of fundamental niches we are not at all assuming that the likelihood of population persistence (as encapsulated geometrically in the fundamental niche) directly feeds into the determination of the direction of selection. When such is the case, one is concerned with group selection (Wilson, 1983). Instead, we are exploring the consequences of an automatic bias in garden-variety microevolution in spatially heterogeneous environments, a bias that arises simply because more individuals tend to be found within the fundamental niche than outside it.

An ecological framework

It is useful to place our evolutionary question into the context of parallel issues in population and community ecology. To what extent are the dynamics of a given species in a local community explained by endogenous processes versus processes impinging on that area from some larger

landscape within which the local community is embedded? One of us (Holt, 1992) has recently proposed a classificatory scheme for the spectrum of regional processes that can influence local abundance. Most local communities have member species fitting each of these mechanisms. At one extreme, there are 'source pool effects': namely, dispersal may only matter in initially seeding the community with a given species, but thereafter does not affect that species' local abundance. At the other extreme, a species by virtue of the spatial implications of its autoecological requirements may not be able to complete even a single generation confined within the local community (e.g. because of large home range requirements). Its local abundance should reflect processes over a much larger region than just the local community.

A number of possibilities arise between these two extremes. For instance, with 'source-sink dynamics' (Holt, 1985; Pulliam, 1988), a local sink population might deterministically become extinct in the absense of immigration from a persistent source population. A population that occurs in a habitat outside the fundamental niche of a species is necessarily a sink population; its local abundance will reflect a balance between its rate of decline and the rate of immigration. In 'classical metapopulation dynamics' all populations are vulnerable to extinction and recolonization, and local abundance reflects the interplay of local dynamics and the timing of extinctions and colonizations. For both source-sink and metapopulation dynamics, the abundance observed in a given population is likely determined in large measure by processes outside that population.

The phylogenetic envelope

Evolutionary biologists study the relative frequency of characters, rather than absolute abundance, but an equivalent problem arises in evolutionary analyses. What is the proper
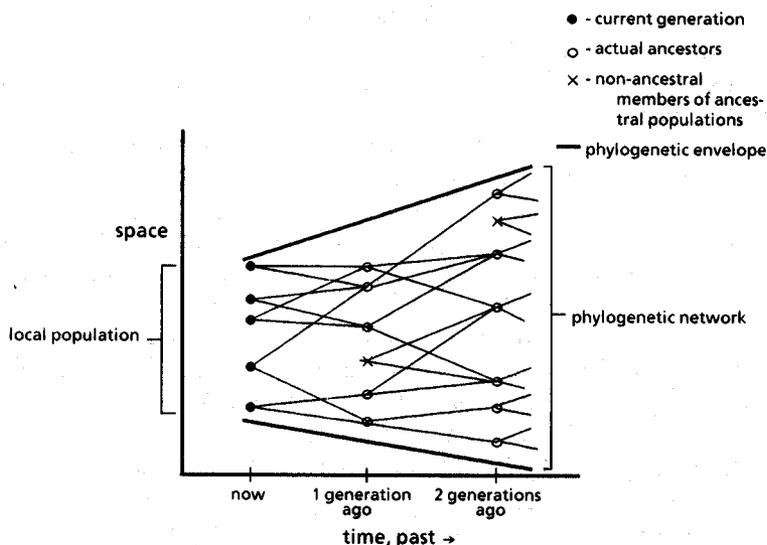

