

Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution

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The most basic adaptation of a species is its ecological niche – that set of environmental conditions, resources, etc. which permit its populations to persist without immigration. Immigration from habitats with conditions within the niche (“source” populations) can sustain populations in habitats outside the niche (“sink” populations). Recent theoretical work on adaptive evolution in source-sink environments suggests that niche evolution should often be conservative, favoring the improvement or maintenance of adaptation to sources, at the expense of improved adaptation in sinks. Niche conservatism requires sinks to remain sinks over evolutionary time-scales. This paper uses models of coupled population and evolutionary dynamics in a spatially heterogeneous environment to examine the effect of density-dependence on niche conservatism and evolution. Density-dependence in birth, death, or dispersal rates can influence the relative evolutionary importance of source and sink habitats. Three distinct dispersal modes are compared. Species with density-dependent, ideal-free dispersal should exhibit niche conservatism. Species with passive or density-independent dispersal are more likely to show niche evolution, but only if rates of dispersal are sufficiently high and fitness in the sink is not too low. Species with active interference leading to a non-ideal free habitat distribution should be expected to be evolutionarily labile in their ecological niches. I conclude that the nature of density-dependence in dispersal may crucially govern the direction of niche evolution.

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The distribution and abundance of a species is largely set by its ecological niche and by density-dependence in birth, death and dispersal rates (Fowler 1987, Sinclair 1989, Royama 1992). Here, the term “niche” denotes the range of abiotic and biotic factors that permit populations of a species to persist (Hutchinson 1981). The niche of a species can be quantified in terms of intrinsic growth rate r (defined to be the expected per capita birth rate – death rate, evaluated in the absence of density-dependent effects) as a function of environmental conditions, resources, etc. A habitat has conditions within the niche of a species if $r > 0$ there, and lies outside the niche if $r < 0$. In habitats within the niche,

mean population abundance will reflect density-dependence in demographic rates.

Given genetic variation, evolution by natural selection can alter both a species’ ecological niche and its density-dependent demographic responses. Many evolutionary biologists (e.g., Coope 1979, Bradshaw 1991, Bradshaw and McNeilly 1991, Holt and Gaines 1992, Ricklefs and Latham 1992) have been struck by the seeming constancy of species’ niches over long spans of evolutionary time, even in the face of pronounced environmental heterogeneity. Understanding the factors leading to niche conservatism, or conversely niche evolution, is becoming increasingly urgent in our

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rapidly changing world (Holt 1990, Travis and Futuyama 1993).

Niche conservatism and source-sink dynamics

In this paper I explore the role of density-dependence in niche conservatism and evolution. We will assume that a species inhabits a heterogeneous landscape with habitats both within and outside the niche (i.e., sites where $r > 0$ and $r < 0$, respectively). Populations maintained by immigration into habitats outside a species' niche are "sink" populations (Shmida and Ellner 1984, Holt, 1985, 1993, Pulliam 1988). A species has "source-sink dynamics" if in "source" habitats, local births exceed local deaths, whereas in "sink" habitats, births do not match deaths. The demographic equation is balanced in all habitats because of a net flow of individuals from sources into sinks. Niche conservatism in a spatially heterogeneous landscape is tantamount to sink habitats remaining sinks over evolutionary time-scales.

The work reported here builds on ideas presented in Holt and Gaines (1992). There I argued that niche conservatism in source-sink environments may reflect an inherent asymmetry – namely, the force of selection for improving adaptation tends to be stronger in sources than in sinks. An evolutionary bias toward sources arises because of two demographic constraints: 1) evolution tends to favor adaptive improvement in habitat types experienced by the greatest number of individuals (often, though not always, habitats within the niche), and 2) evolution tends to favor adaptive improvement in the habitat in which individual fitness is highest (usually also habitats within the niche). There are strong parallels between my suggestion that niche evolution is channeled by demography and the more familiar role of demographic constraints in the evolutionary theory of aging (see Holt in press).

Typically (though not always, see below, Kawecki 1995, Holt in press) source habitats have higher abundances and fitnesses than sink habitats, and hence evolution by natural selection should be stronger for maintaining or improving adaptation in sources, rather than enhancing adaptation to sinks. Using different models, several investigators have recently converged on the conclusion that adaptive evolution has a bias toward sources (Brown and Pavlovic 1992, Holt and Gaines 1992, Houston and McNamara 1992, Kawecki and Stearns 1993). Holt and Gaines (1992) explicitly linked this effect to niche conservatism.

None of these authors, however, have considered in detail how density-dependence might influence this asymmetry in selection. In this paper I examine the interplay of density-dependence and niche evolution, and in particular the effect of density-dependent dispersal on niche evolution. I distinguish several distinct evolutionary roles for density-dependence, and then use

simple models to contrast evolutionary dynamics for three dispersal modes – passive dispersal, ideal-free habitat dispersal, and density-dependent dispersal due to interference. I will show that density-dependence in dispersal may crucially influence the direction of niche evolution in spatially heterogeneous landscapes and the likelihood that niches are evolutionarily conservative. Conversely, the outcome of density-dependent selection in a given habitat may be modified strongly by landscape-level heterogeneity.

The results presented here reinforce my belief that an important (if neglected) link between ecology and evolution comes from recognizing that population dynamics, filtered through dispersal, acts as a constraint on and modulator of evolutionary dynamics (Holt 1987a, in press, Holt and Gaines 1992).

