

Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism

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Summary

I suggest that there may be a fundamental conceptual unity between two seemingly disparate phenomena: (1) senescence (the progressive deterioration in physiological function and, thus, individual fitness with age) and (2) niche conservatism (the observation that species often seem rather fixed over evolutionary time in their basic niche properties). I argue that both phenomena arise from demographic asymmetries. The evolutionary theory of ageing rests on the observation that the force of selection declines with age, reflecting the basic demographic facts that in persistent populations there are always fewer individuals in old than in young age classes and these individuals tend to have lower reproductive value. A similar demographic asymmetry arises when populations inhabit environments with source habitats (i.e. where conditions are within the species' niche) and sink habitats (where conditions lie outside the niche): there tend to be more individuals in sources than in sinks and individuals in sources have relatively higher reproductive values. These demographic asymmetries should often imply that the force of selection is greater in sources than in sinks, leading automatically towards niche conservatism. I suggest that niche evolution is most likely in circumstances where these demographic asymmetries in space weaken or reverse.

Keywords: niche evolution; niche stasis; senescence; source-sink dynamics; stage-structured populations

Introduction

A central aim of science is to seek out simple principles which unify our understanding of disparate phenomena. The purpose of this paper is to point out a fundamental unity in evolutionary explanations that have been proposed for two widespread and important phenomena – ageing or senescence in age-structured populations and the phylogenetic conservatism of species niches. Both phenomena, I suggest, similarly reflect the role of demographic constraints in evolution.

The body of the paper develops an intuitive, verbal argument to support this suggestion; the Appendix presents a more formal analysis. The core ideas described below are, I believe, more general than embodied in the specific models examined by myself and others to date and can be understood and evaluated by readers reluctant to wade through pages of derivations.

Evolutionary explanations for ageing

One of the intellectual triumphs of life-history theory is the development of a general evolutionary theory for ageing or senescence. The evolutionary theory of senescence (Hamilton, 1966; Rose, 1991; Charlesworth, 1993; Charnov, 1993) rests on the simple – but profound – observation that the force of selection declines with age. This decline in the force of selection

reflects two underlying demographic facts: (1) in a persistent, age-structured population, the stable age distribution is always biased toward younger age classes and (2) after the first age of reproduction, younger age classes tend to have relatively high reproductive values, compared to older age classes. The former fact implies that the effects of any given genetic mutation are most likely experienced early in life, rather than later. The latter fact indicates that in evolutionary dynamics, 'success breeds success'. For instance, a small increase in survivorship early in life, relative to a similar increase late in life, is relatively advantageous because (1) it is experienced by a larger fraction of the population (there are more young than old individuals, given a stable age distribution in a persistent population) and (2) an incremental increase in survival at young ages, near the age of first reproduction, moves individuals into ages that are also young, which tend to have a high expected reproductive value (relative to similar increments late in life).

Evolutionary explanations for niche conservatism

A phenomenon that has long puzzled evolutionary biologists is niche conservatism (Bradshaw and McNeilly, 1991; Holt, 1990; Ricklefs and Latham, 1992; Travis and Futuyma, 1993; by 'niche', I mean that range of environmental conditions, resources, etc. which permit a species' populations to persist without immigration). The basic observation is that many phylogenetic lineages seem to retain much the same ecological niches over substantial spans of evolutionary history, in the face of pronounced spatial and temporal heterogeneity in the environment (e.g. Coope, 1979; Bradshaw, 1991). The seeming evolutionary stasis of many species' borders (Mayr, 1963) may reflect niche conservatism. For instance, Huntley *et al.* (1989) observed that the distribution of *Fagus sylvatica* (European Beech) in western Europe has climatic limits quite similar to the climatic range limits of *Fagus grandifolia* (American Beech) in eastern North America. Yet these congeners have been separated from their most recent common ancestor for tens of millions of years! This would seem to be a compelling example of niche conservatism.