Figure 2. Populations are the descendents of phylogenetic networks of individual ancestor–descendent relationships, which can be plotted as links connecting nodes (individuals) on a space–time diagram. Many individuals in past populations did not contribute to the current population; these are represented by x's. The phylogenetic network leading to a given population is in effect bounded by a skin, the 'phylogenetic envelope', that specifies the slice of space–time causally relevant to determining the abundance and composition of that population.
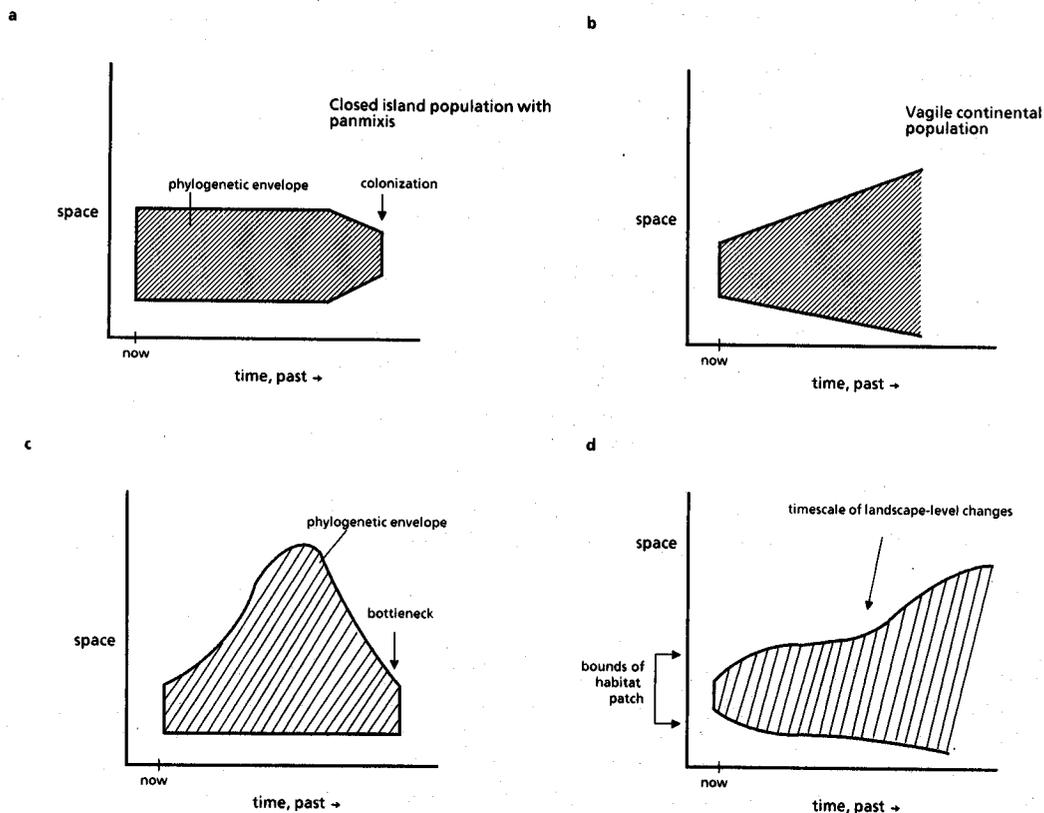
Figure 3. Examples of phylogenetic envelopes. (a) Closed, panmictic island population. (b) Vagile continental population. (c) Vagile continental population that descended from a long-ago bottleneck. (d) Vagile population in heterogeneous habitat. There is dispersal within a given contiguous habitat type, but little across distinct habitats. On long time-scales, the spatial structure of the landscape can change.

spatiotemporal scale for the evolutionary analysis of adaptation? The population one studies today is, in a quite literal sense, the last successful pass of a phylogenetic lineage through a complex sieve of past temporal and spatial environments. The relevant sieve for characterizing the evolutionary forces that led to a given population is a highly biased sample of the array of potentially available past environments. How should we characterize this biased sample?

To characterize heuristically this biased sample of past environments, we display the ancestry of a population as a reticulated web on a space–time plot, where each link in the network couples an actual ancestor with an actual descendant (Fig. 2). Surrounding this web of actual ancestors is a kind of penumbra of potential ancestors, individuals who lived in the same population(s) as those ancestors but did not leave descendents. The web plus this penumbra are bounded by a space–time envelope which we call the 'phylogenetic envelope'. The phylogenetic envelope portrays the slice of the Earth's surface through space and time generating the current local population.

Different species should exhibit quite different phylogenetic envelopes. A population on a small oceanic island occupies a cylinder, stretching back in time, but not in space (Fig. 3a). By contrast, in a vagile continental species, the causal cone rapidly widens, and the ancestors of the
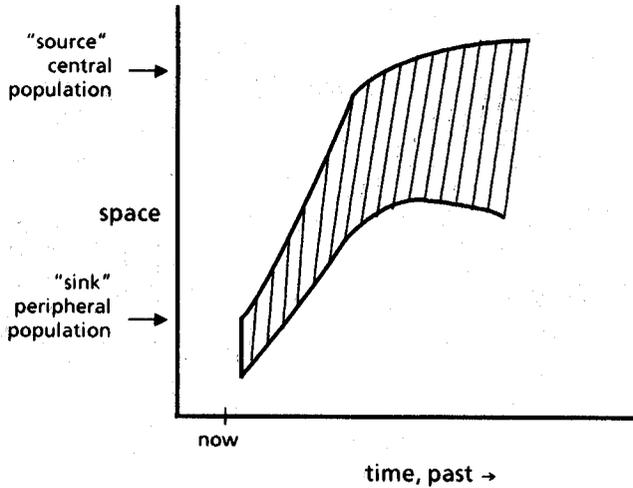
Figure 4. Individuals in sink populations largely descend from individuals in source populations.

current population may have come from many different populations (Fig. 3b). In this case, the selective regime appropriate in the analysis of adaptation involves averaging over many different local populations (which may or may not inhabit distinct environments). Species that stem from a peripheral isolate may have phylogenetic envelopes that shrink as one goes back in time (Fig. 3c). Indeed, the shape of the envelope should reflect the spatiotemporal structuring of the landscape as a whole (Fig. 3d). Sink populations are at the end of phylogenetic envelopes that are mainly located in other habitats (Fig. 4).