Density-dependence: direct and indirect evolutionary effects

Density-dependence can play both direct and indirect roles in evolution (Holt 1987a). Population density directly influences natural selection (viz., density-dependent selection; Boyce 1984, Mueller 1991, Begon 1992, Clarke and Beaumont 1992) if relative fitness varies with density (i.e., the antagonistic pleiotropy in fitness between low and high densities in Fig. 1). Selection favors the phenotype that withstands the highest population density in a given environment (MacArthur 1962, Roughgarden 1981, Charlesworth 1994). With density-dependence, selection may favor different phenotypes in different habitats, even though habitat quality acts in an even-handed, non-selective fashion (e.g., compare low vs high mortality scenarios in Fig. 1).

One indirect role of density-dependence in evolution arises because density-dependence in birth or death

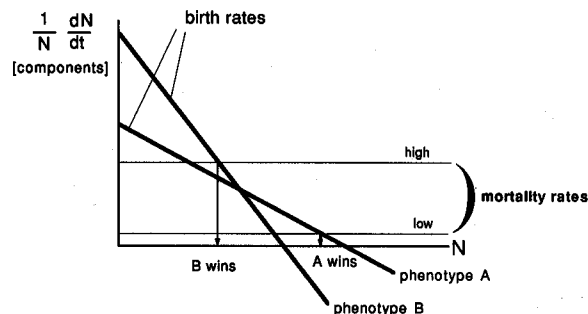


Fig. 1. A graphical model of density-dependent natural selection (after MacArthur 1962). Mortality is density-independent and equal in magnitude for each of two phenotypes; births are density-dependent. Phenotype A has a lower maximal birth rate than phenotype B, but experiences less severe density-dependence in birth. N is total population size. A phenotype is in demographic equilibrium when births equal deaths. In a low mortality environment, phenotype A wins; in a high mortality environment, phenotype B wins.

rates influences local population density. As noted above, adaptive evolution averages across spatial heterogeneity such that there is a bias toward habitats most frequently encountered by individuals, or, more precisely, toward those which contribute disproportionately to the overall population (Brown and Pavlovic 1992, Holt and Gaines 1992, Kawecki 1995, Holt in press). These habitats will usually have a relatively high carrying capacity. A second indirect effect arises from density-dependent dispersal. I will show that making dispersal density-dependent can dramatically change the direction of evolution by natural selection in a spatially heterogeneous environment.

General assumptions

Before describing any models in detail, it is useful to collate simplifying assumptions they all share. All models considered here assume continuous population growth in two habitat patches (one source, and one sink), equal in area and coupled by dispersal, and temporally constant environments (such that populations remain at or near their dynamic ecological equilibria). I further assume negative density dependence in the source (denoted habitat 1); per capita growth rate in habitat 1, F_1 , declines from a maximum of r_1 (the intrinsic rate of increase) with increasing population density, N_1 . In an adjacent sink (habitat 2) per capita growth rate is negative at all densities (with or without negative density-dependence).

As is customary in evolutionary game theory (e.g., Brown and Vincent 1987) I assume the simplest form of genetics, namely asexual clonal variation, with clonal types identified by their different fitnesses in different habitats. I focus on conditions for invasibility by mutant phenotypes of small effect into populations at demographic equilibrium. A population is in an evolutionarily stable state if such mutants fail to increase. Niche conservatism occurs if evolutionarily stable states include sink habitats that remain sinks.

At several points I use fitness sets (Levins 1968), which are graphical depictions of the range of phenotypes available for selection in a population. The outer bounds of fitness sets characterize tradeoffs, either within or between habitats, in performance measures such as density-independent growth rates or sensitivity to density-dependence. Although for concreteness specific models and fitness sets are used (e.g., logistic density-dependence with linear tradeoffs in local intrinsic growth rates) the results presented are indicative of effects in a much broader range of both ecological and genetical models. The results reported here provide springboards for analyzing more realistic, complex models.

Consequences of dispersal mode for niche evolution

Without dispersal, in a temporally constant environment the population equilibrates at densities $N_1^* = K_1$ and $N_2^* = 0$; there is no sink population at all. Sink populations exist only if there is dispersal (Holt 1993). There are three basic ways organisms might potentially move between a source and a sink habitat: 1) density-dependent, ideal-free (sensu Fretwell 1972) dispersal; 2) density-independent (passive) dispersal; 3) density-dependent non-ideal-free dispersal (e.g., due to interference). We will see that these dispersal modes qualitatively vary in their consequences for niche conservatism.

Model 1. Ideal-free habitat selection

Not all density-dependent dispersal produces sink populations. If individuals disperse so as to increase their fitness, and move freely without cost or interference, the population tends toward the spatial distribution known as the "ideal free distribution" (IFD; Fretwell 1972, see Morris 1992 for caveats). The IFD is characterized by the equilibration of fitnesses across space. In a population at demographic equilibrium, the average per capita growth rate is zero; all occupied habitats thus have a zero growth rate (Holt 1985). If the maximal per capita growth rate in a habitat is less than zero (a potential sink), at equilibrium that habitat should not be occupied at all; in other words, the IFD does not contain sink populations (Fig. 2a).

In the IFD (as with zero dispersal), no individuals experience potential sink habitats. Mutants enhancing fitness solely in sink habitats are not favored by selection; those with potentially harmful effects in the sink are not disfavored. Hence, we expect increasing specialization to habitats in which a species is more fit, unhampered by potential (unrealized) fitness costs in alternative, avoided habitats (Holt 1987a, Rosenzweig 1987). Thus, given IFD assumptions, potential sink habitats should remain potential sinks over evolutionary time – that is to say, the species will show niche conservatism.

