VOL. 180, NO. 1 THE AMERICAN NATURALIST JULY 2012

The Evolution of Patch Selection in Stochastic Environments

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Submitted July 25, 2011; Accepted February 8, 2012; Electronically published May 17, 2012

ABSTRACT: A null model for habitat patch selection in spatially heterogeneous environments is the ideal free distribution (IFD), which assumes individuals have complete knowledge about the environment and can freely disperse. Under equilibrium conditions, the IFD predicts that local population growth rates are zero in all occupied patches, sink patches are unoccupied, and the fraction of the population selecting a patch is proportional to the patch's carrying capacity. Individuals, however, often experience stochastic fluctuations in environmental conditions and cannot respond to these fluctuations instantaneously. An evolutionary stability analysis for fixed patch-selection strategies reveals that environmental uncertainty disrupts the classical IFD predictions: individuals playing the evolutionarily stable strategy may occupy sink patches, local growth rates are negative and typically unequal in all patches, and individuals prefer higher-quality patches less than predicted by their carrying capacities. Spatial correlations in environmental fluctuations can enhance or marginalize these trends. The analysis predicts that continually increasing environmental variation first selects for range expansion, then selects for persisting coupled sink populations, and ultimately leads to regional extinction. In contrast, continually increasing habitat degradation first selects for range contraction and may select for persisting coupled sink populations before regional extinction. These results highlight the combined roles of spatial and temporal heterogeneity on the evolution of habitat selection.

Keywords: habitat selection, evolutionarily stable strategies, environmental stochasticity, spatial heterogeneity, source-sink dynamics, ideal free distribution.

Introduction

Habitat selection by individuals can profoundly influence population persistence in heterogenous landscapes (Pulliam and Danielson 1991; Greene 2003; Schmidt 2004), stability of predator-prey interactions (van Baalen and Sabelis 1993; Křivan 1997; Schreiber and Vejdani 2006), and geographical shifts in species distributions in response to climate change (Morris 2011). While there are significant and extensive advances in the evolutionary theory of patch selection for populations living in spatially heterogeneous environments (Morisita 1952, 1969; Fretwell and Lucas 1969; Sutherland 1983, 1996; Tregenza et al. 1996; Kshatriya and Cosner 2002; Cosner 2005; Cantrell et al. 2007, 2010; Morris 2011), the combined effects of temporal and spatial variation on the evolution of patch selection is less understood (Holt and Barfield 2001; Morris 2011). Given the ubiquity of temporal variation and its notable impacts on demography (Boyce et al. 2006) and the evolution of passive dispersal (Johnson and Gaines 1990; Ronce 2007), I examine the evolution of habitat patch selection for freely dispersing individuals in a stochastic environment.

In their seminal article, Fretwell and Lucas (1969) introduced the ideal free distribution (IFD), which describes the patch distribution of freely dispersing individuals that have complete knowledge about spatial variation in individual fitness. For population exhibiting this distribution, individual fitness is equal in all occupied habitat patches and individuals would decrease their fitness by moving into unoccupied patches. This distribution has been explored under a variety of conditions, including interference competition (Sutherland 1983, 1996; Tregenza et al. 1996), exploitative competition (Sutherland 1983; Milinski and Parker 1991; Oksanen et al. 1995; Křivan 2003), and multispecies interactions (van Baalen and Sabelis 1993, 1999; Křivan 1997; Cressman et al. 2004; Schreiber and Vejdani 2006). Surprisingly, while many of these studies assert that the ideal free distribution is an evolutionarily stable strategy (ESS), only recently has a delicate nonlinear analysis verified the ESS conditions (Cressman et al. 2004; Cressman and Křivan 2006, 2010; Cantrell et al. 2007, 2010). Under equilibrium conditions, the IFD predicts that the fraction of individuals selecting a source patch is proportional to the carrying capacity of the source patch (Holt and Barfield 2001). Consequently, all sink patches are unoccupied as their carrying capacity is zero (Holt 1985). Neither of these predictions, however, agrees fully with empirical observations.

Observed patch distributions are frequently less extreme than predicted by the IFD: individuals underexploit higher-quality patches (i.e., undermatching) than predicted by the IFD and overuse lower-quality patches (i.e., overmatching; Milinski 1979, 1994; Abrahams 1986; Kennedy and Gray 1993; Tregenza 1995). Explanations for

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Am. Nat. 2012. Vol. 180, pp. 17–34.
DOI: 10.1086/665655

these deviations include perceptual constraints (Abrahams 1986; Gray and Kennedy 1994), demographic stochasticity (Regelmann 1984; Miller and Coll 2010), sampling variation (Regelmann 1984; Earn and Johnstone 1997), and environmental stochasticity (Hakoyama 2003; Jonzén et al. 2004). Of greatest relevance here, Hakoyama (2003) showed that if stochastic variation in resource availability in higher-quality patches is sufficiently greater than stochastic variation in lower-quality patches, populations playing the ESS for patch selection undermatch the higher-quality patches. This study, however, does not account for population growth or resource depletion due to consumption. Consequently, ecological feedbacks on the evolution of patch selection are missing. In another study, Jonzén et al. (2004) examined the effects of environmental stochasticity and population dynamics on patch distributions using a heuristic stochastic patch selection rule. However, Jonzén et al. (2004, p. E110) readily admit that it "is not clear to what extent the stochastic habitat selection rule implemented here would also be [an] ESS." Hence, it remains to be understand how environmental stochasticity and ecological feedbacks determine the ESS for patch selection.

Contrary to the predictions of the classical IFD theory, sink populations exist in a diversity of taxa, including viruses (Sokurenko et al. 2006), plants (Anderson and Geber 2010), birds (Tittler et al. 2006; Møller et al. 2006), fish (Barson et al. 2009), and mammals (Naranjo and Bodmer 2007; Sulkava et al. 2007; Robinson et al. 2008). These population exhibit an extreme form of overmatching, as sink patches cannot sustain population growth in the absence of immigration. Under equilibrium conditions, one explanation for the existence of these sink populations is maladaptive patch choice (Holt 1997). Alternatively, theory suggests that sink populations may evolve when temporal variation is sufficiently great in source patches (Holt 1997; Jansen and Yoshimura 1998; Holt and Barfield 2001). When this occurs, numerical simulations by Holt and Barfield (2001) show that the geometric mean of fitness, a natural measure of fitness in fluctuating environments, is not equal in all occupied patches. In contrast, if all patches are sources, their simulations suggests that the geometric mean of fitness is approximately equal in all patches. These contrasting outcomes raise the question of whether, if at all, there is a simple rule of thumb analogous to the classical IFD for stochastically fluctuating environments. Emphasizing this point, Holt and Barfield (2001, p. 94) assert that "it will be an important task in future work to assess the generality of these conclusions."

Given that global climate models predict increasing temporal variability in environmental conditions in the next century (Schär et al. 2004; Tebaldi et al. 2006) and that increased variability in these conditions may have already lead to shifts in species distributions (Allen and Breshears 1998), it is becoming increasingly important to understand how environmental fluctuations influence species' habitat choices. As a step toward this understanding, I present a general analysis of the evolution of patch selection strategies for freely dispersing populations living in spatially and temporally heterogeneous landscapes. For these populations, I derive an analytic characterization for the ESS in these stochastic environments. Using this characterization, I examine how spatial correlations and temporal fluctuations inhibit or enhance the evolution of sink populations, result in undermatching of higher-quality patches, determine local stochastic growth rates, and influence the evolution of species ranges in response to increased environmental variation or habitat destruction.

Model and Methods

Local and Regional Population Dynamics

I model a population with overlapping generations living in a spatially heterogeneous environment consisting of k distinct patches. These patches may represent distinct habitats, patches of the same habitat type, or combinations thereof. The abundance of the population in the ith patch at time t is N_t^i. Its rate of change is determined by a mixture of deterministic and stochastic environmental forces. More specifically, the change $\Delta N_t^i = N_{t+\Delta t}^i - N_t^i$ in small time step Δt satisfies

$$\begin{aligned}\mathbb{E}[\Delta N_t^i | N_t^i] &= \int_t^{t+\Delta t} \mathbb{E}[f_i(N_s^i) N_s^i | N_t^i] ds \\ &\approx f_i(N_t^i) N_t^i \Delta t,\end{aligned} \tag{1}$$

where f_i is the average per capita growth rate in patch i and $\mathbb{E}[X|Y]$ denotes the conditional expectation of a random variable X given the random variable Y. To account for intraspecific competition and population regulation within the patch, I assume that f_i is a decreasing function of local population abundance in patch i and is negative when the local population abundance is sufficiently large, that is, $f_i(N^i) < 0$ for N^i sufficiently large.