One explanation for niche conservatism is the absence of appropriate genetic variation a condition called 'genostasis' by Bradshaw (1991). Another class of explanations comes from the interplay of evolutionary and population dynamics (Bell, 1988; Gomulkiewicz and Holt, in press). Recently in this journal (Holt and Gaines, 1992; see also Holt, in press; T.J. Kawecki, 1995) I presented an ecological explanation for niche conservatism based on the influence of demographic constraints on selection in spatially heterogeneous environments. The basic idea is that stabilizing selection on the niche may automatically arise from the population dynamic consequences of species' having niches in the first place, given environmental heterogeneity at spatial scales sufficiently large to encompass habitats both within and outside a species' niche (Holt and Gaines, 1992).

Habitats within a species' niche can sustain 'source' populations, which via dispersal maintain 'sink' populations in habitats outside the niche (Shmida and Ellner, 1984; Holt 1985; Pulliam 1988). Source-sink dynamics may be common at species' borders. The reason to expect niche conservatism in environments with a source-sink structure is simply stated: the force of selection is stronger in the source than in the sink, because (1) evolution tends to favour adaptive improvement in the habitat that harbours the greatest number of individuals and (2) evolution tends to favour adaptive improvement in the habitat in which individual fitness is highest (Holt and Gaines, 1992). Typically (if not always, see Pulliam, 1988; Holt, in press; T.J. Kawecki, 1995, sources have higher abundances and fitnesses than do sinks and, hence, evolution by natural selection should be biased toward honing adaptation to sources, rather than to sinks.

In effect, demographic asymmetries (both in habitat-specific abundance and fitness) 'weight' the direction of selection towards source habitats. In a remarkable flurry of intellectual

convergence, four groups of investigators coming from quite different initial questions have independently discovered that in a spatially heterogeneous environment, adaptive evolution tends to be biased toward sources and away from sinks (Brown and Pavlovic, 1992; Holt and Gaines, 1992; Houston and McNamara, 1992; Kawecki and Stearns, 1993. Holt and Gaines (1992) explicitly drew out the consequences of this observation for niche evolution and conservatism (see also Holt, *in press*; T.J. Kawecki, 1995), using a particular two-patch model. The models considered by these authors differ considerably in detail. The broad similarity in our results suggests that my assertion that adaptive evolution in source-sink environments tends to be biased toward sources may be quite robust.

The simple model examined in Holt and Gaines (1992; see also Holt, 1987; McPeck and Holt, 1992) assumed two habitat patches of equal area are coupled symmetrically by dispersal, but differ in abiotic or biotic factors that influence absolute fitness (i.e. local population growth rates). This and similar models (e.g. T.J. Kawecki, 1995) are examples of stage-structured population models (Caswell, 1989), in which 'stage' can be identified with the occupancy of a particular habitat patch. In a patchy environment with dispersal, the stable patch distribution (namely, the fraction of individuals found in each patch at demographic equilibrium) tends to be biased toward source habitats and, moreover, individuals in sources have higher mean fitnesses (as measured by reproductive value) than do individuals in sinks.

Using either the formal machinery of eigenvalue sensitivity analysis developed by Caswell (1989) or brute force analyses (as in Holt and Gaines, (1992), Holt, (*in press*) and T.J. Kawecki (1995)) one can show that the force of selection does tend to be stronger in source habitats, particularly at low dispersal rates. In the Appendix, I present an eigenvalue sensitivity analysis for a two-patch source-sink model. This analysis helps distinguish circumstances tending towards niche conservatism from those which promote niche evolution.

Demographic constraints in evolution: a unifying principle

I suggest that there exists a fundamental conceptual unity between the evolutionary theory of ageing and evolutionary theories of conservatism in niche evolution: both phenomena reflect how demography channels adaptive evolution. The idea that demography can constrain evolution is not entirely new. For instance, Van Valen (1967, p. 124, personal communication) in a discussion on mortality selection in human newborns noted that 'selection [operates] most strongly on the most numerous classes of any phenotype'. However, I believe the importance of demographic constraints for evolution has not yet been accorded the importance it deserves in the thinking of evolutionary biologists. Once our conceptual antennae are appropriately tuned, I suspect we will detect the importance of demographic constraints all over the evolutionary landscape.