Model 2. Sinks resulting from passive dispersal

Sink populations exist only because of mechanisms forcing some individuals to reside in habitats with lower fitness than the population average. One such mechanism is density-independent dispersal (Holt 1985, 1993). As Brown and Pavlovic (1992) observe, such dispersal can be viewed as a factor of the environment to which the population may evolutionarily respond.

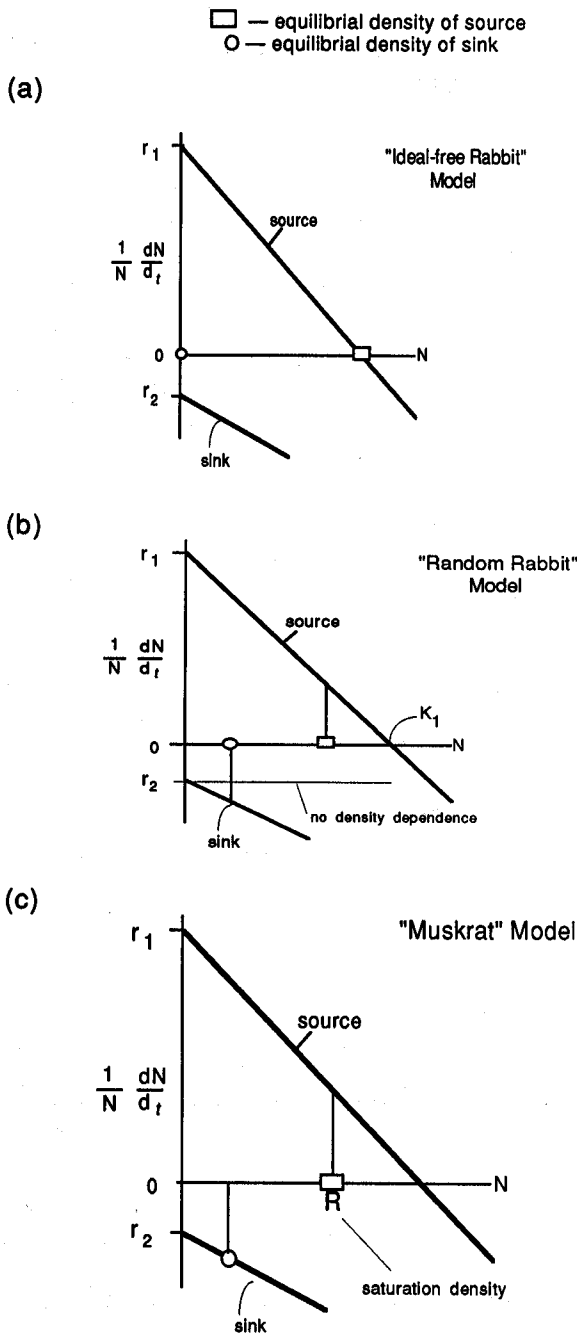


Fig. 2. Effects of dispersal on local density. In each case, habitat 1 is a source, and habitat 2 a sink. In this and subsequent figures, N denotes the density in either habitat. (a) In an ideal-free habitat distribution (sensu Fretwell 1972), at demographic equilibrium no individuals will be found in a sink habitat. (b) If there is passive dispersal, at equilibrium population density in the source is suppressed, and a population is sustained in the sink. (c) The source saturates at R individuals, with excess recruitment driven into the sink. The three graphical models are named for mammals, in honor of the VIth Theriological Congress, where this paper was presented.

For simplicity, assume that dispersal rates are equal in the two habitats, and that the two habitats are juxtaposed

(so there is no mortality during dispersal) and of equal size. Let N_i be population density in patch i , F_i the per capita growth rate there (including density-dependence), and ϵ a per capita, density-independent dispersal rate. A general model for dynamics in the two coupled patches is:

$$\frac{dN_1}{dt} = N_1 F_1(N_1) - \epsilon N_1 + \epsilon N_2,$$

$$\frac{dN_2}{dt} = N_2 F_2(N_2) + \epsilon N_1 - \epsilon N_2. \quad (1)$$

At equilibrium the habitat with higher carrying capacity sustains more individuals, with higher average per capita growth rates, than the other habitat (Holt 1985) (see Fig. 2b).

Brown and Pavlovic (1992) and Holt and Gaines (1992) have explored some aspects of evolution in heterogeneous environments using specific versions of (1). Here, I extend this earlier work by explicating the role of density-dependence, and by analyzing the evolutionary stability of sink habitats.

First consider a sink with no direct density-dependence, and logistic density-dependence in the source:

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

$$\frac{dN_2}{dt} = r_2 N_2 + \epsilon N_1 - \epsilon N_2. \quad (2)$$

Fig. 2b shows habitat-specific fitness functions matching the model (2). The parameters r_1 , ϵ and d (a measure of density-dependence) are positive; r_2 is negative. Without dispersal, the source equilibrates at its carrying capacity, $N_1^* = r_1/d$. Analyzing linear habitat-specific fitness functions is a useful point of departure, but it should be noted that fitness functions are often nonlinear (Sinclair 1989, Morris in press). Instead of parameterizing logistic growth with the usual r - K notation, I use r and d . The d parameter measures the strength in density-dependence (i.e., the marginal reduction in local growth resulting from a small increase in density); carrying capacity emerges as a balance between a population's inherent propensity to grow and density-dependence.