To capture the role of stochastic forces, the covariance in the growth of the populations in patches i and j over a time interval of length Δt satisfies

$$\mathrm{Cov}\,[\Delta N_t^i, \Delta N_t^j | N_t^i, N_t^j] \approx \sigma_{ij} N_t^i N_t^j \Delta t,$$

where $\mathrm{Cov}\,[X, Y|Z, W]$ denotes the covariance between random variables X and Y given the random variables Z and W. The covariance matrix $\Sigma = (\sigma_{ij})$ captures the spatial dependence between the temporal fluctuations in patches. Taking the limit as Δt gets infinitesimally small,

Table 1: Definitions of key terms

Term	Definition
E_t^i	Environmental noise in patch i
$p = (p_1, \ldots, p_k)$	Patch selection strategy with fraction of p_i individuals living in patch i
$f_i(N_t^i)$	Per capita growth rate in patch i
σ_{ij} (with $\sigma_i^2 = \sigma_{ii}$)	Covariance in temporal fluctuations between patch i and patch j
$f_i(0) - \sigma_i^2/2$	Intrinsic stochastic growth rate in patch i
$\hat{N}(p)$	Stochastic equilibrium for a population with patch selection strategy p
$\mathbb{E}[f_i(p_i\hat{N}(p))] - \sigma_i^2/2$	Local stochastic growth rate in patch i
$\sigma(p)^2 = \sum_{i,j} p_i p_j \sigma_{ij}$	Total temporal variation experienced by a population playing the patch selection strategy p
Sink patch	Patch in which $f_i(0) - \sigma_i^2/2 < 0$; local population persists only due to immigration
Deterministic sink patch	Sink patch in which $f_i(0) < 0$
Stochastic sink patch	Sink patch in which $f_i(0) - \sigma_i^2/2 < 0$ but $f_i(0) > 0$

the spatially uncoupled local population dynamics are given by the Itô stochastic differential equations (Gardiner 2009)

$$dN_t^i = N_t^i(f_i(N_t^i)dt + dE_t^i), \tag{2}$$

where $(E_t^1, \ldots, E_t^k)$ is a multivariate Brownian motion with covariance matrix Σ. For convenience, I refer to the environmental variance σ_{ii} in patch i as σ_i^2.

When populations in the different patches are uncoupled, Itô's formula (Itô 1950; Gardiner 2009) implies that the rate of change of the log population abundance in patch i satisfies the Itô stochastic differential equation

$$d\log N_t^i = \left(f_i(N_t^i) - \frac{\sigma_i^2}{2}\right)dt + dE_t^i.$$

Since dE_t^i is on average equal to zero, the mean change in the log abundance over a small time interval Δt satisfies

$$\mathbb{E}[\Delta \log (N_t^i)|N_t^i] \approx \left(f_i(N_t^i) - \frac{\sigma_i^2}{2}\right)\Delta t,$$

where $\Delta\log(N_t^i) = \log(N_{t+\Delta t}^i) - \log(N_t^i)$. Hence, unlike the mean per capita change $f_i(N_t^i)$ in abundance (conditioned on the current abundance), the mean change in log abundance (conditioned on the current abundance) decreases with the variance in environmental fluctuations. This reduction plays a crucial role in determining population persistence.

The sign of the intrinsic stochastic growth rate $f_i(0) - \sigma_i^2/2$ in patch i determines population persistence and invasion success (Lewontin and Cohen 1969; Gillespie 1977; Lande et al. 2003). This intrinsic stochastic growth rate is the continuous-time analog of the geometric mean of fitness discussed extensively in the bet-hedging literature (Gillespie 1977; Childs et al. 2010); by decreasing temporal variation in their reproductive success, individuals can increases their fitness. When this intrinsic stochastic growth rate is negative, patch i is a sink and, in the absence of immigration from other patches, populations restricted to this patch go extinct. I make a distinction between two types of sinks (table 1). If the deterministic intrinsic rate of growth $f_i(0)$ is negative, then patch i is a sink for all levels of environmental stochasticity. I call such patches "deterministic sinks." In contrast, if $f_i(0) > 0$ and $f_i(0) - \sigma_i^2/2 < 0$, patch i is a stochastic sink, as stochastic fluctuations drive the local population to extinction in the absence of immigration. Unlike deterministic sinks, stochastic sinks exhibit periods of positive population growth and, consequently, can contribute to regional persistence. In contrast to sinks, patch i is called a source when $f_i(0) - \sigma_i^2/2$ is positive. Populations in source patches are able to persist in the sense that N_t^i converges in probability to a positive random variable $\hat{N}^i$ whenever $N_0^i > 0$ (Braumann 1999). When the population persists in the absence of immigration, the local stochastic growth rate $\mathbb{E}[f_i(\hat{N}^i)] - \sigma_i^2/2$ at this stochastic equilibrium is zero; on average the population is neither increasing nor decreasing.

To couple the population dynamics across patches, let p_i be the fraction of the population selecting patch i. The patch selection strategy $p = (p_1, \ldots, p_k)$ may be a pure type in which each individual occupies only one patch, or a mixed type in which individuals spends a proportion p_i of their time in patch i (Morris 2011). With this notation, $N_t^i = p_i N_t$, where $N_t = N_t^1 + \ldots + N_t^k$ is the total population abundance at time t. Summing equation (2) across all patches yields the Itô stochastic differential equation for the total population abundance:

$$dN_t = \sum_{i=1}^{k} p_i N_t (f_i(p_i N_t)dt + dE_t^i). \tag{3}$$

Since $\sum_i p_i E_t^i$ is a Brownian motion with variance

$t\sum_{i,j} p_i p_j \sigma_{ij}$ at time t, the dynamics of equation (3) are equivalent to

$$dN_t = N_t\left(\sum_i p_i f_i(p_i N_t)dt + \sigma(p)dB_t\right), \tag{4}$$

where $\sigma(p)^2 = \sum_{i,j} p_i p_j \sigma_{ij}$ and B_t is a standard Brownian motion (i.e., variance at time t equals t). As in the case of the single-patch model, if the regional intrinsic stochastic growth rate $\sum_i p_i f_i(0) - \sigma(p)^2/2 > 0$, then the population persists and N_t converges in probability to a unique positive random variable $\hat{N}(p)$ whenever $N_0 > 0$. In contrast, the population becomes extinct with probability 1 whenever $\sum_i p_i f_i(0) - \sigma(p)^2/2 < 0$. Table 1 summarizes the key terms presented here.

Invasion Rates and the ESS for Patch Selection

Given the uncertainty in local growth rates, one can ask from an evolutionary perspective, what is the optimal patch selection strategy? To identify this "optimal" strategy, I use the noninvasibilty criterion for an ESS (Maynard Smith and Price 1973). More specifically, assume there is a resident population playing strategy $p = (p_1, \ldots, p_k)$ competing with a "mutant" population playing strategy $q = (q_1, \ldots, q_k)$. Let N_t and M_t denote the total population abundance of the resident strategy and the mutant strategy, respectively. If these populations only differ in their patch selection strategy, then the population dynamics of these competing strategies are given by the following system of Itô stochastic differential equations:

$$dN_t = N_t \sum_i p_i f_i(p_i N_t + q_i M_t)dt + N_t \sigma(p) dB_t, \tag{5}$$

$$dM_t = M_t \sum_i q_i f_i(p_i N_t + q_i M_t)dt + M_t \sigma(q) dB_t. \tag{6}$$

When the resident population is at its stochastic equilibrium, the intrinsic stochastic growth rate of the mutant population equals

$$\mathcal{I}(p, q) = \sum_i q_i \mathbb{E}[f_i(p_i \hat{N}(p))] - \frac{1}{2}\sigma(q)^2,$$

where $\hat{N}(p)$ is the stochastic equilibrium associated with the resident strategy. When $\mathcal{I}(p, q) > 0$, the mutant can invade. Conversely if $\mathcal{I}(p, q) < 0$, the mutant population fails to invade. A sufficient condition for p to be an ESS is that all mutant strategies cannot invade, that is, $\mathcal{I}(p, q) < 0$ for all $q \neq p$.

While I will show that there is a unique ESS and provide an analytic characterization of it, one cannot in general write down an explicit formula for the ESS. To solve for the ESS numerically, I derive in appendix A an evolutionary dynamic on the strategy space in which small mutations occurring at a rate μ randomly shuffle the "infinitesimal" weights of the patch selection strategy:

$$\frac{dp_i}{dt} = \mu p_i\left\{\mathbb{E}[f_i(p_i \hat{N}(p))] + \sum_{j,k} p_j\left(\frac{p_k \sigma_{jk}}{2} - \sigma_{ij}\right)\right\}. \tag{7}$$

An explicit representation of this dynamic is possible for linear per capita growth rates: $f_i(N^i) = b_i(1 - N^i/K_i) - d_i$, where b_i, d_i, and K_i are the per capita birth rate, per capita death rate, and the "reproductive carrying capacity" of patch i. This representation of the logistic equation allows for deterministic sink patches (i.e., when $b_i < d_i$) as well as source patches and stochastic sink patches. For the numerical results, equation (7) with the linear f_i was simulated with the deSolve package of R (R Core Devlopment Team 2008) for 1,000 time steps. Extensive simulations suggest that these evolutionary dynamics always converge to a globally stable equilibrium corresponding to the ESS for patch selection after the 1,000 time steps.

Results

To Persist or Not to Persist?

In order for there to be an ESS, the population needs to persist: there is a patch selection strategy p for which the regional intrinsic stochastic growth rate $\sum_i p_i f_i(0) - \sigma(p)^2/2$ is positive. Evans et al. (2012) developed an algebraic solution to maximizing this intrinsic stochastic growth rate with respect to the patch selection strategy. Appendix B uses this algebraic solution to provide an explicit, analytical expression for when this intrinsic stochastic growth rate is positive for some p. While this condition is quite unwieldy, it provides some useful insights.

Not surprisingly, persistence is always possible when there is at least one source patch and impossible if all patches are deterministic sinks. Unlike deterministic sinks, stochastic sinks ensure that there are opportunities for population growth. Consequently, consistent with earlier work on discrete time models (Holt 1997; Jansen and Yoshimura 1998; Bascompte et al. 2002), persistence is possible in environments with only sink patches, provided that at least one of them is a stochastic sink. For example, if all patches have similar intrinsic rate of growth (i.e., $f_i(0) = r$ for all i) and experience similar environmental variation (i.e., $\sigma_{ii} = \sigma^2$), then persistence requires

$$r > \frac{\sigma^2}{2k}[1 + \rho(k-1)], \tag{8}$$

where ρ is the correlation in environmental fluctuations between any pair of patches (i.e., $\sigma_{ij} = \rho\sigma^2$ for all $i \neq j$) and k is the number of patches.