Genetic mechanisms for niche conservatism

As in the evolutionary theory of ageing, a full understanding of niche conservatism will require a consideration both of the selective environment (including demographic constraints) and genetics. The genetic mechanisms that may underlie senescence include the biased accumulation of deleterious mutations acting at later rather than earlier age classes ('the mutation theory of senescence') and trade-offs between gene effects early and late in life ('the antagonistic pleiotropy theory of senescence') (Rose, 1991). A very active area of empirical work is discerning which of these plausible mechanisms actually accounts for senescence in natural or laboratory populations (e.g. Charlesworth, 1993).

I suggest that a similar classification of genetic mechanisms may pertain to the phenomenon of niche conservatism. Consider first the fate of deleterious mutations with habitat-specific effects.

As shown in Holt and Gaines (1992), selection often acts more weakly to remove mutants with deleterious effects in the sink habitat. If the abundance of deleterious mutants in the population is maintained in a mutation-selection balance, a greater load of habitat-specific mutants should be maintained which are expressed in the sink environment, than of mutants with deleterious effects in the source environment. The existence of this genetic load increases the fitness differential between habitats, which tends to further weaken selection against sink-specific deleterious mutations; thus, the degree of maladaptation to the sink habitat might increase over evolutionary time. Moreover, because selection against variant phenotypes is weaker in sink environments, one might expect increased genetic variance in such environments, for instance because of poorer canalization in development (as suggested by Van Valen (1967) and more recently by S. Stearns and T. Kawecki (personal communications)).

Part of the folk wisdom of evolutionary biology is that specialization leads to adaptive decay for environments outside the domain of specialization. Jaenike (1993) has recently described a lovely example of rapid niche decay in a nematode, *Howardula aoronymphium*, which parasitizes species of mushroom-breeding *Drosophila*. Jaenike (1993) cultured a strain of the nematode which initially could parasitize several alternative host species on a single host species. After 50 generations, this strain had lost its ability to parasitize two of these alternative hosts. Jaenike (1993) suggests that by having restricted the parasite to just a single host species, any alleles specifically beneficial on alternative host species were, in effect, rendered neutral and so could be lost by drift; likewise, deleterious mutations on these alternative hosts would not be selectively eliminated and could have increased by drift. This and other like examples may in a real sense instantiate 'the mutation theory of niche conservatism'.

An alternative class of genetic explanations for niche conservatism can be dubbed 'the antagonistic pleiotropy theory of niche conservatism'. If trade-offs among habitats are sufficiently strong, a species' niche may be evolutionarily conservative even if some individuals are persistently found in sink populations outside the niche (Brown and Pavlovic, 1992; Holt and Gaines, 1992; Holt in press; T.J. Kawecki, 1995; Table 3 in the Appendix). The relevant trade-offs involve fitness.

Fitness, of course, is a function of a broad spectrum of factors, including individual phenotypic traits, habitat-specific density-dependence, habitat selection (Rosenzweig, 1987), abiotic factors and interspecific interactions such as competition and predation. Ascertaining the nature of the trade-offs underlying observed instances of niche conservatism will require one to weave together threads from individual, population and community ecology. Moreover, the evolutionary response of a lineage to a spatially heterogeneous environment depends on both its dispersal biology (e.g. density-independent versus density-dependent dispersal; see Holt (in press), and Appendix) and the spatial structure of the landscape (T.J. Kawecki, 1995). If we are to develop mechanistic explanations for niche conservatism, we must thus seriously foster the long-announced (Lewontin, 1968) – but rarely consummated – marriage of ecology and evolution.

Strong and weak asymmetries in evolution

The near-universality of senescence rests on the fact that time flows in only one direction (Charnov, 1993). In stationary populations in their stable age distributions, the unidirectional flow of time necessarily implies that the number of individuals present declines monotonically with age; a complementary effect is that reproductive value typically (but not necessarily) declines with age after the first age of reproduction.