The proper spatiotemporal arena for adaptive analysis is the sample of environments actually experienced by the individuals within the phylogenetic envelope. Consider an early successional species, such as a dandelion, which invades transient patches of open habitat that rapidly become unsuitable during succession as the canopy closes. All local dandelion populations may become extinct because of directional environmental changes during succession, and the species may persist regionally only because frequent colonizations balance local extinctions. Thus, the species occupies a highly variable ecological environment. Nonetheless, the selective environment (*sensu* Antonovics *et al.*, 1989) of the dandelion may be quite constant when measured within the phylogenetic web. If all transient patches are on average the same, there is no reason to expect dandelions to be maladapted to the transient environments that are selectively relevant to their lineage.

Contrast this with the scenario for the evolutionary stability of the species' border sketched by Mayr (1963), which emphasized substantial gene flow from central to peripheral populations. In this scenario, many ancestors of individuals in the border population will have lived in central populations. Traits adaptive in the central population may be maladaptive in the peripheral population. A sustained asymmetry in dispersal should lead to the peripheral population being, to a degree, maladapted to its environment. Mayr's explanation of the species border can be generalized to any species in a spatially heterogeneous environment: if most individuals in a population trace their ancestry in the recent past to sites outside that population, it can potentially exhibit maladaptation to the local environment, to the extent that the local environment deviates from that experienced by the ancestral lineage.

Another way to state this is that if one examines the ancestry of populations not sustained by immigration, these ancestral populations to a first approximation should all have occupied habitats within their own fundamental niches.

An automatic bias in the evolution of the fundamental niche

Our main message is as follows: species adapt to conditions within their realized niches. Adaptation within the realized niche is weighted toward those regions of niche space in which abundance is greatest (see also Brown and Pavlovic, 1992). Because, on average, relatively few individuals of a persistent species are found outside the fundamental niche, species cannot readily adapt to regions of niche space outside their fundamental niches. This makes evolutionary changes in the fundamental niche an inherently conservative process.

We will illustrate this message with several simple models. Consider first a haploid population with discrete generations growing in two patches, equal in area, coupled by dispersal (as in Holt, 1987). We assume that *per capita* growth rates in the ancestral population are density-independent constants, R_i. Following reproduction, a fraction e of the subpopulation in each patch disperses to the other patch; the population is censused following dispersal. If $e < 0.5$, there is partial philopatry; if $e = 0.5$, the population is uniformly distributed, and if $e > 0.5$, individuals preferentially disperse from their natal habitat. In matrix form, this two-patch geometric growth model is

$$\begin{bmatrix} N_1(t+1) \\ N_2(t+1) \end{bmatrix} = \begin{bmatrix} R_1(1-e) & R_2e \\ R_1e & R_2(1-e) \end{bmatrix} \begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} \tag{1}$$

Because the entries in the matrix are assumed to be constant, we know (as with any projection matrix model) that: (1) the population settles into a stable patch distribution, with a constant proportion of the total population in each patch, and (2) in this stable patch distribution, the population grows at a constant rate. For the above model, the asymptotic growth rate of the population is

$$\overline{R} = \frac{1}{2}\left[(R_1 + R_2)(1-e) + \sqrt{[(R_1 + R_2)^2(1-e)^2 - 4R_1R_2(1-2e)]}\right] \tag{2}$$

The ancestral population is described by a pair of growth rates (R_1, R_2). To examine the direction of evolution of the fundamental niche, we consider the fitness of mutant alleles that increase by a small amount the fitness in one habitat, possibly (but not necessarily) at the cost of decreasing fitness in the other habitat. All genotypes are assumed to disperse at the same rate. The subpopulation spawned by any given mutant will itself be described by a pair of growth rates, (R_1', R_2'), leading to its own stable patch distribution and long-term growth rate (both typically different from that of the ancestral clone).