Equation (8) implies that persistence occurs provided there are many uncorrelated patches even if all are stochastic sinks. With many uncorrelated stochastic sinks, positive growth is likely in at least one of the patches at any point in time. Hence, by utilizing many patches, populations experience less environmental variation and may persist; the variance term $\sigma(p)^2$ in the regional intrinsic stochastic growth rate $\sum_i p_i f_i(0) - \sigma(p)^2/2$ becomes smaller. In contrast, equation (8) implies persistence in a landscape of sink patches is impossible whenever environmental fluctuations in patches are highly correlated (i.e., $\rho \approx 1$). With strong spatial correlations, individuals experience the same environmental conditions in all patches, and consequently, selecting multiple patches does not reduce the environmental variation experienced by the population.

The symmetry in the preceding example implies that a population playing the ESS is uniformly distributed across patches. To get a sense of how spatial heterogeneity in local demography generates nonuniform distributions requires a general characterization of the ESS for patch selection.

What Types of Patches Are Occupied by Populations Playing the ESS?

Most of the analytic results involve an ESS for which multiple patches are selected (app. C). There are two ways in which this occurs. As in the case in the deterministic theory (Fretwell and Lucas 1969; Holt and Barfield 2001), all source patches are occupied by populations playing the ESS. Hence, provided there are multiple source patches, a population playing the ESS occupies multiple patches.

Unlike the deterministic theory, even if there is only one source patch, call it patch i, populations playing the ESS may also select a sink patch, say patch j, provided that intrinsic stochastic growth rate $f_j(0) - \sigma_j^2/2$ in this sink patch is not too negative (see app. C):

$$f_j(0) - \frac{\sigma_j^2}{2} > -\frac{\sigma_j^2}{2} + \sigma_{ij} - \frac{\sigma_i^2}{2}. \tag{9}$$

Since σ_{ij} corresponds to the covariation in fluctuations between the source patch i and sink patch j, inequality (9) implies that selection of a sink patch is more likely as σ_{ij} decreases, and especially if $\sigma_{ij} < 0$. Intuitively, strong negative correlations imply that at any point in time, environmental fluctuations increase population growth in one patch and decrease population growth in the other patch. Spending time in both patches (or distributing offspring to both patches) reduces the temporal variation experienced by an individual (or by its offspring). More precisely, when the environmental fluctuations are perfectly negatively correlated in these two patches (i.e., $\sigma_{ij} = -\sigma_i\sigma_j$), inequality (9) requires that the local stochastic growth rate in the sink patch exceed $-(\sigma_i + \sigma_j)^2/2$. Therefore, provided that environmental fluctuations are sufficiently strong in either patch, strong negative correlations ensure that populations playing the ESS always select the sink patch. When environmental fluctuations between the source and sink patches covary perfectly (i.e., $\sigma_{ij} = \sigma_i\sigma_j$ and $\sigma_i = \sigma_j$ for all i, j), the population playing the ESS does not select the sink patch, as spending time in both patches does not reduce the environmental variation experienced by an individual (or its offspring).

Provided all patches experience environmental fluctuations and these fluctuations do not perfectly covary across the landscape (i.e., Σ is positive definite), appendix C shows that all local stochastic growth rates $\mathbb{E}[f_i(p_i\hat{N}(p))] - \sigma_i^2/2$ are negative. Consequently, unlike the deterministic ideal free distribution where the per capita growth rates in all patches equal zero (Fretwell and Lucas 1969; Holt and Barfield 2001; Cantrell et al. 2007), populations playing the ESS in stochastic environments are living in a landscape composed of sink patches and pseudo-sink patches (Watkinson and Sutherland 1995). Pseudo-sinks are source patches in which density-dependent feedbacks cause the local stochastic growth to be negative, that is, patches where $\mathbb{E}[f_i(p_i\hat{N})] - \sigma_i^2/2 < 0$ and the intrinsic stochastic growth rate $f_i(0) - \sigma_i^2/2$ is positive.

What Is Balanced by Populations Playing the ESS?

Under the assumption of multiple patches being selected, appendix C shows that the ESS p for patch selection satisfies

$$-\frac{\sigma(p)^2}{2} = \mathbb{E}[f_i(p_i\hat{N}(p))] - \sum_j p_j\sigma_{ji} \tag{10}$$

for all occupied patches (i.e., i such that $p_i > 0$). Equation (10) implies that the differences between two local demographic quantities are equal in all occupied patches. In patch i, these demographic quantities are the average per capita growth rate $\mathbb{E}[f_i(p_i\hat{N}(p))]$ in patch i, and the covariance $\sum_j p_j\sigma_{ji}$ between the environmental fluctuations E_t^i within patch i and the environmental fluctuations $\sum_j p_j E_t^j$ experienced by the "average" individual. All other things being equal, preferred patches are more "out of sync" with the environmental fluctuations experienced in the other patches, considered collectively. The difference $\mathbb{E}[f_i(p_i\hat{N}(p))] - \sum_j p_j\sigma_{ji}$ need not be equal to the local stochastic growth rate $\mathbb{E}[f_i(p_i\hat{N}(p))] - \sigma_i^2/2$. Consequently, in contrast to the deterministic theory, one does not generally expect the local stochastic growth rates to be equal in all occupied patches for populations playing the ESS.

Patch Selection in Spatially Uncorrelated Environments

To gain more detailed insights into the effects of environmental stochasticity on patch selection, it is useful to examine the simpler case of spatially uncorrelated temporal fluctuations, that is, $\sigma_{ij} = 0$ for $i \neq j$. In the absence of these correlations, appendix C shows that all stochastic sinks are occupied by populations playing the ESS. To understand why this occurs, consider a population that doesn't occupy a stochastic sink, say $p_j = 0$, where patch j is a stochastic sink. If an individual, unlike the rest of the population, spends a small fraction ε of time in patch j, then the deterministic component of this individual's stochastic growth rate increases approximately by $f_j(0)\varepsilon$, which is positive as patch j is a stochastic sink. On the other hand, the environmental variance experienced by this individual only increases at most by $\varepsilon^2\sigma_j^2$. Since the added benefit $\varepsilon f_j(0)$ of entering patch j exceeds the cost $\varepsilon^2\sigma_j^2/2$ of entering patch j for small ε, individuals selecting patch j would increase their stochastic growth rate and could invade the resident population. Hence, any ESS for patch selection has individuals occupying all stochastic sinks.

Deterministic sinks may or may not be occupied by populations playing the ESS. Expansion into deterministic sink patches, say patch j with $f_j(0) < 0$, is selectively advantageous whenever the rate of population decline $(1/2)\sum_i p_i^2\sigma_i^2$ due to environmental stochasticity exceeds the deterministic rate $-f_j(0)$ of decline in the sink patch. Hence, sufficiently large stochastic fluctuations in source patches or stochastic sink patches select for the occupancy of deterministic sink patches. Since the additional environmental variation experienced by an individual using patch j only increases quadratically with p_j, large stochastic fluctuations in deterministic sinks do not select against their occupancy. These large stochastic fluctuations, however, may select for fewer individuals residing in deterministic sinks, that is, p_j is positive but small.

When multiple patches are selected, equation (10) implies that the quantities $\mathbb{E}[f_i(p_i\hat{N})] - p_i\sigma_i^2$ are equal to $-\sum_i p_i^2\sigma_i^2$ in all occupied patches. While $\mathbb{E}[f_i(p_i\hat{N})] - p_i\sigma_i^2$ is determined by the local demography, these quantities do not generally equal the local stochastic growth rates $\mathbb{E}[f_i(p_i\hat{N})] - \sigma_i^2/2$. However, when there are sufficiently many patches selected by the ESS and the p_i are small (i.e., the population selects many patches), the terms $p_i\sigma_i^2$ and $\sum_i p_i^2\sigma_i^2$ are approximately zero and one recovers a classical prediction of IFD that the average per capita growth rates $\mathbb{E}[f_i(p_i\hat{N})]$ are (approximately) equal to zero in all occupied patches.

To further explore these trends, I ran the evolutionary dynamic in equation (7) to determine how the ESS responds to spatial variation in the per capita birth rates b_i and environmental variation σ_i where $f_i(N^i) = b_i(1 - N^i/K_i) - d_i$. In both scenarios, the spatial variation is chosen such that the intrinsic stochastic growth rates decrease in a Gaussian manner with respect to the patch index i, that is, $b_i - d_i - \sigma_i^2/2 = \alpha\exp(-\beta i^2) + \gamma$ for n constants α, β, and γ.

Figures 1 and 2*A* report the numerical results for spatial variation in per capita birth rates. When there is little environmental stochasticity, all stochastic sink patches are occupied but no deterministic sinks are occupied (fig. 1*A*, 1*B*). At higher levels of environmental stochasticity, a population playing the ESS occupies all deterministic sinks (fig. 1*C*, 1*D*). More generally, continually increasing environmental stochasticity selects for range expansion, then selects for persistence of coupled sink populations and ultimately leads to extinction (fig. 2*A*). Alternatively, continually increasing the per capita death rates d selects for range contraction, then selects for persistence of coupled sink populations (provided environmental stochasticity is initially sufficiently large) and ultimately leads to extinction (fig. 2*B*).

Along gradients of environmental stochasticity, individuals preferentially select patches with less environmental stochasticity (fig. 3*A*; analytical predictions in appendix C). However, higher per capita birth rates ameliorate this bias by reducing the spatial variation in intrinsic stochastic growth rates. Surprisingly, the highest within-patch abundances occur at the lowest per capita birth rates (lower left in fig. 3*A*); strong preferences for patches with less environmental stochasticity increases local population abundances within these patches, despite the low regional population abundance $\mathbb{E}[\hat{N}(p)]$.