Niche conservatism, I have suggested here, may arise in part because of an analogous asymmetry in the demographic impact of habitats respectively within ('sources') and outside

('sinks') a species' niche. In a stationary population, the reproductive value of individuals in sources always exceeds that of individuals in sinks (see the Appendix). A complementary demographic effect is that the stable patch distribution is typically (but not necessarily) biased toward source habitats.

However, because spatial flows can be in two directions, niche conservatism intrinsically rests on a weaker asymmetry than does senescence in life histories. Recognizing this fact provides useful pointers as to when niches should be evolutionarily labile, rather than conservative. In some circumstances, substantial sink populations can be maintained (Pulliam, 1988) and contribute to the total breeding pool, setting up the pre-conditions for shifts or expansions in species niches (for theoretical examples, see Holt and Gaines (1992), Holt (in press), T.J. Kawecki, 1995 and the Appendix).

Moreover, natural systems are typically heterogeneous in time as well as space. A given habitat may be a sink for a particular species at some times (e.g. because a competitor or predator is abundant) but not at others (e.g. when those species are rare or absent), leading to variability in both expected spatial reproductive values and the stable patch distribution across habitats. Such variability can open up opportunities for rapid niche evolution. This contingency does not arise in life-histories: there are always more young than old individuals in a stationary population in its stable age distribution.

Towards a conceptual framework for interpreting niche conservatism and evolution

I believe that we are on the verge of developing a conceptual framework for interpreting the full range of evolutionary dynamics observed in the niches of species occupying heterogeneous environments – from rapid niche evolution to stasis. This framework will surely include as a major structural component asymmetries in the 'weights' arising from habitat-specific demography and dispersal in guiding the overall evolutionary trajectory of species.

It may be helpful to end with some concrete predictions as to when one might expect niche conservatism, versus niche evolution. I use as an illustrative system the two-habitat model analysed in the Appendix, which assumes that individuals disperse from a source to a sink at per capita rate e , that individuals back-disperse from sink to source at a rate e' and that the rate of population decline in the sink is $F_2 < 1$. The following paragraphs summarize salient conclusions from this model.

The force of selection for improved adaptation in the sink is weak – tending towards niche conservatism – in three broad circumstances, particularly if there are trade-offs in fitness between the habitats:

(1) The rate of movement from source to sink (e) is low. In this case, relatively few individuals are found in the sink. As Rosenzweig (1987) notes (see also Holt, 1987), if organisms are not found in a given habitat (either due to active habitat selection or simply due to low rates of dispersal), there is no opportunity for evolution to 'test' mutations that are potentially beneficial in those habitats. Evolution by natural selection is blindly channelled towards those habitats actually experienced by individuals in the current population, irrespective of potential benefits in habitats occupied rarely or not at all.

(2) The rate of movement from sink to source (e') is low. In the limit $e' \rightarrow 0$, we have what I call a 'black-hole sink'. Models for adaptive evolution in black-hole sinks (Holt and Gaines, 1992; R.D. Holt and R. Gomulkiewicz, manuscript in preparation) reveal that mutants with a small effect on fitness in the sink cannot increase by selection. Without back-migration, individuals in sink habitats are irrelevant in determining the direction of adaptive evolution.

(3) The sink is highly unfit (i.e. low F_2) and there are low to moderate dispersal rates (e.g. e and e' are both < 0.5). This implies low abundance in the sink and low reproductive values for those few individuals there; these demographic effects devalue the 'weight' natural selection accords to the sink, relative to the source.

Conversely, high rates of dispersal (i.e. high e and e') and not-too-bad sinks (i.e. F_2 near 1) tend to enhance the force of selection in the sink and thereby favour improved adaptation to the sink. High dispersal permits – and indeed forces – potentially beneficial mutants to be 'tested' in a range of environments (not just in favourable habitats) and this tends to equalize the demographic weightings accorded habitats. In these circumstances, given appropriate genetic variation, niche evolution is much more likely than is niche conservatism.