At equilibrium, source and sink densities and realized fitnesses are, respectively: $N_1^* = [r_1 + \epsilon r_2 / (\epsilon - r_2)] / d$, $N_2^* = N_1^* \epsilon / (\epsilon - r_2)$, $F_1(N_1^*) = -\epsilon r_2 / (\epsilon - r_2) > 0$, and $F_2(N_2^*) = r_2 < 0$. Realized local fitnesses are independent of the source intrinsic growth rate or density-dependence in the source. Population persistence requires $r_1 > -\epsilon r_2 / (\epsilon - r_2) > 0$; extinction is risked if r_2 is too low (Holt 1985). I assume population persistence.

Natural selection with passive dispersal in source-sink environments

A novel clone may experience a different growth rate from the ancestral type in either or both habitats. When the invader is rare, density-dependent effects stem largely from the resident clone, whose numbers can be

assumed fixed during the initial stages of invasion. After an initial transient phase an invader will enter a stable patch distribution and have an asymptotic exponential growth rate (Holt 1985)

$$\bar{r}(q) = \frac{F_1 + F_2}{2} - \varepsilon + \sqrt{\varepsilon^2 + Q^2} \quad (3)$$

where F_i is the realized per capita growth rate of the clone in patch i , and $Q = (F_1 - F_2)/2$ measures the spatial difference in fitness between habitats. I call Q the "fitness gradient". Q is positive (because habitat 1 is a source, and habitat 2 a sink). For model (2), at demographic equilibrium Q increases with decreasing r_2 .

Now assume the resident clone has phenotype $q = q'$ and is at demographic equilibrium, so $r(q') = 0$. To determine if an invading clone with a slightly different phenotype can increase when rare, we evaluate the sign and magnitude of

$$\frac{dr(q)}{dq} = \frac{1}{2} \left[\frac{dF_1}{dq} \left(1 + \frac{Q}{\sqrt{\varepsilon^2 + Q^2}} \right) + \frac{dF_2}{dq} \left(1 - \frac{Q}{\sqrt{\varepsilon^2 + Q^2}} \right) \right] \quad (4)$$

where the derivatives and fitness gradient Q are evaluated at $q = q'$ (as in Holt and Gaines 1992). The quantities dF_i/dq measure the marginal change in habitat-specific fitnesses generated by a small increase in q . The two terms in parentheses on the right side of (4) can be viewed as habitat-specific "weighting factors", determined jointly by habitat-specific demography and dispersal. These terms set the relative importance of each habitat in guiding the direction of evolution.

In the above model, the weight accorded by selection to the source always exceeds that given to the sink. Moreover, the fitness gradient Q is larger at greater rates of decline in the sink. This implies that the greater is the fitness gradient, the more heavily weighted selection will be towards the source.

Density-dependence plays a subtle role in generating the fitness gradient. Emigration depresses the source below its carrying capacity, leading to a compensatory increase in local fitness. The amount of back-migration from the sink into the source declines with decreasing sink fitness; the reduction in immigration secondarily decreases source abundance, further enhancing fitness in the source because of compensatory density-dependence. Both effects increase the fitness gradient as r_2 decreases, and hence the bias in selection toward adaptive improvement in the source.

In model (2), the evolutionary bias against the sink depends only on the degree of maladaptation in the sink and the dispersal rate. Demographic parameters in the source (i.e., r_1 and d) do not directly influence Q , and thus the relative evolutionary importance of source

and sink habitats. This effect changes dramatically with density-dependent dispersal driven by interference (see below).

The evolutionary stability of sink populations

We now turn to ascertaining the evolutionary stability of habitat sinks, qua sinks. First imagine that the phenotypic variation available for selection influences the intrinsic rate of increase (r), but not the strength of density-dependence (d , the slope of the fitness function in Fig. 1). One can then replace dF_i/dq with dr_i/dq . Fig. 3 shows an example of a fitness set bounding potentially available phenotypic variation. A source-sink population with habitat 1 as the source falls in the lower right quadrant. Open circles indicate starting conditions, and arrows relative strengths of selection provided by increasing habitat-specific fitnesses (with no fitness tradeoff between habitats).

Now assume the initial population is on the edge of the fitness set; improvement to one habitat thus implies decreased fitness in the other. For illustrative purposes, let this edge be represented by a straight line, $r_2 = M - sr_1$, where $M > 0$ is the maximal feasible growth rate in habitat 2, and the quantity $s > 0$ describes the strength of the tradeoff in habitat-specific intrinsic growth rates. Fig. 4 shows a family of possible

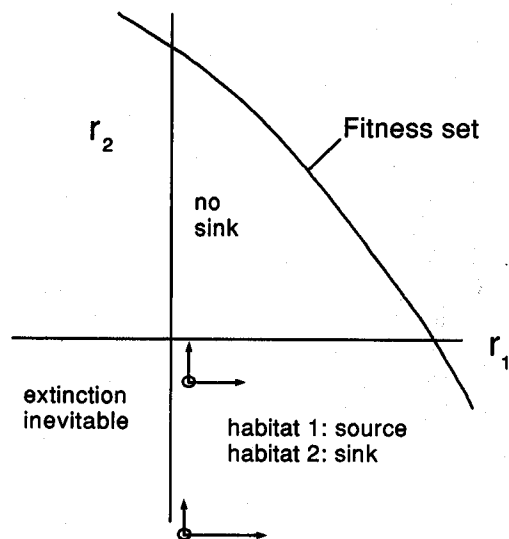


Fig. 3. A fitness set for intrinsic rates of increase in two habitats, the horizontal axis for habitat 1, the vertical axis for habitat 2. Points below the line denoted "Fitness set" are assumed to represent accessible phenotypic variation. A source-sink system occurs when one habitat has a positive r , the other habitat, a negative r . The two open circles show different initial combinations of source and sink growth rates. The relative lengths of the arrows denote the relative strengths of selection toward increasing growth rates in the two habitats, for a subset of variants that improve fitness in one habitat without cost in the other. The relative magnitude of selection improving fitness in the sink decreases as the sink becomes less fit.