As predicted by the analytic results, the local stochastic growth rates are not equal in all occupied patches, even when they are all source patches (figs. 1*B*, 1*D*, 3*B*). The differences in local stochastic growth rates are most pronounced between source patches and sink patches and at higher levels of environmental stochasticity. Sufficiently many independent patches, however, can marginalize these differences and result in the average per capita growth rates $\mathbb{E}[f_i(p_i\hat{N})]$ being approximately equal in all occupied patches (fig. D1 in app. D).

Patch Selection in Spatially Correlated Environments

With perfect environmental covariation in all patches (i.e., $\sigma_{ij} = \sigma^2$ for all i, j), the characterization of the ESS in equation (10) implies that the local stochastic growth rates are zero in all occupied patches, that is, $0 = \mathbb{E}[f_i(p_i\hat{N}(p))] - \sigma^2/2$ for all i such that $p_i > 0$. In particular,

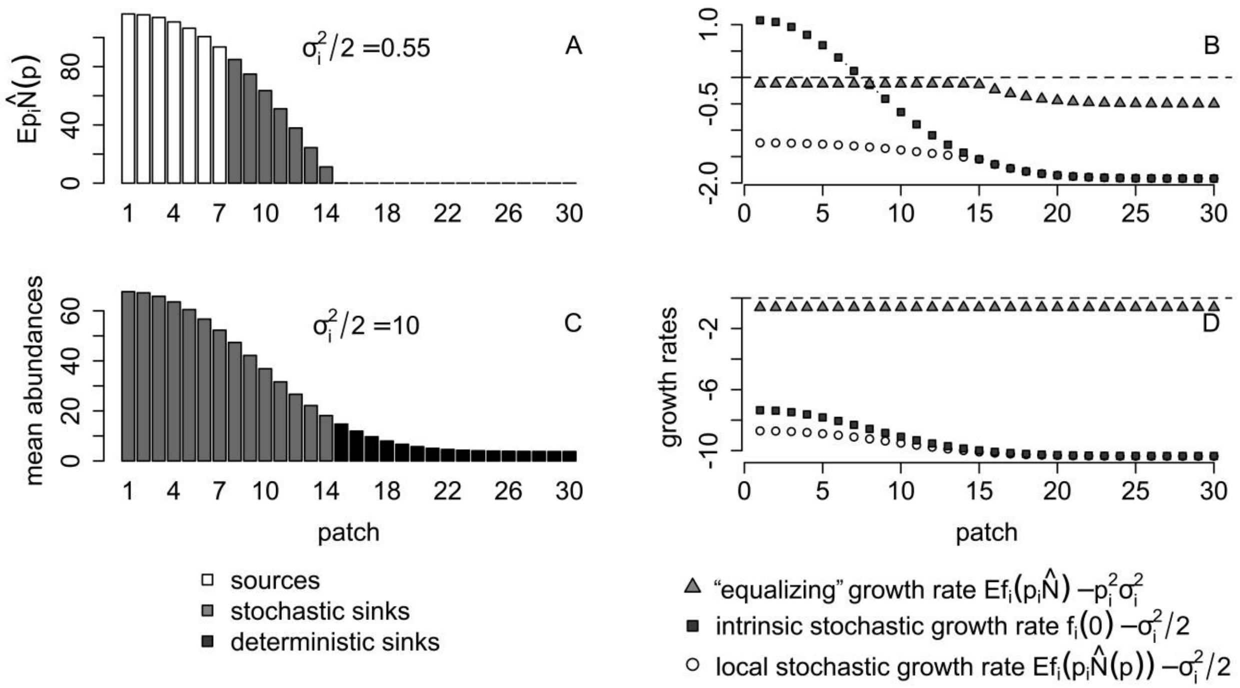

Figure 1: Spatially uncorrelated environmental stochasticity favors selection of sink patches. *A*, *C*, Mean abundance $\mathbb{E}[p_i\hat{N}(p)]$ in each patch is plotted along a gradient of patches where per capita birth rates decrease in a Gaussian manner from patch 1 to patch 30. *B*, *D*, Intrinsic stochastic growth rate $f_i(0) - \sigma_i^2/2$, the local stochastic growth rate $\mathbb{E}[f_i(p_i\hat{N}(p))] - \sigma_i^2/2$, and the "equalizing" stochastic growth rate $\mathbb{E}[f_i(p_i\hat{N}(p))] - p_i\sigma_i^2$ are plotted for each patch. Parameters: $f_i(N_i) = b_i(1 - N_i/K_i) - d_i$ with $b_i = 3\exp(-i^2/300) + 1$, $d_i = 1.5$, $K_i = 200$, and $\sigma_{ii} = \sigma_i^2$ as shown and $\sigma_{ij} = 0$ for $i \neq j$.

no sink patches are occupied. Intuitively, when environmental fluctuations are perfectly correlated, spending time in sink patches does not reduce the environmental variance experienced by an individual. Figure 4 illustrates how partial spatial correlations influence the ESS along a spatial gradient of varying per capita birth rates. Spatial correlations marginalize the degree to which selecting multiple patches reduces the environmental variation experienced by an individual. Consequently, increasing spatial correlations selects for range contraction and reduces the equilibrium population abundance in all patches (fig. 4*A*).

For linear per capita growth rates $f_i(N^i) = b_i(1 - N^i/K_i) - d_i$ and perfectly covarying environmental fluctuations, the ESS for patch selection corresponds to the classical "patch matching rule": the fraction of individuals in patch i is proportional to the local population abundance at equilibrium. More specifically, the equilibrium abundance for populations restricted to patch i equals

$$\tilde{N}^i = K_i\left(1 - \frac{d_i + \sigma^2/2}{b_i}\right)$$

whenever $b_i - d_i > \sigma^2/2$, and $\tilde{N}^i = 0$ otherwise. The ESS for patch selection is

$$p_i = \frac{\tilde{N}^i}{\sum_j \tilde{N}^j}.$$

Since the local equilibrium abundances $\tilde{N}^i$ decrease with increasing environmental variation σ^2, patch preferences p_i become less differentiated at higher levels of environmental variation.

To illustrate the role of partial spatial correlations on overmatching or undermatching along a spatial gradient of varying per capita birth rates, figure 4*B* plots the difference between the ESS patch selection preferences p_i and classical patch matching rule $\tilde{N}^i/\sum_j \tilde{N}^j$. Partial spatial correlations results in overmatching of the lower-quality patches (i.e., greater fraction of individuals selecting the lower-quality patches than predicted by the local equilibrium abundances) and undermatching of the higher-quality patches. Somewhat unexpectedly, the greatest overmatching occurs at strong spatial correlations despite

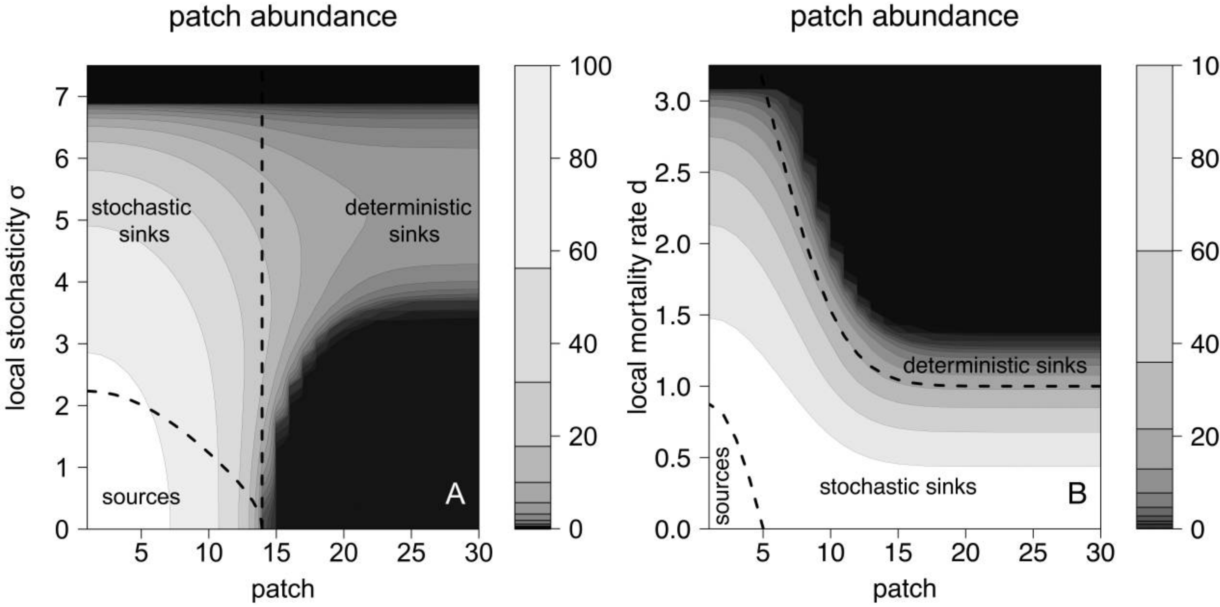

Figure 2: Range shifts, persistence of coupled sink populations, and extinction in response to increasing environmental variation (*A*) or patch degradation (*B*). Contour plots of the mean patch abundances $p_i\mathbb{E}[\hat{N}(p)]$ for populations playing the evolutionarily stable strategy in a landscape where per capita birth rates decrease in a Gaussian manner. Dashed contours corresponds to where the deterministic and stochastic intrinsic growth rates, $f_i(0)$ and $f_i(0) - \sigma_i^2/2$, equal zero. Labels indicate patch and parameter combinations that correspond to sources ($f_i(0) > \sigma_i^2/2$), stochastic sinks ($0 < f_i(0) < \sigma_i^2/2$), and deterministic sinks ($f_i(0) < 0$). Parameters: $f_i(N_i) = b_i(1 - N_i/K_i) - d_i$, $K_i = 200$ for all i, $\sigma_{ij} = 0$ for $i \neq j$; $b_i = 3\exp(-i^2/300) + 1$ and $d_i = 1.5$ in *A*; $b_i = 3\exp(-i^2/150) + 1$ and $\sigma_{ii} = 2.5$ in *B*.

perfect matching occurring in perfectly covarying environments.