In conclusion, recognizing conceptual linkages between the evolutionary theory of ageing and the evolutionary theory of niche conservatism should help sharpen potential research agendas in future studies of niche evolution. These might include analyses of the genetic bases for niche conservatism, a sharper characterization of spatio-temporal structures in the environment which promote niche evolution versus conservatism and the development of laboratory bottle experiments to test theories of niche conservatism (akin to *Drosophila* experiments in ageing research; Charlesworth, 1993). All of these are ripe for further empirical and theoretical study.

Appendix

Here I present a formal model that buttresses the assertions made in the main text. The model permits one to make more precise predictions about niche conservatism and evolution, at least in certain limiting cases. For simplicity, assume there are two habitat patches occupied by a species with discrete generations. Let $N_i(t)$ be the population size in habitat i in generation t , a_{ii} the contribution to population recruitment made by patch i to itself and a_{ij} the cross-patch contribution from patch j to patch i . (In general, the a_{ij} may be functions of population density in each patch.) The following matrix model describes the dynamics of these two coupled patches:

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \end{pmatrix} \quad (\text{A1})$$

Special cases of this model have been analysed elsewhere (Holt, 1987; Holt and Gaines, 1992; McPeck and Holt, 1992; T.J. Kawecki, 1995). To facilitate synthesizing this earlier work and to set the stage for future work, I first present some basic machinery using the general matrix notation of Equation A1. I then analyse a concrete model with asymmetric dispersal and density dependence in one habitat (the source patch).

Given constant growth and dispersal rates, as with any matrix model (Caswell, 1989) the population settles into a *stable patch distribution* (the right eigenvector of the above matrix) with a defined fraction of the population in each patch, growing at rate $\lambda = (a_{11} + a_{22} + Q)/2$ (the dominant eigenvalue of the matrix), where $Q = (a_{11} - a_{22})^2 + 4a_{12}a_{21}$. A right eigenvector describing the stable patch distribution is $(w_1, w_2) = (\psi/2a_{21}, 1)$, where for notational convenience $\psi \equiv (a_{11} - a_{22} + Q)$. The fraction of the total population found in patch 1 is $w_1/(w_1 + w_2)$.

In an age-structured matrix model, the left eigenvector describes reproductive value – the contribution of an individual to future generations as a function of its age. For the above stage-structured patch model, the left eigenvector is $(v_1, v_2) = (\psi/2a_{12}, 1)$. The elements in this vector describe *spatial reproductive value* – the contribution of an individual to future generations (in both patches) as a function of which habitat it is now in. The relative contribution of an individual in, say, patch 1 to future generations is $v_1/(v_1 + v_2)$.

Note that $\psi = 2(\lambda - a_{22})$. For the population to be in demographic equilibrium, patch-specific fitnesses must be such that $\lambda = (a_{11} + a_{22} + Q)/2 = 1$. In general, this requires density dependence in at least one patch. At equilibrium, $\psi = 2(1 - a_{22})$. The spatial reproductive value and stable patch distribution vectors simplify respectively to $(v_1, v_2) = ([1 - a_{22}]/a_{12}, 1)$ and $(w_1, w_2) = ([1 - a_{22}]/a_{21}, 1)$.

Using this machinery, we now consider a more specific scenario. Let the net reproductive rate in patch i be F_i . Habitat 1 is a source (conditions there are within the species' niche) and habitat 2 is a sink (conditions there are outside the niche). Given no dispersal, we assume the sink population declines geometrically at rate $F_2 < 1$ and that the per capita growth rate in the source declines with density, such that $F_1(0) = F > 1$ and $F_1(K_1) = 1$ for $N_1 = K_1 > 1$. (I assume that density dependence is sufficiently weak to preclude stable population cycles or chaotic dynamics.) Without dispersal, the species equilibrates at K_1 in the source and disappears from the sink.