By formulating the model in this fashion, we are following the traditional practice of evolutionary genetics, which is to identify 'strategies' with fitness values. In evolutionary ecology, one instead usually starts with a strategy (e.g. body size), and then evaluates the fitness consequences of that strategy (e.g. as in the approach of Brown and Pavlovic, 1992; and see below). Because the fundamental niche is defined in terms of absolute fitness, we feel that it is useful to begin with the evolutionary genetics formulation.

Selection should favour a mutant that has a greater longterm growth rate than does the resident. There are two effects that should be considered. First, to evaluate whether or not a mutant slightly increasing, say, R_1 is deterministically favoured, we evaluate the sign of $\partial \overline{R}/\partial R_1$. Second, among those mutants that are deterministically favoured, selection needs to be strong enough to overcome stochastic effects on the chance of survival of a rare favourable allele

(Fisher, 1958). Increasing the magnitude of $\partial \bar{R}/\partial R_1$ (the strength of selection) increases the chances of fixation for a favourable mutation. Now,

$$\frac{\partial \bar{R}}{\partial R_1} = \frac{1}{2} \left[(1 + \frac{\partial R_2}{\partial R_1}) (1-e) + \frac{(R_1+R_2)(1 + \frac{\partial R_2}{\partial R_1}) (1-e)^2 - 2(1-2e)(R_2+R_1\frac{\partial R_2}{\partial R_1})}{\sqrt{[(R_1 + R_2)^2(1-e)^2 - 4R_1R_2(1-2e)]}} \right] \quad (3)$$

A similar expression (with indices 1 and 2 reversed) describes $\partial \bar{R}/\partial R_1$. We will not attempt a full explication of the range of implications of this expression here, but instead examine some illustrative special cases.

Let us first examine cost-free mutations: i.e. $\partial R_2/\partial R_1 = \partial R_1/\partial R_2 = 0$. By convention, we assume $R_1 > R_2$. Manipulating the above explanation leads to

$$\frac{\partial \bar{R}}{\partial R_1} \rangle \frac{\partial \bar{R}}{\partial R_2} \quad (4)$$

if $e < 0.5$. If $e = 0.5$, the inequalities become equalities; if $e > 0.5$, the inequalities are reversed. In other words, if we compare favourable mutants, each of which respectively increases the fitness within one or the other of the two loosely coupled patches by an equivalent small amount, the one more likely to be fixed is the one that improves fitness in the patch which initially had the higher growth rates, which is the one within the fundamental niche. Indeed, the relative strength of selection in the two habitats, in the limit $R_2 \to 0$, is $(\partial \bar{R}/\partial R_1)/(\partial \bar{R}/\partial R_2) = (2 - e)/3e$, which is large at small e.

The reason that mutants which improve fitness within the fundamental niche are at an advantage relative to mutants that improve adaptation outside the niche is simply that when the population is in its stable patch distribution, relatively more individuals are found in the patch with higher fitness (i.e. inside the fundamental niche). As such mutants arise and become fixed, the disparity in local growth rates faced by additional mutants increases. This enhances the relative advantage of mutants that improve fitness in the habitat to which the population is already better adapted.
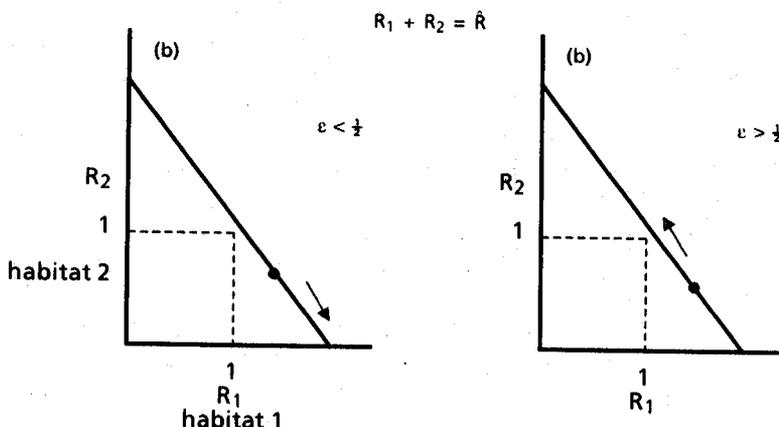

Figure 5. Evolution of patch-specific fitnesses, when summed fitness across the two habitats is unity. (a) With a modicum of philopatry ($e < 0.5$), selection favours increasing the fitness in the habitat in which fitness was initially higher. (b) With high migration rates ($e > 0.5$), selection favours equilibration in fitness across both habitats.