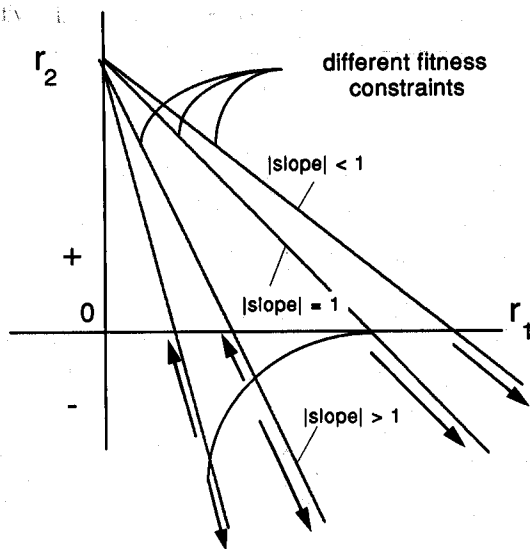


Fig. 4. Potential evolutionary outcomes for linear fitness constraints. Any point along a constraint line can represent a potential initial state. The arrows depict the direction of evolution, when mutants arise of small effect, but constrained to this line. As explained in the text, sinks are evolutionarily stable if the tradeoff constraint is sufficiently shallow, or if initial fitness in the sink sufficiently low.

linear fitness sets differing in s . The condition for fitness to increase in the source, at the expense of fitness in the sink, is

$$\frac{1 + \frac{Q}{\sqrt{\varepsilon^2 + Q^2}}}{1 - \frac{Q}{\sqrt{\varepsilon^2 + Q^2}}} > s \quad (5)$$

(With a nonlinear boundary for the fitness set circumscribing the intrinsic growth rates, the appropriate condition is found by replacing s with $|\partial r_2 / \partial r_1|$ in expression (5).)

Expression (5) quantitatively defines a condition for evolutionary stability of the sink habitat. Because $Q > 0$, (5) is always satisfied if $1 > s$. Thus, the sink is evolutionarily stable if along the edge of the fitness set near $r_2 = 0$, an increase in r_1 decreases r_2 by an absolutely smaller amount. Moreover, for any tradeoff s , there is some Q (which increases with $|r_2|$, the degree of maladaptation in the sink), above which selection favors continued improvement in the source – ensuring evolutionary stability of the sink, and thus niche conservatism.

Making the above inequality into an equality and solving numerically generates the curved line in Fig. 4, a threshold separating evolutionarily stable sink states from those which should be evolutionarily transient. If the initial population state lies above this line, evolution favors increased fitness in the sink. With sufficient time, via the accumulation of small adaptive improvements

the sink character of habitat 2 should disappear, and the population will be well-enough adapted there to persist without immigration. Thus, some sinks may be evolutionarily transient, and the species' niche will not be conservative over evolutionary time.

If, instead, the initial state lies below the threshold line, selection will not improve fitness in the sink habitat via cumulative, small adaptive changes. Decreasing ε (i.e., lower dispersal rates) presses the threshold line towards the R_1 -axis. As mutants which lower fitness in the sink arise and become fixed, the habitat fitness gradient Q increases; the positive feedback between the direction of evolution and the fitness gradient reinforces the evolutionary stability of the sink. The threshold line shown in the figure separates evolutionarily stable from evolutionarily unstable sink populations. For the former, in a constant environment the only evolutionary escape from a sink is for mutants to arise which either have large effect or break the constraint.

In this model three broad circumstances produce evolutionary stability of sinks. First, if adaptive improvement in the source is not too costly (as measured by decreased fitness in the sink) the sink will remain a sink. Second, if initial fitness in the sink habitat is too low, selection is weighted toward the source sufficiently to preclude adaptive improvement in the sink, even if adaptation to the source comes at substantial cost for individuals unlucky enough to occur in the sink. Third, in both cases evolutionary stability of the sink is more likely at lower dispersal rates (and evolution toward lower dispersal is predicted in spatially heterogeneous environments, see Morris 1991a, McPeck and Holt 1992). Fig. 5 illustrates how selection tends to shift

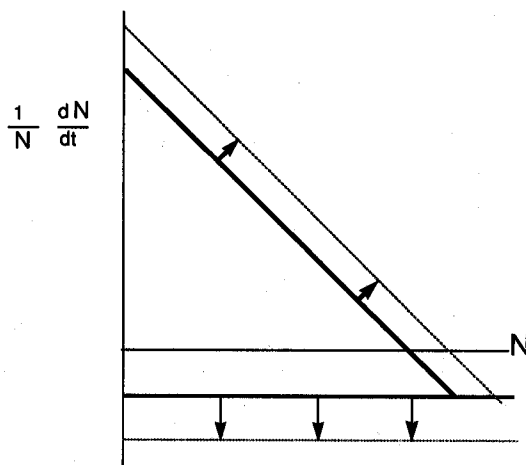


Fig. 5. The direction of evolution of habitat-specific fitness functions when a sink is evolutionarily stable, and the evolutionary trade-off is between intrinsic growth rates in the two habitats (with no density-dependence in sink; see text). The heavy lines are the initial state of the population. Variants arise along the edge of the linear fitness set shown in Fig. 4. In conditions described in text, selection increases r in the source, at expense of r in the sink.