Spatial correlations, in and of themselves, can influence the evolution of patch selection. To see why, consider a landscape where there are a finite number of distinct regions or habitats. Patches within different regions only differ to the extent the temporal fluctuations are correlated, that is, $f_i = f_j$ and $\sigma_i^2 = \sigma^2$ for all i, j but σ_{ij} for $i \neq j$ may vary. Let k_i be the number of patches in the ith region and $k = k_1 + \ldots + k_n$ be the total number of patches. In the absence of any variation in the spatial correlations, individuals select all patches with equal likelihood, that is, $p_1 = p_2 = \ldots = p_k = 1/k$. In contrast, assume the correlation between patches within region i is ρ_i and patches from different regions are uncorrelated. Appendix D shows individuals playing the ESS preferentially select patches in regions for which $\rho_i(k_i - 1)$ is smaller and show no preference for patches within a given region. All else being equal, individuals preferentially select patches within regions with fewer patches or lower spatial correlations; both of these preferences reduce the environmental variation experienced by an individual and, thereby, increases their fitness. Patches within regions with lower values of $\rho_i(k_i - 1)$ support larger populations, and consequently, the local stochastic growth rates in these regions are more negative.

A surprising consequence of these analytical results is that patch destruction within a region can select for individuals exhibiting greater preference for the remaining patches in the perturbed region. To illustrate this counterintuitive prediction, I simulated a landscape consisting of two regions with 20 patches in region 1 (before patch destruction) and 10 patches in region 2. Figure 5 illustrates that patch destruction in region 1 always results in a lower fraction of individuals selecting region 1 and a lower mean total population abundance. Despite this regional trend, individuals may exhibit a greater preference for patches within region 1 following patch destruction. For instance, if spatial correlations within both regions are equal ($\rho_1 = \rho_2 = 0.5$), then as predicted by the analytic results, individuals exhibit greater preference for patches in region 2 before patch destruction as there are fewer patches in region 2. However, if patch destruction results in region 1 having fewer patches, then there is selection for the opposite preference. Intuitively, this phenomena occurs because patches in each region offer special opportunities to buffer fluctuations in fitness across the entire ensemble of patches. So, as patches in one region get scarce, they

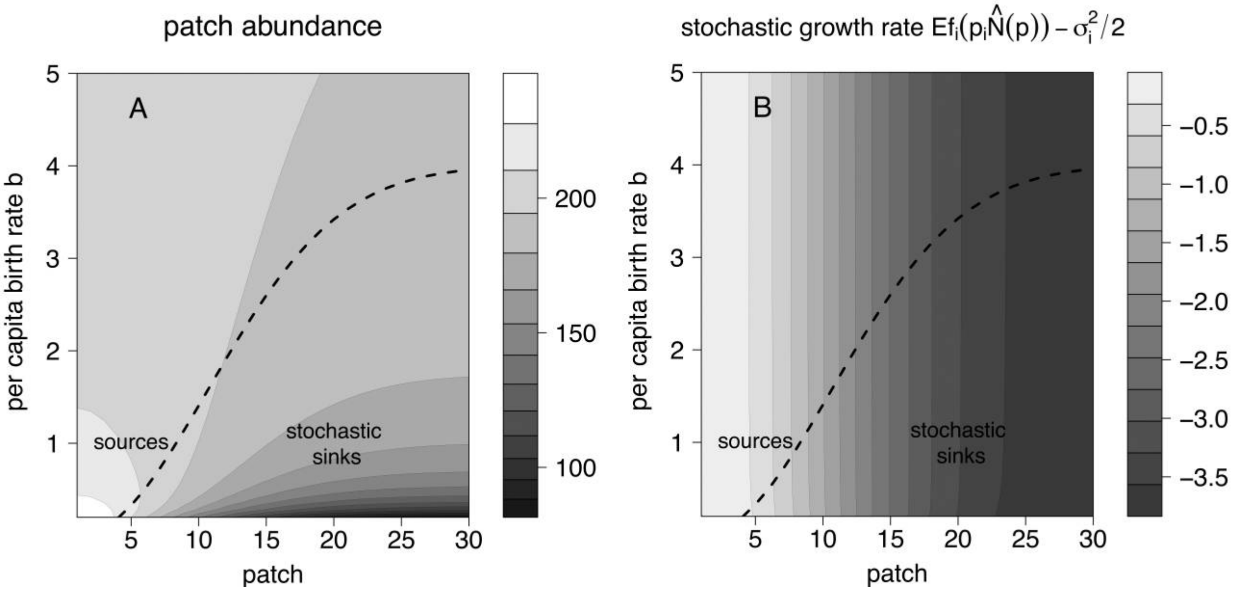

Figure 3: Selection for patches with lower environmental uncertainty. Contour plots of the mean patch abundances $p_i\mathbb{E}[\hat{N}(p)]$ in *A* and local stochastic growth rates $\mathbb{E}[f_i(p_i\hat{N})] - \sigma_i^2/2$ in *B* for populations playing the ESS. Dashed contours as in figure 2. Parameters: $f_i(N_i) = b_i(1 - N_i/K_i) - d_i$ with $d_i = 0$, $K_i = 200$, $\sigma_i^2 = 8 - 8\exp(-i^2/600)$ and $\sigma_{ij} = 0$ for $i \neq j$.

offer an increasingly precious commodity—a habitat with out-of-sync fluctuations in quality. When patches in region 1 are more correlated than patches in region 2, greater patch destruction is required for an evolutionary reversal in patch preferences. Alternatively, when patches within region 1 are sufficiently less correlated than patches within region 2, no amount of patch destruction reverses patch preferences; patches within region 2 are preferred at all levels of patch destruction. Intuitively, weaker correlations amongst patches in region 1 increases their value as patches with out-of-sync fluctuations in quality.

Discussion

Global climate models predict that increasing temporal variability in temperature, precipitation, and storms in the next hundred years (Schär et al. 2004; Tebaldi et al. 2006). For example, Schär et al. (2004) predict temperature variability in Europe may increase up to 100% with maximum changes in central and eastern Europe. Changes in mean temperature and increased variability in rainfall have already led to shifts in species distributions (Allen and Breshears 1998; Parmesan and Yohe 2003; Kelly and Goulden 2008). Evolution of patch selection may play an important role in these shifts (Parmesan 2006; Morris 2011). Morris (2011) recently reviewed how the deterministic theory of patch selection serves as a powerful tool for making predictions about future shifts in patch use. This deterministic theory predicts that the ESS for patch selection is an ideal free distribution for which the per capita growth rates of individuals in occupied patches equal zero, sink patches are unoccupied, and the fraction of individuals selecting a patch is proportional to the "carrying capacity" of the patch (Holt and Barfield 2001; Cressman et al. 2004; Cressman and Křivan 2006; Morris 2011). Morris (2011, p. 2408) concludes with a call to arms as "there is much work that needs our attention" especially stochastic effects as they "produce results that can depart rather dramatically from deterministic solutions." In response to this call, I analyzed the evolution of patch selection for a general class of stochastic models accounting for any number of patches, general patterns of spatial-temporal covariance, and general forms of density-dependent population growth. The analysis of these models shows that all of the classical IFD predictions can break down in the face of environmental stochasticity.

A powerful prediction of the classical deterministic theory is that evolution of patch selection equalizes local per capita growth rates across all occupied patches. For the empiricist, this prediction is testable (Abrahams 1986; Milinski and Parker 1991; Tregenza 1995; Oksanen et al. 1995). For the theoretician, this prediction often reduces solving the ESS to an algebraic problem (Cressman and Křivan 2006). My analysis of models accounting for environmental stochasticity reveals that the evolution of patch selection generally does not equalize any local de-

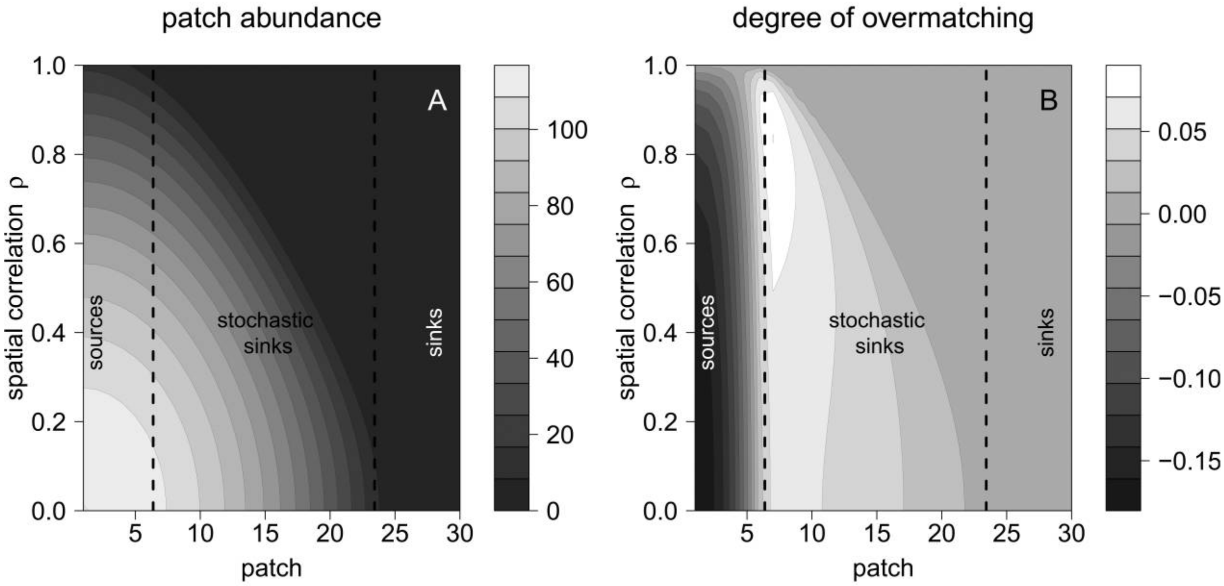

Figure 4: Spatial correlations select for range contraction. *A*, Contour plots of the mean patch abundances $p_i\mathbb{E}[\hat{N}(p)]$ for populations playing an ESS as a function of the patch location and the spatial correlation ρ. *B*, Contour plots of the difference $p_i - \tilde{N}_i^*/\sum_j \tilde{N}_j^*$ between the evolutionarily stable strategy preferences and classical patch matching rule are shown. Positive values correspond to overmatching and the negative values correspond to undermatching. Dashed contours as in figure 2. Parameters: $f_i(N_i) = b_i(1 - N_i/K_i) - d_i$, $b_i = 3\exp[-(15 - i)^2/75] + 1$, $d_i = 1.5$, $K_i = 100$, $\sigma_{ii} = 2.1$, and $\sigma_{ij} = 2.1\rho$ for $i \neq j$.