Of course, in the absence of any constraints, there are no ultimate limits on the evolutionary expansion of the fundamental niche. Such limits can be expressed as trade-offs, so that an increase in the growth rate in one habitat leads to a decrease in growth rate in the other habitat. As a simple example, let us assume that all feasible mutations are contained within a set, the outer boundary of which is described by a straight constraint line $R_1 + R_2 = R^*$ (which states that there are equitable trade-offs between fitness in the two habitats). The interesting evolutionary dynamics involves movement along the outer bound of this set (Fig. 5). Manipulating the above expression leads to

$$\frac{\partial \bar{R}}{\partial R_1} \quad \propto (1 - 2e)(R_1 - R_2)$$

$$\frac{\partial \bar{R}}{\partial R_2} \quad \propto (1 - 2e)(R_2 - R_1) \tag{5}$$

There are three cases to consider:

Case 1: $e = 0.5$ (i.e. a fine-grained distribution of individuals across habitats). Because $\partial R/\partial R_1 = \partial R/\partial R_2 = 0$, there is no selection for or against mutants along the constraint line.

Case 2: $e < 0.5$ (i.e. some philopatry). If $R_1 > R_2$, then

$$\frac{\partial \overline{R}}{\partial R_1} \; \rangle \; 0 \; \rangle \; \frac{\partial \overline{R}}{\partial R_2} \tag{6}$$

Hence selection favours an increase in fitness in habitat 1, but disfavours an increase in fitness in habitat 2: selection drives the population toward increasing specialization in the habitat in which fitness was initially the highest, and decreases adaptation in the habitat outside the fundamental niche. Evolution by natural selection is biased toward the habitat which initially contains the greater number of individuals, a situation that is automatically guaranteed if one couples by dispersal habitats within and outside the fundamental niche.

It is intriguing that this result depends only on the relative magnitudes of the habitat-specific fitnesses and not their absolute magnitudes; a species may start out with both habitats within its fundamental niche, and then evolve so that it drops one of them (see also Rosenzweig, 1974).

Case 3: $e > 0.5$ (i.e. there is a regular shuttling of individuals between the two habitats). Now Inequality 6 is reversed, and selection pushes the population toward equalization in fitness in both habitats (i.e. increasing generalization).

The simplicity of the above results depends upon the assumption of a linear constraint function of slope -1 describing the fitness trade-off between the two habitats. More generally, one describes the outer bound of the feasible fitness set by $F(R_1, R_2) = k$, where F has a negative slope. It would be desirable to examine this general model more fully. Here, we merely note that in the important limiting case where $R_2 \to 0$, selection prevents improvement of adaptation in habitat 2 (and thus expansion of the fundamental niche), when

$$\frac{2 - e}{3e} \; \rangle \; | \frac{\partial R_2}{\partial R_1} | \tag{7}$$

Thus, for selection to favour expansion in the fundamental niche, when originally the habitat outside has a very low fitness, the following are required: (1) a large increase in R_2, relative to the magnitude of the decrease in R_1, and (2) substantial mixing. For any given trade-off cost, there is a value of e below which selection favours only adaptations to habitat 1.

   The simple message of this model is that if a species straddles two habitats, one inside and one outside its fundamental niche, and dispersal occurs at slow enough a rate that it is reasonable to consider the system to be comprised of two populations coupled by dispersal, natural selection tends to favour continued improvement in the habitat that is already inside the fundamental niche, even at the expense of fitness outside it.

Evolution in sink populations

Density-dependence

One limitation of the above model might seem to be that it does not include density-dependence. The model developed above, taken at face value, leads to a population that eventually grows (or declines) geometrically. Some readers might therefore discount our suggestion that evolution is biased toward honing adaptation within the fundamental niche, because in nature most populations are expected to experience density-dependence. It therefore is useful to discuss a source-sink model with density-dependence to show that adding this does not affect our basic conclusion.

   The continuous-time clonal selection model we consider comes from Holt (1985, 1992). In the source patch the population experiences logistic population growth; dispersal occurs in a density-independent manner; and, the sink population in the absence of immigration declines exponentially. Within each habitat, the intrinsic growth rate is a function of an individual phenotypic variable, q. The model is as follows:

$$\frac{dN_1}{dt} = N_1[r_1 - bN_1] - \epsilon N_1 + \epsilon N_2 \tag{8}$$

$$\frac{dN_2}{dt} = r_2 N_2 + \epsilon N_1 - \epsilon N_2 \tag{9}$$

Assume first that the population is fixed for $q = q'$, $r_1 > 0$, and $r_2 < 0$. In the absence of dispersal, the source population equilibriates at $N_1 = r_1/b$, and the sink population equilibrates at $N_2 = 0$. With dispersal, the equilibrial densities of the source and sink are respectively $N_1^* = [r_1 + \epsilon r_2/(\epsilon - r_2)]/b$, and $N_2^* = N_1^*\epsilon/(\epsilon - r_2)$.