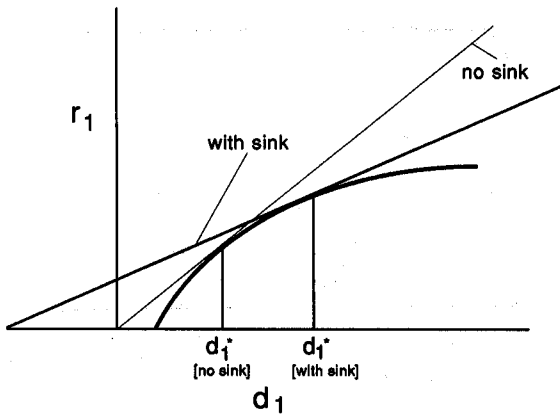


Fig. 6. Effect of sink on evolutionary balance between intrinsic growth rate (r_1) and sensitivity to density-dependence (d_1) in the source. The solid line shows that phenotypes with higher maximal growth rates are more sensitive to density-dependence. The optimal combination of parameters occurs when $\partial r_1 / \partial d = N_1^*$, which can be represented as a tangent line (thin lines in figure). The sink lowers N_1^* , and indirectly shifts the evolutionary balance towards higher maximal growth rates in the source.

habitat-specific fitness functions, given an evolutionarily stable sink.

There is a general message about the relation of population limitation and evolution implicit in these results. It might seem intuitive, indeed commonsensical, to believe that if a given ecological factor becomes increasingly severe in limiting a population, perforce the intensity of selection to adapt to that factor should be stronger. The above model demonstrates an exactly opposite relation between population limitation and selection. For fixed dispersal rates, an increase in the strength of an ecological factor depressing growth rate in the sink *reduces* the strength of selection favoring improved adaptation there. Such shifts in limiting factors also increase the risk of extinction; hence, those populations most in "need" of evolutionarily responding in their niches are the very ones least likely to do so.

The effect of sinks on density-dependent selection in the source

Now consider another kind of trade-off. Following MacArthur (1962) (and many others since), assume that an increase in r_1 comes at the expense of an increase in d (as in Fig. 6). The evolutionarily stable state of the source occurs when $\partial r_1 / \partial d = N_1^*$. The population dynamic effect of the sink is to decrease population size in the source, which declines with decreasing r_2 . At lower densities, the selective effect of density-dependence is weakened, concurrent with an increase in the selective advantage of high- r phenotypes. This conclusion echoes the usual reasoning about density-dependence in closed populations; emigration to a sink is akin to lowering population size by mortality (as in Fig. 1). Fig. 7 shows how selection should shift the habitat-specific fitness

functions, given a tradeoff between intrinsic growth rate and density-dependence in the source. Density-dependence is predicted to become stronger in a source, when coupled to a sink.

As noted earlier, in this model at demographic equilibrium realized patch-specific fitnesses (and hence Q) depend only on the dispersal rate and the rate of decline in the sink. Hence, a shift in density-dependent selection in the source due to coupling with a sink does not affect adaptive evolution in the sink, and in particular the relative weightings of sink and source habitats in niche evolution.

Trade-offs in density-dependence in source and sink

For simplicity we have assumed no density-dependence in the sink. Now assume that fitness in habitat i is given by $F_i = r_i - d_i N_i$; the sink habitat has $r < 0$. The strength of density-dependence d_i may differ between habitats (as in Fig. 2b, heavy lines).

Before examining evolution in the strength of density-dependence, first consider how adding negative density dependence in the sink modifies our earlier conclusions. Density-dependence in the sink lowers fitness in the sink, F_2 , below r_2 and indirectly depresses source density, thus increasing F_1 . Both these effects increase Q , further magnifying the weight given by selection to the source and devaluing the sink. Thus, incorporating negative density-dependence in the sink heightens the likelihood that a sink will remain evolutionarily stable. Because of the indirect effect that density-dependence in the sink has on lowering equilibrial density in the source, the selective balance between r and d in the source is pushed toward higher r , exaggerating the effect of the sink on density-dependent selection in the source described above.

Now let clonal variation exist for the strength of density-dependence in the two habitats, but not in the

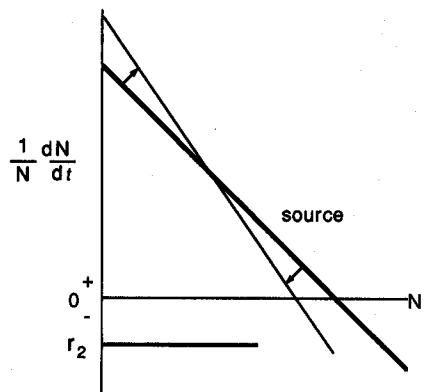


Fig. 7. The effect of coupling to a sink on the shape of the fitness-density relation in the source. As in Fig. 5, heavy lines are an initial population state, and arrows denote how the fitness functions are expected to change. The evolutionary changes in r and carrying capacity reflect the outcome of density-dependent natural selection.