Immigration can maintain a sink population (Shmida and Ellner, 1984; Pulliam, 1988); moreover, emigration can depress source populations (Holt, 1985). I assume that each generation a bout of density-independent dispersal follows survival and reproduction in each habitat. A fraction e of individuals move from source to sink; a fraction e' move from sink to source. We census immediately following dispersal.

With these assumptions, $a_{11} = (1-e)F_1$, $a_{12} = e'F_2$, $a_{21} = eF_1$, and $a_{22} = (1-e')F_2$. I assume the population is at equilibrium, so $\lambda = 1$. This requires $F_1 > 1 > F_2$ (see Equation A5 below). Emigration lowers source density with a concomitant increase in fitness there, permitting the population to reach equilibrium. (Note: if the maximal per capita growth rate in the source is too low, the entire population risks extinction (Holt, 1985). Here, I assume source reproductive capacity suffices for persistence.)

I assume that available genetic variation is clonal or haploid in character and that mutations arise which can improve fitness in the sink. A rare mutant will initially experience density dependence mainly from the resident population. Such a mutant itself will spawn a clone, whose dynamics is described by a matrix model such as Equation A1 above; the eigenvalue of this matrix defines the rate of increase of this subpopulation when it has achieved its own stable patch distribution. The strength of selection associated with improving fitness in habitat i can be gauged by examining the marginal effect on λ of increasing F_i (see, e.g. Holt and Gaines, 1992).

In general, the sensitivity of the dominant eigenvalue to an increase in the matrix entry a_{ij} is proportional to $v_i w_j$ (Caswell, 1989). Selection is relatively stronger for transitions from classes that numerically dominate the population (i.e. large w_j) into classes with a high generalized reproductive value (i.e. large v_i). In a spatially structured population, the densities and fitnesses of source habitats tend to exceed those of sink habitats (with important exceptions; see Pulliam (1988) and below). This qualitatively supports the suggestion that the strength of selection may be greater in source than in sink habitats (i.e. $v_1 w_1 > v_2 w_2$).

Quantitative support for this assertion requires one to account for how changes in habitat-specific fitness simultaneously alter multiple elements in the transition matrix. We note that (following Caswell, 1989)

$$\frac{\partial \lambda}{\partial F_i} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial F_i} = \frac{1}{\langle v, w \rangle} \sum_{i,j} v_i w_j \frac{\partial a_{ij}}{\partial F_i} \quad (\text{A2})$$

(The normalizing constant $\langle v, w \rangle$ is the inner product of v and w .) After substitution, we arrive at the following expression for the sensitivity of the dominant eigenvalue to each patch-specific fitness (recall $\psi \equiv (a_{11} - a_{22} - Q)$):

$$\frac{\partial \lambda}{\partial F_i} = G \left[\frac{\psi^2}{4a_{12}a_{21}} \frac{\partial a_{11}}{175F_i} + \frac{\psi}{2a_{12}} \frac{\partial a_{12}}{\partial F_i} + \frac{\psi}{2a_{21}} \frac{\partial a_{21}}{\partial F_i} + \frac{\partial a_{22}}{\partial F_i} \right]$$

where $G = a_{12}a_{21}/[(1-a_{12})^2 + a_{12}a_{12}]$. The coefficients in the bracketed term describe how selection differentially 'weights' potential changes in fitness in the two habitats.

With the forms for a_{ij} assumed in the concrete two-patch model, we have

$$\frac{\partial a_{11}}{\partial F_1} = 1 - e, \quad \frac{\partial a_{12}}{\partial F_1} = e \frac{\partial F_2}{\partial F_1}, \quad \frac{\partial a_{21}}{\partial F_1} = e, \quad \frac{\partial a_{22}}{\partial F_1} = (1 - e) \frac{\partial F_2}{\partial F_1}$$

and

$$\frac{\partial a_{11}}{\partial F_1} = (1 - e) \frac{\partial F_1}{\partial F_2}, \quad \frac{\partial a_{12}}{\partial F_2} = e, \quad \frac{\partial a_{21}}{\partial F_2} = e \frac{\partial F_1}{\partial F_2}, \quad \frac{\partial a_{22}}{\partial F_1} = 1 - e$$