   Now consider the initial fate of a mutant that arises in an equilibrial population with a slightly different value for q, but the same b (i.e. it experiences density-dependence in the same way as the resident clone, but may grow at different rates in the two habitats). When rare, it will not perturb the equilibrial densities, and so its initial growth can be described as exponential growth in two patches coupled by dispersal. Let N'_i be the abundance of this clone in patch i, and F_i be its fitness (= *per capita* growth rate, discounting dispersal) there; in our system, $F_1 = r_1(q) - bN_1^* > 0$, $F_2 = r_2(q) < 0$. The asymptotic exponential rate of growth of this clone is (Holt, 1985)

$$\bar{r}(q) = \frac{F_1 + F_2}{2} - \epsilon + \sqrt{(\epsilon^2 + Q^2)} \tag{10}$$

where $Q = (F_1 - F_2)/2 > 0$. To determine if the invading clone can increase when rare (note that the resident clone is at equilibrium, so $(q') = 0\bar{r}$, we evaluate the sign and magnitude of

$$\frac{d\bar{r}(q)}{dq} = \frac{1}{2}\left[\frac{dr_1}{dq}\left(1 + \frac{Q}{\sqrt{(\epsilon^2 + Q^2)}}\right) + \frac{dr_2}{dq}\left(1 - \frac{Q}{\sqrt{(\epsilon^2 + Q^2)}}\right) \right] \tag{11}$$

where the derivatives and Q are all evaluated at $q = q'$. The quantities dr_i/dq describe the marginal effect of a small change in q on fitness in the source and sink habitats. The terms in parentheses determine the relative weighting given to these marginal effects in determining the overall direction of selection. Inspecting these weighting terms shows that because $Q(q') > 0$ (i.e. for the resident clone, fitness in the source is greater than fitness in the sink), the marginal effect in the source is always weighted more heavily than the marginal effect in the sink. Moreover, an increase in Q (corresponding to an increase in the fitness difference between the source and the sink) diminishes the importance of the marginal effect on fitness in the sink. In the limiting case of $Q \gg \epsilon$, (e.g. the sink has quite low fitness, or there is low dispersal) the overall direction of selection is almost entirely dominated by fitness maximization in the source, irrespective of the effect in the sink.

Hence, introducing density-dependence does not modify the conclusion that adaptive evolution is biased toward the source patch, which is the one already within the fundamental niche.

Unidirectional dispersal

Another seeming limitation of the above model is that it assumes symmetrical *per capita* dispersal rates between the two habitats. It is useful to distinguish two distinct kinds of sink populations: 'black hole sinks', and 'leaky sinks'. A black hole sink is one in which there is immigration but no back-migration to the source population. A leaky sink, by contrast, is one in which there is some dispersal from the sink back into the source. The above models deal with evolution in leaky sink populations.

The following argument suggests that selection will have a difficult time improving adaptation in a black hole sink, at least if we consider evolution via the accumulation of mutations, each of small effect. Assume that the sink dynamics are described by a model of geometric decline (at rate $R < 1$) with a constant rate of immigration from the source:

$$N(t + 1) = N(t)R + I. \tag{12}$$

Thus, there is no inherent density-dependence in the sink (at the densities one is concerned with), and the population becomes extinct without immigration (as it should if the local habitat is outside the species' fundamental niche).

The sink population persists at an equilibrial size of $N^* = I/(1 - R)$. Now consider the fate of an allele initially at a low abundance N' that increases fitness in the sink habitat from R to R'; the allele is not present in the source, and thus not in the immigrants. The dynamics of this subpopulation is described by a geometric growth model: $N'(t + 1) = N'(t)R'$. The frequency of this locally-favoured allele in generation $t + 1$ is

$$p(t + 1) = N'(t + 1)/(N'(t + 1) + N(t + 1)) = R'N'(t)/(I + RN(t) + R'N'(t)). \tag{13}$$

Dividing through by $N(t) + N'(t)$ leads to

$$p(t + 1) = R'p(t) / [(I / [N(t) + N'(t)]) + R(1 - p(t)) + R'p(t)]$$

Assuming that the immigrant clone is at its equilibrial population size, and that the immigrant clone is rare, leads to $p(t + 1) = p(t)R'$.