mographic measure of fitness across all occupied patches, a finding consistent with discrete-time, two-patch models (Schmidt et al. 2000; Holt and Barfield 2001). Rather, correlations in temporal fluctuations between patches result in a nonlocal measure of fitness being equal in all occupied patches: the difference between the expected per capita growth rate within a patch and the covariance between environmental fluctuations within this patch and the average environmental fluctuations experienced by the population across all patches. For two special cases, however, local demography determines the ESS for patch preferences. First, if environmental fluctuations tightly covary across the landscape, then one recovers a stochastic analog of the deterministic theory for which the local stochastic growth rates $\mathbb{E}[f_i(p_i\hat{N})] - \sigma_i^2/2$ are equal to zero in all occupied patches. Second, if environmental fluctuations are uncorrelated between patches, then a nonstandard but locally determined stochastic growth rate $\mathbb{E}[f_i(p_i\hat{N})] - p_i\sigma_i^2$ is equal in all occupied patches. When there are only two patches and there is not a strong skew in patch preferences, this nonstandard growth rate $\mathbb{E}[f_i(p_i\hat{N})] - p_i\sigma_i^2$ is approximately equal to the local stochastic growth rate. This may explain why Holt and Barfield (2001) observed the geometric mean of fitness (a discrete time analog of the local stochastic growth rate) being equal in occupied source patches in simulations of discrete-time models with two patches.

At a demographic equilibrium, populations conforming to the ideal free distribution never enter sink patches and have balanced birth and death rates in all source patches. In sharp contrast, my analysis shows that environmental stochasticity results in local stochastic growth rates being negative in all occupied patches. Hence, all local populations are either sink populations or pseudo-sink populations that only exhibit a negative local stochastic growth rate due to density-dependent feedbacks (Watkinson and Sutherland 1995). Intuitively, across all patches, the population maintains a larger, stable size in the long term by reducing the temporal variance. In particular, this implies that any particular patch represents some sort of a sink, because the isolated population cannot realize this variance-reducing effect.

When correlations in environmental fluctuations between patches are weak, populations playing the ESS occupy all stochastic sink patches. In addition, if environmental variations are sufficiently great in source patches and stochastic sink patches, populations playing the ESS also occupy deterministic sink patches. This latter result is consistent with earlier studies using discrete-time, two-patch models (Holt 1997; Jansen and Yoshimura 1998;

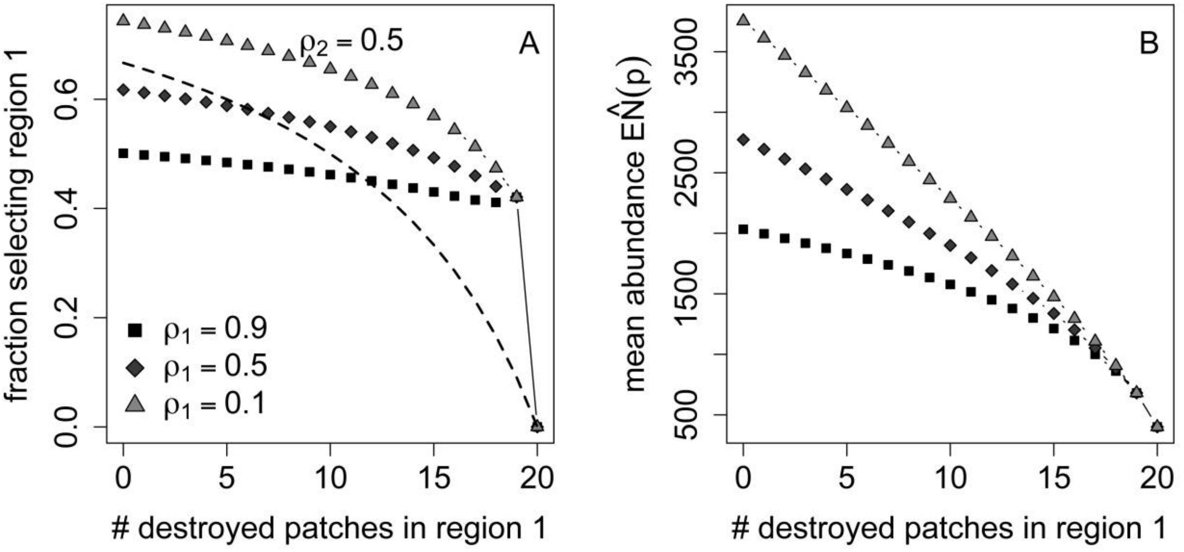

Figure 5: Evolutionary responses of patch selection to patch destruction. Prior to destruction, there are two regions with 20 patch patches in the first region and 10 patch patches in the second region. The temporal correlation between patches within region i is ρ_i. Patches from different regions are uncorrelated. In A, the total fraction of individuals selecting patches in region 1 is plotted as a function of the number of patches lost in region 1. The dashed curve represents the fraction of patches found in region 1. Points lying above the dashed curve correspond to individuals preferring patches within region 1 and points lying below this curve correspond to individuals preferring patches within region 2. In B, the mean abundance $\mathbb{E}[\hat{N}(p)]$ of the total population is plotted. Parameters: $f_i(N^i) = b(1 - N^i/K) - d$ with $b = 2$, $K = 200$, and $d = 0.5$.

Holt and Barfield 2001). However, these earlier studies did not predict the evolution of stochastic sink populations for arbitrarily small Gaussian fluctuations in source patches. My analysis also reveals that strong correlations between patches prevent the evolution of sink populations and lead to local stochastic growth rates being close to zero in occupied patches.

Under equilibrium conditions, the IFD predicts the fraction of individuals selecting a patch is proportional to the carrying capacity of the patch (i.e., the equilibrium abundance supported by the patch in isolation of other patches). When environmental fluctuations are synchronous across all patches and per capita growth rates are linear, this prediction still holds with respect to the mean population abundance supported by a patch. However, when environmental fluctuations are not perfectly covarying, populations playing the ESS overmatch their usage of lower-quality patches and undermatch their usage of higher-quality patches as predicted by the mean population abundances. These predictions are consistent with results of Hakoyama (2003) on optimal patch selection for landscapes with stochastic variation in resource supply rates. Even if local demography is statistically similar in all patches, I also show that correlations in the environmental fluctuations, in and of themselves, lead to undermatching. For example, all else being equal, individuals are less likely to select patches in regions experiencing stronger correlated environmental fluctuations than patches in regions experiencing weaker correlations.

Climate change have resulted in shifts in species geographical distribution in response to changes in mean temperature (Parmesan and Yohe 2003; Parmesan 2006). For example, in a meta-analysis involving more than 1,700 species, Parmesan and Yohe (2003) categorized 434 species as exhibiting a range shift in the past 17–1,000 years (median 66 years). Of these, 80% shifted as predicted by changes in mean temperature with range expansions as species colonized previously cool regions or range contractions in the case of some arctic species. Alternatively and consistent with prior work (Holt and Barfield 2001; Holt 2003), my analysis reveals that increasing environmental variation can select for species range expansions if this variability is weakly or negatively correlated across space or range contractions if this variability is highly correlated across space. Since there is evidence that some species ranges have been altered due to increasing environmental variability (Allen and Breshears 1998; McLaughlin et al. 2002; Parmesan 2006), it would be interesting to see how often these changes can be explained by the theory presented here.

When environmental variation is too great, population models predict populations are extinction prone (Lande et al. 2003). For example, McLaughlin et al.'s (2002) analysis on long-term time series of two checkerspot butterfly populations in California concludes their extinctions were hastened by increasing variability in precipitation, a phenomenon predicted by global climate models. If this environmental variation increases sufficiently slowly to allow a population's patch selection strategy to evolve, my analysis suggests that extinction is preceded by populations persisting solely in sink patches. Hence, persistence of coupled sink populations, which to some extent have been a fascinating theoretical curiosity (Jansen and Yoshimura 1998; Roy et al. 2005; Matthews and Gonzalez 2007; Schreiber 2010), may be an inescapable reality for populations subject to increasing levels of environmental variation.