There are two ways to interpret the partial derivatives in the above expressions (corresponding to the two genetic models mentioned in the main text). First, the pool of variation in question may affect fitness only in habitat-specific ways. In this case, we set $\partial F_2/\partial F_1$ and $\partial F_2/\partial F_1 = 0$ and consider the effect of varying, say F_2 while keeping F_1 fixed. Second, we could imagine that variants lie along the edge of a fitness set (as in Rosenzweig, 1987), implying a functional relation between F_2 and F_1 . Given trade-offs in performance between habitats, both $\partial F_2/\partial F_1$ and $\partial F_1/\partial F_2 < 0$.

We now assume that we are examining evolution in a population at demographic equilibrium, so $\lambda = 1$. After substitution, we have

$$\frac{\partial \lambda}{\partial F_i} = G \left[\frac{(1 - a_{22})^2}{a_{12}a_{21}} (1 - e) + \frac{1 - a_{22}}{a_{12}} e' \frac{\partial F_2}{\partial F_1} + \frac{1 - a_{22}}{a_{21}} e + (1 - e) \frac{\partial F_2}{\partial F_1} \right]$$

and

$$\frac{\partial \lambda}{\partial F_i} = G \left[\frac{(1 - a_{22})^2}{a_{12}a_{21}} (1 - e) + \frac{\partial F_1}{\partial F_2} + \frac{1 - a_{22}}{a_{12}} e' + \frac{1 - a_{22}}{a_{21}} e \frac{\partial F_1}{\partial F_2} + e + (1 - e) \right] \quad (A3)$$

It can be shown that $\lambda = 1$ implies the following expression for realized source fitness:

$$F_1 = \frac{1 - (1 - e)F_2}{(1 - e) - (1 - e - e')F_2} > 1 > F_2 \quad (A4)$$

The first column of Table 1 shows for various limiting cases the realized fitness in the source that permits the population as a whole to be in demographic equilibrium. The set of fitnesses F_1 (given by Equation A5) and F_2 defines the initial condition against which the selective fate of new mutations of small effect are assessed.

The matrix elements a_{ij} can now be expressed entirely in terms of the dispersal parameters (e and e') and the sink fitness parameter (F_2). These can be substituted into Equation A3 to produce explicit expressions for the marginal effect on overall fitness of a small increase in F_i . To make further progress one must characterize the trade-off between fitness in the two habitats. As in Holt and Gaines (1992), it is useful to examine several simple but illuminating cases.

'Cost-free mutations'

If the class of phenotypic variants in question only affects fitness in a single habitat, (i.e. $\partial F_2/\partial F_1 = 0$), then $\partial \lambda/\partial F_i > 0$ for both $i = 1, 2$. However, if this is near zero, selection will be weak,

Table 1. Strengths of selection for 'cost-free' variation

Limiting cases	Source habitat fitness	Strength of selection in source	Strength of selection in sink	Bias toward source?
$e \rightarrow 0$	1	1	0	Yes
$e \rightarrow 1$	$\frac{1-(1-e')F_2}{e'F_2}$	$\frac{e'F_2}{2-(1-e')F_2}$	$\frac{1}{F_2[2-(1-e')F_2]}$	No
$e' \rightarrow 0$	$\frac{1}{1-e}$	$1-e$	0	Yes
$e' \rightarrow 1$	$\frac{1}{1-e+eF_2}$	$\frac{(1-e+eF_2)^2}{1-e+2eF_2}$	$\frac{e}{1-e+2eF_2}$	Yes, at lower e^a
$F_2 \rightarrow 0$	$\frac{1}{1-e}$	$1-e$	$\frac{ee'}{1-e}$	Yes at lower e, e'^b
$F_2 \rightarrow 1$	1	$\frac{e'}{e+e'}$	$\frac{e}{e+e'}$	Yes, if $e' > e$

^aThe precise condition is $1-3e+e^2F_2^2 > 0$.