Thus, a locally favoured allele increases when rare only if it has an absolute fitness exceeding one, regardless of its relative fitness. This will not be the case if the mutant has a small effect on fitness – given that the ancestral condition in the sink habitat, maintained by immigrants each generation, has absolute fitness less than one. This implies that a population which cannot persist except by the influx of immigrants is unlikely to evolve improved adaptations to its environment by the cumulative impact of mutants, each of small effect.

A quantitative genetic approach to fundamental niche evolution

One criticism that might be levelled at the above models is that they rely on unrealistic assumptions about the genetic basis of the characters that determine the fundamental niche. Elsewhere, we intend to examine more closely models that couple selection on a quantitative character and population dynamics, along the lines sketched in Pease *et al.* (1989) and Holt (1990). The essential ideas, though, can be laid out schematically without developing models in any detail.

A closed population outside its fundamental niche in generation *t* declines at a rate of $R(t)$, its mean absolute fitness in that generation. If the assumptions of Fisher's Fundamental Theorem (Fisher, 1958; Hartl and Clark, 1989; Holt, 1990) are met, at least to a reasonable approximation, then the per generation rate of increase in the mean absolute fitness of a sink population is equal to the additive genetic variance in fitness, $G(t)$, available to selection in that generation. Taking this idea at face value, the joint recursion in population size and population growth rates is $N(t + 1) = R(t)N(t)$, and $R(t + 1) = R(t) + G(t)$, where $R(0) < 1$. In a deterministic world, so long as $R(0) > 0$ and $G(t) > 0$, there will come some time in the future when $R(t) > 1$, and, presto, the population will have evolved such that the environment it inhabits is now within its fundamental niche!

So there appear to be no intrinsic limits to how labile the fundamental niche of a species might be. But there are several weak links in the argument leading to this conclusion. (1) It neglects the fundamental demographic fact that the population is initially declining. Unless $G(t)$ is large, the population is likely to decrease to levels where it is likely to become extinct because of demographic stochasticity. If absolute fitness sharply declines for environmental states outside the fundamental niche, populations outside their ancestral fundamental niche are not likely to persist long enough for evolution to change their niche characteristics. (2) It assumes that selection does not severely deplete genetic variance in fitness, but this may be false (Charlesworth, 1987). Populations that are declining suffer increasingly severe genetic bottlenecks as time proceeds, depleting the pool of variation available for selection. (3) It ignores the potentially complex effects of immigration, which both continually re-introduces individuals maladapted to the local environment, thereby diluting the effects of local selection, and replenishes the pool of genetic variation available for selection. All these effects become more pronounced, the lower the initial growth rate of the sink population and the smaller its initial population size.

Conditions favouring evolution of the fundamental niche

These observations lead to a number of tentative conclusions about the circumstances allowing evolution in the fundamental niche in a heterogeneous environment where individuals encounter different environments in a coarse-grained fashion. If populations are to come to occupy successfully environmental states from which they were once excluded, the environmental states in question should not be too different from the environments to which the species is already adapted; otherwise, the local population is likely to become extinct rapidly before selection can be effective (in the case of a secular environmental change), or too few individuals will be able to persist outside the fundamental niche for them to weigh heavily in selection (in the case of two coupled habitats). We might be more likely to observe adaptive modification in the fundamental niche along gradual spatial gradients in the environment, which ensures the juxtapositions of habitats only slightly deviating from the conditions required for population persistence, than where there are abrupt transitions. However, if the gradients themselves are shifting through time, the main response of the species may be to track an optimum across space rather than to change in fundamental niche (Pease *et al.*, 1989).

Consider a population which experiences a constant environment at state A in Fig. 1. This population has equilibrated at N^*. The environment now suddenly shifts to state B, and in this new environment the population has a constant *per capita* growth rate $R < 1$. The population will be in imminent danger of extinction when its abundance has declined to N_{crit}. The number of generations T_{crit} elapsing before that critical threshold is reached is $T_{crit} = (\log[N^*] - N_{crit})/|\log[R]|$. The larger the initial population size, the more generations natural selection will have to modify the fundamental niche in a direction permitting the population to persist, and the larger the pool of variation is likely to be on which selection can act (for the reasons sketched in Holt, 1987). Moreover, if the new environment is only slightly outside the original fundamental niche, $|\log[R]|$ is small, and many generations will be available for selection to operate. In a changing environment, adaptive evolution is most likely to be observed if the changes occur slowly and continuously, so that populations are never pushed too far outside their fundamental niche. In other words, the opportunity for evolution in the fundamental niche should reflect the spatiotemporal texture of the environment as experienced within the phylogenetic envelope.