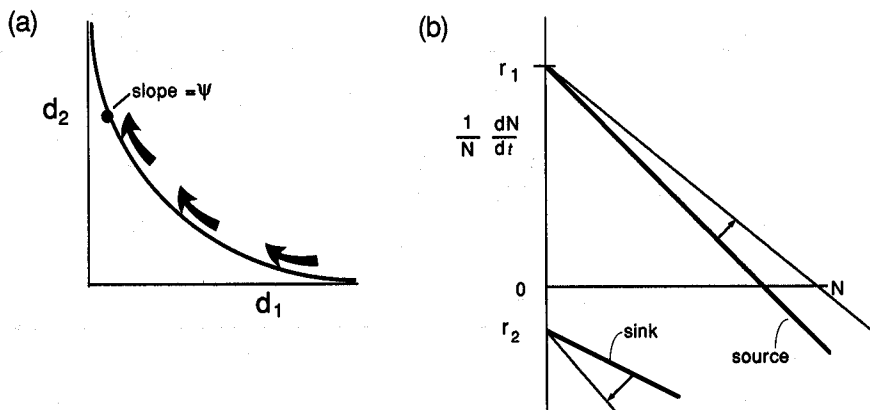


Fig. 8. (a) Tradeoffs in the strength of density dependence in the source (d_1) and in the sink (d_2). The arrows show the likely evolutionary trajectory, starting from an initial system with little density-dependence in the sink (see text). (b) Shifts in habitat-specific fitness functions resulting from coupled density-dependent natural selection in source and sink.

r_1 . Fig. 8a shows as an example a concave fitness set in the d_1 (biologically, available phenotypes must lie outside the line, away from the d_1 -axis; otherwise, there is no density-dependence in the source, leading to unbounded population growth). After substitution into (4), we find that equilibrium occurs at the point on the fitness set edge with tangent slope Ψ equal to

$$\frac{N_1^* \left(1 + \frac{Q}{\sqrt{Q^2 + \varepsilon^2}}\right)}{N_2^* \left(1 - \frac{Q}{\sqrt{Q^2 + \varepsilon^2}}\right)} = \Psi \quad (6)$$

This quantity exceeds unity in magnitude. In the example shown of a concave fitness set, density-dependence should evolve to become stronger in the sink (Fig. 8b). One can explicitly solve for N_1^* (roots of a cubic), and substitute into (6) to show that the adaptive balance between source and sink depends upon the strength of density-dependence in each. The algebra is messy and not particularly illuminating, so this effect is not pursued further here.

Model 3. Sinks resulting from active interference

It stretches credulity to imagine that the above model applies even as a metaphor to many vertebrates, which are more like to disperse in direct response to changes in population density than at some fixed, density-independent rate (though see Gaines and McClenaghan 1980).

If dispersal occurs because of interference, sink populations can be sustained by density-dependent dispersal. Pulliam (1988) has proposed a simple model for source-sink dynamics appropriate for many vertebrates, in which a fixed number of high-quality sites are occupied in one habitat, and the reproductive excess are forced

into another, inferior habitat where the population could not persist without immigration. A similar model was examined in Holt (1987b) in the context of competition for refuges: one habitat has a limited number of refuges from density-independent mortality factors, and competition for refuges occurs when the population exceeds that number. The refuge is the source habitat; space outside the refuge is the sink habitat. Here I explore adaptive evolution in a continuous-time model incorporating competition for space.

Let R denote the limited number of high-quality/safe sites in habitat 1 (denoted as "suitable" sites hereafter). Once these sites are occupied, the reproductive output of residents are forced into a lower-quality sink habitat (i.e., strong pre-emptive competition; see Fig. 2c). The growth rate of the total population ($N = R + N_2$) is

$$\frac{dN}{dt} = F_1(R)R + N_2 F_2(N_2) \quad (7)$$

As before, assume that sink dynamics consists of immigration coupled with exponential decline at rate $r_2 < 0$. The equilibril population size in the sink is $N_2^* = F_1(R)/|r_2|$ (Holt 1993).

Several models of evolutionary dynamics are consistent with this population dynamic model. If individuals are forced from the source and neither they nor their descendants ever return, the system is what I call a "black hole" sink. As discussed elsewhere (Holt and Gaines 1992, Holt and Gomulkiewicz unpubl.), there are substantial constraints on adaptive evolution in black hole sinks (and of course no reciprocal effect on evolution back in the source).

Alternatively, there could be an ongoing equitable lottery among all individuals, both in and out of the source, for access to suitable sites in the source. Expressing the above model in terms of per capita growth rates gives

$$\frac{1}{N} \frac{dN}{dt} = F(R) \frac{R}{N} + r_2 \left(1 - \frac{R}{N} \right) \quad (8)$$

Consider the fate of a clone which arises with different habitat-specific fitnesses, but with the same propensity to win the lottery for suitable sites as the resident clone. When rare, this clone will mainly compete with the resident, which we assume to be at its equilibrium abundance. After some manipulation, we arrive at the following expression for the effect of a small phenotypic change on the asymptotic growth rate of the invader:

$$\frac{d\bar{r}(q)}{dq} = \frac{|r_2|}{|r_2| + F(R)} \left(\frac{dF(R)}{dq} \right) + \frac{F(R)}{|r_2| + F(R)} \left(\frac{dr_2}{dq} \right) \quad (9)$$

In striking contrast with sinks maintained by passive dispersal, evolution may now be less heavily weighted toward adaptive improvement in the source. The reason is that the fraction of the population outside the source may exceed that within if $|r_2| < F_1(R)$. With density-dependent dispersal, selection may be more heavily weighted toward adaptive improvement in the *sink* than in the source. This effect should make it more difficult for a sink to be evolutionarily stable, compared to passive dispersal.