To keep the models general yet tractable, I made several simplifying assumptions that could be relaxed in future studies. First, the focal species does not interact with any other species. It is well known that in deterministic patch selection theory, species interactions can substantially alter patterns of patch use (van Baalen and Sabelis 1993; Schmidt et al. 2000; Schreiber et al. 2000; Cressman et al. 2004; Schreiber and Vejdani 2006). For example, prey may select resource poor patches to escape predation and predators may select resource-rich patches to capture more nutritious prey (Fox and Eisenbach 1992; Schreiber et al. 2000; Schreiber and Vejdani 2006). It remains to be understood whether stochasticity in the environment exaggerates or ameliorates these contrary choices exhibited by prey and their predators. Second, the analysis assumes that individuals have unlimited, cost-free access to potential patches. However models accounting for search costs indicate that optimal patch selection behavior may involve a willingness to settle in low-quality patches, even when higher-quality patches are accessible (Ward 1987; Stamps et al. 2005). In light of the results presented here, it seems likely that environmental stochasticity in conjunction with search costs will further increase preferences for low-quality patches. Finally, populations may experience inverse density dependence at low densities due to cooperative behavior, mate limitation, or predator saturation (Courchamp et al. 1999). For populations exhibiting an IFD, this inverse density dependence can generates alternative stable states corresponding to all possible combinations of occupied patches and unoccupied patches (Fretwell and Lucas 1969; Greene 2003). Since environmental stochasticity can promote the evolution of sink populations, it seems reasonable to conjecture that inclusion of environmental stochasticity in these models with inverse density dependence will reduce the number of alternative states.

To conclude, patch selection strategies that evolve in stochastically varying environments can differ significantly from ideal free distributions under equilibrium conditions. In particular, undermatching of higher-quality patches, avoidance of clusters of highly correlated patches, and selection of sink patches can be optimal in stochastically fluctuating environments. These results highlight that the spatial covariance structure of environmental stochasticity plays a crucial role on the evolution of patch selection and deserve further empirical and theoretical attention.

Acknowledgments

Many thanks to B. Alger, M. Baskett, C. Boetigger, N. Fabina, H. Hakoyama, B. Meeker, M. Meisner, J. Moore, S. Patel, J. Rosenheim, J. Stamps, and an anonymous reviewer for providing many useful comments on previous drafts of this manuscript. This work was supported by National Science Foundation grants EF-0928987 and DMS-1022639.

APPENDIX A

An Evolutionary Dynamic

In general, getting an explicit tractable form of the evolutionarily stable strategy (ESS) is difficult. Hence, when this is not possible, it is useful to introduce an evolutionary dynamic that can be used to solve for the ESS numerically. The basic idea behind the evolutionary dynamic is that mutations arise that randomly reallocate time spent in one patch with time spent in another patch. This reassignment is only "adopted" by the population if it increases $\mathcal{I}(p, q)$. More formally, if time is discretized into units of length $\varepsilon > 0$ and e_i denotes the standard unit vector whose

ith component is 1 and remaining components are 0, then a mutation from p to $p+\varepsilon e_i-\varepsilon e_j$ occurs with probability $\mu p_i p_j$ and establishes with probability

$$\mathcal{I}(p, p+\varepsilon e_i-\varepsilon e_j)^+,$$

where $x^+=\max\{0,x\}$ denotes the positive part of a real number. The establishment probability is consistent with standard branching process approximations. The mutation probability is a choice of convenience. More general forms of mutation probabilities can be used. Discretizing mutation sizes as ε is done out of notational convenience. More general scalings proportional to ε simply correspond to rescaling time. Under these assumptions,

$$\begin{aligned} p_i(t+\varepsilon)-p_i(t) &\approx \mu p_i \sum_j p_j\{\mathcal{I}(p,p+\varepsilon(e_i-e_j))^+-\mathcal{I}(p,p-\varepsilon(e_i-e_j))^+\} \\ &\approx \mu p_i \sum_j p_j\left(\frac{\partial \mathcal{I}(p,q)}{\partial q_i}\bigg|_{q=p}-\frac{\partial \mathcal{I}(p,q)}{\partial q_j}\bigg|_{q=p}\right)\varepsilon. \end{aligned}$$

Hence, taking the limit as $\varepsilon \to 0$ yields

$$\begin{aligned} \frac{dp_i}{dt} &= \mu p_i \sum_j p_j\left(\frac{\partial \mathcal{I}(p,q)}{\partial q_i}\bigg|_{q=p}-\frac{\partial \mathcal{I}(p,q)}{\partial q_j}\bigg|_{q=p}\right) \\ &= \mu p_i\left(\frac{\partial \mathcal{I}(p,q)}{\partial q_i}\bigg|_{q=p}-\sum_j p_j\frac{\partial \mathcal{I}(p,q)}{\partial q_j}\bigg|_{q=p}\right). \end{aligned}$$

I claim that if $p_i(0)\ge 0$ for all i and $\sum_i p_i(0)=1$, then $p_i(t)\ge 0$ for all i with $t\ge 0$ and $\sum_i p_i(t)=1$ for all $t\ge 0$. This claim follows from two observations. First, the system of equations are conservative as $\sum_i dp_i/dt=0$. Hence, if $\sum_i p_i(0)=1$, then $\sum_i p_i(t)=1$ for all $t\ge 0$. Second, since $p_i'(t)=0$ whenever $p_i(t)=0$, $p_i(t)\ge 0$ for t provided that $p_i(0)\ge 0$.

Since

$$\frac{\partial \mathcal{I}}{\partial q_i}(p,p)=\mathbb{E}[f_i(p_i\hat{N}(p))]-\sum_j p_j\sigma_{ij},$$

this system of differential equations becomes

$$\begin{aligned} \frac{dp_i}{dt} &= \mu p_i\left(\mathbb{E}[f_i(p_i\hat{N}(p))]-\sum_j p_j\sigma_{ij}-\sum_j p_j\left\{\mathbb{E}[f_j(p_j\hat{N}(p))]-\sum_k p_k\sigma_{jk}\right\}\right), \\ &= \mu p_i\left(\mathbb{E}[f_i(p_i\hat{N}(p))]-\sum_j p_j\sigma_{ij}+\frac{1}{2}\sum_{j,k} p_j p_k\sigma_{jk}\right), \end{aligned}$$

where the second line follows from $\sum_j p_j\mathbb{E}[f_j(p_j\hat{N}(p))]-(1/2)\sum_{j,k}p_jp_k\sigma_{j,k}=0$; that is, the average stochastic growth rate equals zero at the stationary distribution for the resident population.

When the per capita growth rates are linear, that is, $f_i(N^i)=b_i(1-N^i/K_i)-d_i$, a more explicit representation of the dynamic is possible as

$$\mathbb{E}[f_i(p_i\hat{N}(p))]=b_i\left(1-\frac{p_i\mathbb{E}[\hat{N}(p)]}{K_i}\right)-d_i,$$

and $\mathbb{E}[\hat{N}(p)]$ must satisfy the zero stochastic growth rate equation

$$0=\sum_i p_ib_i\left(1-\frac{\mathbb{E}[\hat{N}(p)]}{K_i}\right)-\sum_i p_id_i-\frac{\sigma(p)^2}{2}.$$

Solving for $\mathbb{E}[\hat{N}(p)]$ yields

$$\mathbb{E}[\hat{N}(p)] = \frac{\sum_i p_i(b_i - d_i) - \sigma(p)^2/2}{\sum_i p_i b_i/K_i},$$

which can be substituted into the evolutionary dynamic equation to yield an explicit system of differential equations.

APPENDIX B

Persistence

In order for an evolutionarily stable strategy (ESS) analysis to be meaningful, there needs to be a patch selection strategy p such that $\sum_i p_i f_i(0) - \sigma(p)^2/2 > 0$. When this occurs, there is a unique positive stationary distribution for this strategy and the population persists (Braumann 1999). Whether such a p exists reduces to maximizing the function $g(p) = \sum_i p_i f_i(0) - \sigma(p)^2/2$ subject to the linear constraints $p_i \geq 0$ for all i and $\sum_i p_i = 1$. Under the assumption that the optimal p, call it p^*, satisfies $\prod_i p_i^* > 0$ and the covariance matrix Σ is invertible, Evans et al. (2012) showed that

$$p^* = \Sigma^{-1}\left(r - \frac{\mathbf{1}^T\Sigma^{-1}r - 1}{\mathbf{1}^T\Sigma^{-1}\mathbf{1}}\mathbf{1}\right), \tag{B1}$$

where $\mathbf{1} = (1, \dots, 1)$ and $r = (f_1(0), \dots, f_k(0))$. Equation (1) defines the optimal vector p^* provided that it belongs to the interior of the probability simplex $\Delta = \{p : p_i \geq 0, \sum_i p_i = 1\}$. Otherwise, one can perform similar analyses on the faces of the probability simplex Δ. Hence, persistence requires that $g(p^*) > 0$.

For the special case where $\sigma_{ii} = \sigma^2$ and $\sigma_{ij} = \rho\sigma^2$ for $i \neq j$ and $f_i(0) = r$ for all i, symmetry implies that $p_i^* = 1/k$, in which case

$$\begin{aligned} g(p^*) &= r - \frac{1}{2}\sum_{i,j}\frac{1}{k^2}\sigma_{ij}, \\ &= r - \frac{1}{2}\left(\sum_i \frac{1}{k^2}\sigma^2 + \sum_{i\neq j}\frac{1}{k^2}\sigma^2\rho\right), \\ &= r - \frac{\sigma^2}{2}\left(\frac{1}{k} - \frac{k-1}{k}\rho\right) = r - \frac{\sigma^2}{2k}[1 - (k-1)\rho], \end{aligned}$$

as claimed in the main text.