^bThe precise condition is $1 > 2e+e^2+ee'$.

Table 2. Qualitative conclusions for 'cost-free' selection

Parameter change	Effect on strength of selection	
	In source	In sink
Source-to-sink $e: 0 \rightarrow 1$	Weaker	Stronger
Sink-to-source $e': 0 \rightarrow 1$	Stronger	Stronger
Sink 'quality' $F_2: 1 \rightarrow 0$ (moderate to low dispersal, $e, e' > 0.5$)	Stronger	Weaker
$F_2: 1 \rightarrow 0$ (high dispersal, $e, e' > 0.5$)	Weaker	Stronger

permitting locally advantageous alleles to be lost or deleterious alleles to spread, because of drift. (This case is the 'deleterious mutation theory of niche conservatism'.) Holt and Gaines (1992) showed for the special case $e = e' < 0.5$ that $\partial\lambda/\partial F_1 < \partial\lambda/\partial F_2$: advantageous mutants (with a given effect on fitness) spread more rapidly in the source than in the sink and deleterious mutants are selected against more strongly in the source. The magnitude of this difference increases at small e and low F_2 .

Table 1 shows the strength of selection for limiting cases in our more general model, which permits asymmetry in dispersal. Table 2 describes the qualitative effect of parameter changes on the strength of selection on habitat-specific fitnesses. In general, the strength of selection is weak to negligible in the sink if rates of dispersal either into or out of the sink are low. Moreover, when dispersal is low, decreasing fitness in the sink weakens the strength of selection in the sink and indirectly increases it in the source.

Table 3. Qualitative conclusions for 'rigid trade-off'

Limiting cases	Is sink evolutionarily stable? (\Rightarrow niche conservatism)
$e \rightarrow 0$	Yes
$e \rightarrow 1$	No
$e' \rightarrow 0$	Yes
$e' \rightarrow 1$	Yes, if $0 < 1 - 3e + e^2 + 2eF_2(1-e)e^2F_2^2$ (e.g. low e) No, otherwise
$F_2 \rightarrow 0$	Yes, if $2e - e^2 + ee' < 1$ (e.g. both $e, e' < 0.5$) No, otherwise
$F_2 \rightarrow 1$	Yes, if $e < e'$ No, if $e > e'$

'Rigid trade-off'

If there is a symmetrical, linear trade-off between the source and sink, such that $\partial F_2 / \partial F_1 = \partial F_1 / \partial F_2 = -1$, we have a special case of the 'antagonistic pleiotropy theory of niche conservatism'. Holt and Gaines (1992) showed that if $e = e' < 0.5$, the only mutants which can increase when rare are those which improve fitness in the source, at the expense of the sink.

After substitution into Equation A4, we can more generally address the question: When is the sink evolutionarily stable (tantamount to niche conservatism)? This is equivalent to determining conditions for $\partial \lambda / \partial F_2 < 0$, which says that selection actively impedes adaptation to the sink (because such adaptation is too costly back in the source).

Table 3 reports a number of limiting cases. The evolutionary stability of the sink habitat is more likely if dispersal rates are low (either into or out of the sink or both) and if the sink has low fitness to start with. This tendency towards niche conservatism is weakened if the sink has fitnesses not much less than one. Moreover, niche evolution is more likely if dispersal forces individuals into the sink and there is a high rate of dispersal back into the source.

Although here (as in Holt and Gaines, 1992) I have concentrated on a particular system (two patches with density-dependence in just the source), the general machinery provided above permits one to examine a variety of alternative dispersal mechanisms and assumptions about trade-offs in assessing the likelihood of niche conservatism versus niche evolution (e.g. see Kawecki (1995) for an analysis of niche evolution given habitats differing in area and Holt (in press) for an analysis of the consequences of density-dependent dispersal).

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