Using the same family of linear fitness sets relating r_1 to r_2 as before, the condition for evolutionary stability of the sink can be shown to be: $|r_2|/F(R) > s$. The sink is more likely to be evolutionarily stable if it is a very unfit place to live (i.e., high $|r_2|$), comparable with what we found for passive dispersal. However, in sharp contrast to passive dispersal, increasing productivity in the source automatically shifts the weight in selection toward the sink (because a larger fraction of individuals are forced to be there). Increasing the strength of interference may reduce the number of individuals in suitable sites, decreasing R and increasing $F(R)$, and thus shifting selection in favor of adaptation to the sink. Conversely, an increase in the number of suitable sites or the strength of density-dependence d_1 allows the source population to more nearly approach its inherent carrying capacity. This depresses the reproductive output of the source $[F(R)]$ and reduces the number of individuals forced into the sink. A diminution in exposure to the sink indirectly weakens selection for adaptation to the sink, and thereby makes evolutionary stability of the sink more likely.

Thus, given density-dependent dispersal driven by interference, mild sinks (viz., $|r_2|$ near zero) will often be evolutionarily unstable. In contrast, we showed above that with passive dispersal, even mild sinks can be evolutionarily stable if improved fitness in the sink was too costly in the source. The evolutionary tran-

sience of a sink habitat in this model arises because interference competition maintains a large standing crop of individuals forced to reside in sinks. Selection is automatically funneled toward the habitat encountered by the average individual in the population – which can be sink habitats given density-dependent dispersal.

The main conclusion of the above model is that density-dependent dispersal, driven by interference competition, tends to promote adaptive evolution to the sink environment, as compared with passive, density-independent dispersal. This conclusion rests on the assumption that all individuals have a comparable chance of entering the source habitat. I conjecture that the evolutionary stability of sink environments should become more likely, to the degree that individuals residing in sinks are disadvantaged in competing for suitable sites in the source.

Future directions

One weakness of the above models is that they focus on just a single species evolving in a fixed heterogeneous environment. But in nature sinks may often arise from competitive and predator-prey interactions (Holt 1984, 1993, Danielson and Stenseth 1990). A broader understanding of the evolutionary stability of sink habitats, and how this phenomenon bears on the broader problem of niche conservatism, will require developing multispecies versions of the above models, placing source and sinks in a broader community context (Brown and Vincent 1987, Danielson 1992, Danielson and Stenseth 1992) that permits species to respond differently to the available palette of habitats (Rosenzweig 1991).

We have also focused on a radically simple landscape – two habitats, equal in area, coupled either by symmetrical dispersal (the passive dispersal model) or threshold interference (the habitat saturation model). A challenging task for future work will be to examine niche evolution in more complex landscapes and with a broader spectrum of dispersal syndromes. For instance, one might expect evolution to proceed differently in environments with smooth gradients than with sharp spatial transitions between habitat extremes, or in landscapes with fractal or hierarchical spatial structures [where individuals in high-quality habitats may experience lower quality conditions in their daily movements (Morris 1991b, 1992, pers. comm.)]. If sources and sinks differ greatly in areal extent, density-independent dispersal can be asymmetrical between habitats, which can either facilitate or inhibit niche evolution (Kawecki 1995, Holt in press).

Conclusions

The basic conclusion I draw from the above models is that the nature of density-dependence crucially matters in determining the direction of adaptive evolution in heterogeneous environments comprised of source and sink populations coupled by dispersal. If density-dependence acts on local birth and death rates, but dispersal is density-independent, then evolution is automatically biased toward further improvement in sources, even at the expense of potential adaptive improvement in sinks. These biases can be expressed either in the intrinsic rate of increase or in the strength of density-dependence. The effect arises because of two complementary consequences of population dynamics: 1) more individuals tend to occur in the source than in the sink, which weights selection in favor of the source, and 2) individuals in the source have a higher reproductive value than in the sink. The force of selection is therefore stronger for improvement to the source habitat (Holt in press). Moreover, coupling between a source and sink can shift the outcome of density-dependent selection in each.

These conclusions may be weakened or reversed if dispersal is strongly density-dependent, driven by interference. This reversal in the expected bias in the direction of adaptive evolution is most likely if individuals in sinks have a reasonable likelihood of re-entering sources, and there are a large number of such individuals. Transitions through "sink" habitats may in effect constitute normal phases in a life cycle (e.g., juveniles may persist in a habitat distinct from that occupied by breeding, behaviorally dominant adults). When this occurs, we should expect substantial adaptation to sinks as well as to sources, leading possibly to the evolutionary transience of sinks. However, even in this case, sinks which are sufficiently unfit can be evolutionarily stable, so that adaptive evolution hones organismic performance mainly to conditions in the source.

My earlier conclusion (Holt and Gaines 1992) that adaptive evolution in source-sink environments tends to favor continued adaptation to the source, hence leading to evolutionary conservatism in species niches (Holt in press), thus needs to be tempered. If dispersal is density-dependent and driven by interference, selection may strongly favor improved adaptation in the sink, and hence expansion of the species' niche.

The models presented here are complementary intellectual tools, rather than competing hypotheses about source-sink populations, because they pertain to very different kinds of species. The results I have presented point to a rich body of contingent theory describing how different evolutionary routes are open to species with different syndromes of density-dependence. For organisms with passive dispersal (e.g., plants?), one might expect to see considerable niche conservatism over evolutionary time (for evidence on this point, see Bradshaw 1991 and Ricklefs and Latham 1992). The

same may be true for species able to finely discriminate among habitats and move without interference, approximating an ideal-free distribution (such species should never have sink populations in the first place). By contrast, for organisms with strong interference in optimal habitats forcing density-dependent dispersal, coupling sources to substantial sink populations, niches may evolutionarily labile (e.g., some mammals?). Density-dependence in dispersal may thus exert a far-reaching influence on broad patterns in evolutionary history.

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