It is of course possible that changing the assumptions in the above models about how density-dependence operates, or introducing asymmetrical dispersal, might facilitate evolution of adaptation to the sink habitat. An assumption of the above models is that the source and sink habitats are of the same areal extent, so that relative densities reflect relative local population sizes. When this is not true, in some circumstances sink populations can sometimes contain more total individuals than do the source populations (Pulliam, 1988); this is most likely if there is strong compensatory density-dependence in the source, and a slow rate of population decline in the sink (i.e. the sink habitat is near the edge of the fundamental niche; Holt, 1992). This could provide another route for the evolution of the fundamental niche.

Another mechanism that might permit shifts in the fundamental niche arises from the multidimensional character of the niche, and functional interactions among different niche
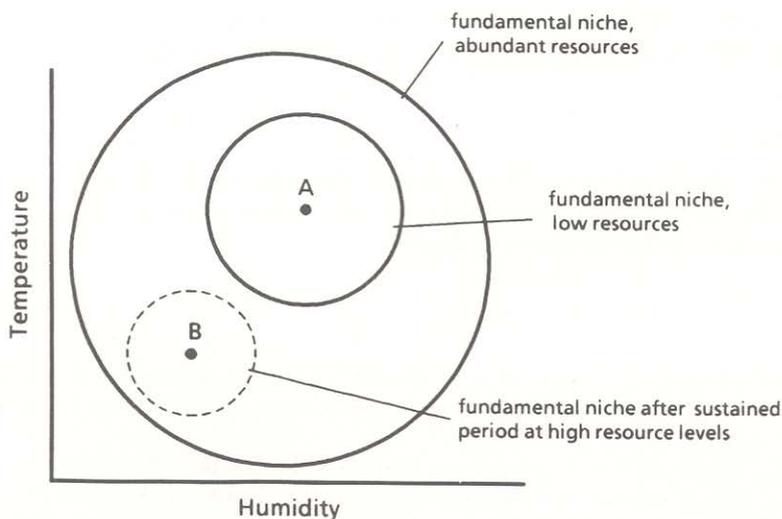

Figure 6. The fundamental niche for two abiotic conditions, as a function of resource levels. Populations can persist over a wider range of abiotic conditions when resources are abundant. This allows colonization, with subsequent adaptation to, abiotic conditions that are impossible to colonize during lean resource years. (See text)

dimensions. In Fig. 6, we indicate how the fundamental niche with respect to our two environmental variables of temperature and humidity might vary in response to fluctuations in a third, resource level. Initially resources are low, and for the reasons sketched above, adaptive evolution improves the species ability to utilize a habitat at state A, even at the expense of its ability to persist in a habitat at state B. If resource levels now increase, and remain high for substantial periods of time, a population can become established and persist in the state B habitat. Once there, selection can hone adaptation to the new environment, and if the environment eventually becomes impoverished the niche boundaries of the population may have shifted sufficiently for it to persist. In terms of the phylogenetic envelopes of Fig. 3, for a population to move its fundamental niche from point A to point B, there must be some trajectory of intermediate environments occupied by a chain of ancestral populations, each within or very near the fundamental niche of its own ancestral population.

Interpreting the adaptive evolution of the fundamental niche of a species therefore requires us to analyse the continuity in space and time of the environments sampled by its constituent populations as they weave together to form the phylogenetic web. If the experienced environment varies smoothly rather than in large, discrete jumps, this makes it more likely for the fundamental niche to itself evolve, thereby allowing a phylogenetic lineage to bootstrap itself through niche space. This obviously must happen in evolution, but we suspect that often the texture of the environment includes step functions, across which adaptive evolution is unlikely to happen. Stasis in the fossil record may sometimes reflect a basic conservatism in species' fundamental niches, circumscribing the range of relevant selective environments, rather than developmental or genetic constraints on the variation exposed to selection in those environments.

If fundamental niches are indeed evolutionarily conservative characters, as we have argued, in a certain sense organisms inherit their environments, as well as their genes, from their ancestors. Because evolution patently requires the persistence of phylogenetic lineages over many generations, the populations comprising those lineages must all to a reasonable approximation be within their fundamental niches. Thus, all of microevolution, necessarily, occurs within the constraints of the evolutionary dynamics of the fundamental niche. The fundamental niche thus proves to be even more fundamental than one might at first think, in that it is – or should be – a fundamental concept for the analysis of character evolution, as well as in ecology.

Acknowledgements

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