APPENDIX C

The Evolutionarily Stable Strategy (ESS)

Assume the covariance matrix Σ is positive definite and p is an ESS. Then p is a local maximum for the function $q \mapsto \mathcal{I}(p, q)$ subject to the constraints $h(q) = \sum_i q_i = 1$ and $q_i \geq 0$ for all i. By the method of Lagrange multipliers there exists a scalar λ such that

$$\lambda = \lambda\frac{\partial h}{\partial q_i}(p) = \left.\frac{\partial \mathcal{I}(p, q)}{\partial q_i}\right|_{q=p} = \mathbb{E}[f_i(p_i\hat{N}(p))] - \sum_j p_j\sigma_{ij} \tag{C1}$$

for all i such that $p_i > 0$. Multiplying both sides of equation (C1) by p_i and summing with respect to i yields

$$\lambda = \sum_i p_i\lambda = \sum_i p_i\mathbb{E}[f_i(p_i\hat{N}(p))] - \sigma(p)^2. \tag{C2}$$

On the other hand, at the stochastic equilibrium, the stochastic growth rate of the population equals zero:

$$0 = \sum_i p_i \mathbb{E}[f_i(p_i \hat{N}(p))] - \frac{\sigma(p)^2}{2}. \tag{C3}$$

Combining the last two equations yields

$$\lambda = -\frac{\sigma(p)^2}{2}.$$

This expression for λ combined with equation (C1) yields the ESS characterization (10) provided in the main text. Since $q \mapsto \mathcal{I}(p, q)$ is a strictly concave down function, any p satisfying the Lagrange multiplier condition is a global maximum for this function and, consequently, an ESS.

Unlike the deterministic case for which an ESS p for patch selection only satisfies the weak noninvasibilty condition $\mathcal{I}(p, q) \leq 0$ for all $q \neq p$, any ESS p for patch selection in a stochastic environment satisfies the strong noninvasibility condition: $\mathcal{I}(p, q) < 0$ for all $q \neq p$. This observation implies that the stochastic growth rate is negative in all occupied patches whenever multiple patches are occupied. To understand why, consider the mutant strategy q where $q_i = 1$ for some patch i selected by the ESS (i.e., $p_i > 0$). Since the invasion rate $\mathcal{I}(p, q) = \mathbb{E}[f_i(p_i \hat{N}(p))] - \sigma_i^2/2$ equals the stochastic growth rate in patch i and $\mathcal{I}(p, q) < 0$ by the ESS noninvasibility condition, the stochastic growth rate in patch i is negative.

In the special case of linear per capita growth rates $f_i(N_i) = b_i(1 - N_i/K_i) - d_i$, the ESS characterization becomes

$$0 = b_i\left(1 - \frac{p_i \mathbb{E}[\hat{N}(p)]}{K_i}\right) - d_i + \sum_{jk} p_j p_k \left(\frac{\sigma_{jk}}{2} - \sigma_{ji}\right). \tag{C4}$$

To solve for $\mathbb{E}[\hat{N}(p)]$, one can use the fact that the stochastic growth rate at the stochastic equilibrium is zero:

$$0 = \sum_i p_i b_i \left(1 - \frac{p_i \mathbb{E}[\hat{N}(p)]}{K_i}\right) - \sum_i p_i d_i - \frac{\sigma(p)^2}{2}.$$

Hence,

$$\mathbb{E}[\hat{N}(p)] = \frac{\sum_i p_i(b_i - d_i) - (\sigma(p)^2/2)}{\sum_i p_i^2 b_i/K_i}. \tag{C5}$$

Combined, equations (C4)and (C5) provide an implicit algebraic characterization of the ESS for this special case of linear per capita growth rates.

In general, all source patches must be occupied at an ESS. Indeed, assume that patch k is a source patch ($f_k(0) > \sigma_{kk}/2$) and p is a strategy such that $p_k = 0$. Let $q = (0, \ldots, 0, 1)$. Then $\mathcal{I}(p, q) = f_k(0) - \sigma_{kk}/2 > 0$ and p is not an ESS. Hence, a population playing the ESS must occupy all of the source patches.

To see that all the stochastic sinks are occupied in spatially uncorrelated environments, consider a strategy p such that $p_i = 0$ for some i. Without loss of generality, assume that $p_k = 0$. Consider the mutant strategy $q(\varepsilon) = q$ with $q_i = (1 - \varepsilon)p_i$ for $i < k$ and $q_k = \varepsilon$. Let $g(\varepsilon) = \mathcal{I}(p, q(\varepsilon))$, in which case

$$g(\varepsilon) = \sum_i (1 - \varepsilon) p_i \mathbb{E}[f_i(p_i \hat{N}(p))] + \varepsilon f_k(0) - (1 - \varepsilon)^2 \frac{1}{2} \sum_{i,j} p_i p_j \sigma_{ij} - \varepsilon(1 - \varepsilon) \sum_i p_i \sigma_{ik} - \frac{\varepsilon^2}{2}\sigma_{kk}.$$

Strategy p can be an ESS only if $g'(0) \leq 0$, where

$$\begin{aligned} g'(0) &= f_k(0) - \sum_i p_i \mathbb{E}[f_i(p_i \hat{N}(p))] + \sum_{i,j} p_i p_j \sigma_{ij} - \sum_i p_i \sigma_{ik}, \\ &= f_k(0) + \frac{1}{2} \sum_{i,j} p_i p_j \sigma_{ij} - \sum_i p_i \sigma_{ik}. \end{aligned}$$

This is only possible if $\sum_i p_i \sigma_{ik}$ is sufficiently positive or $f_k(0)$ is sufficiently negative. If the correlations between patch k and the other patches is too weak and $f_k(0) + \sigma(p)^2/2 > 0$, then $g'(0) > 0$ and one needs $p_k > 0$ at the ESS. In particular, this means that if $f_k(0) > 0$, then the patch is occupied even if it is a stochastic sink. It also means that indeterministic sinks are occupied if the reduction of the population growth rate due to noise is greater than the reduction in of the population growth rate for individuals living in the sink patch.

To understand the effects of spatial correlations, in and of themselves, on the ESS, I assume there are n regions with $k_1, \ldots, k_n$ patches in each region such that $\sum_i k_i = k$. Let σ_i^2 be the variance for patches in region i and ρ_i be the correlation between a pair of patches in region i. Assume that $f_i = f$ for all patches i and that patches in different regions are uncorrelated. Then

$$\sigma(p)^2 = \sum_{i=1}^{n} p_i^2\sigma_i^2 k_i[1+\rho_i(k_i-1)],$$

where p_i is fraction of individuals going to a patch within region i. If there are multiple patches occupied at the ESS, then characterization (10) implies

$$-\frac{1}{2}\sum_{i=1}^{n} p_i^2\sigma_i^2 k_i[1+\rho_i(1-k_i)] = \mathbb{E}[f(p_j\hat{N}(p))] - p_j\sigma_i^2[1+\rho_i(k_i-1)] \tag{C6}$$

for all patches j within region i. Since the right-hand side of equation (C6) is a decreasing function of p_j, occupied patches in regions with larger values of $\sigma_i^2[1+\rho_i(k_i-1)]$ must have smaller values of p_j. When $\sigma_i = \sigma$ for all regions i, patches with a lower value of p_j have a larger value of $\mathbb{E}[f(p_j\hat{N}(p))]$ and, consequently, a larger stochastic growth rate $\mathbb{E}[f(p_j\hat{N}(p))] - \sigma^2/2$.

APPENDIX D

Supplementary Figure

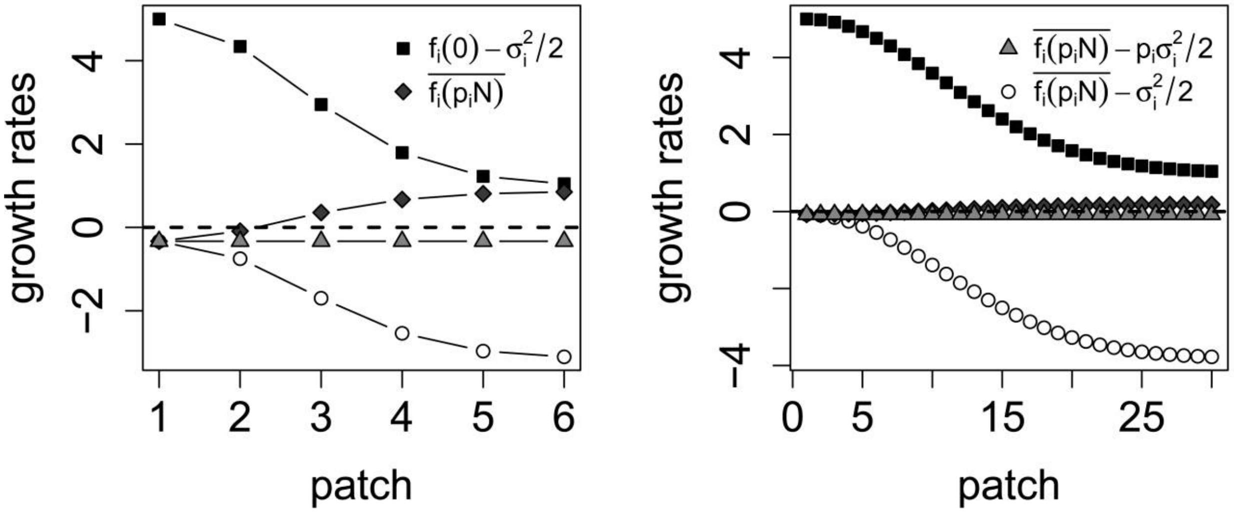

Figure D1: Influence of patch number (6 vs. 30) of stochastic growth rates for populations playing the evolutionarily stable strategy (ESS). Parameters: $f_i(N_i) = b_i(1 - N_i/K_i) - d_i$ with $b_i = 5$, $d_i = 0$, $K_i = 200$, and $\sigma_i^2 = 8 - 8\exp[-3(i/k)^2/2]$ and $\sigma_{ij} = 0$ for $i \neq j$.

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