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Eric M Schauber
*Southern Illinois University Carbondale*

Brett J Goodwin

Clive G Jones

Richard S Ostfeld

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# SPATIAL SELECTION AND INHERITANCE: APPLYING EVOLUTIONARY CONCEPTS TO POPULATION DYNAMICS IN HETEROGENEOUS SPACE

Eric M. Schauber,[1,3,4] Brett J. Goodwin,[2,3] Clive G. Jones,[3] and Richard S. Ostfeld[3]

[1]*Cooperative Wildlife Research Laboratory and Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901 USA*
[2]*Department of Biology, University of North Dakota, Grand Forks, North Dakota 58202 USA*
[3]*Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545 USA*

*Abstract*. Organisms in highly suitable sites generally produce more offspring, and offspring can inherit this suitability by not dispersing far. This combination of spatial selection and spatial inheritance acts to bias the distribution of organisms toward suitable sites and thereby increase mean fitness (i.e., per capita population increase). Thus, population growth rates in heterogeneous space change over time by a process conceptually analogous to evolution by natural selection, opening avenues for theoretical cross-pollination between evolutionary biology and ecology. We operationally define spatial inheritance and spatial selective differential and then combine these two factors in a modification of the breeder's equation, derived from simple models of population growth in heterogeneous space. The modified breeder's equation yields a conservative criterion for persistence in hostile environments estimable from field measurements. We apply this framework for understanding gypsy moth population persistence amidst abundant predators and find that the predictions of the modified breeder's equation match initial changes in population growth rate in independent simulation output. The analogy between spatial dynamics and natural selection conceptually links ecology and evolution, provides a spatially implicit framework for modeling spatial population dynamics, and represents an important null model for studying habitat selection.

*Key words: dispersal; fitness; inheritance; modeling; natural selection; population dynamics; spatial heterogeneity; suitability.*



## Introduction

An organism's ability to survive and reproduce is profoundly tied to the suitability of its local environment, defined as its expected fitness in situ. Factors that determine environmental suitability (e.g., resource availability or risk of attack) typically show positive autocorrelation in space and time, so an offspring settling near its natal site will generally experience an environment more like that of its parents than if it had dispersed far away. Therefore, environmental suitability can be considered inheritable (although non-genetically) when suitability is spatiotemporally autocorrelated and dispersal distance is limited. The inheritance of space has become part of the parlance of ecology, in which philopatric animals are described as inheriting home ranges or burrow systems (Boero 2003, Hale et al. 2003, Kitchen et al. 2005) and lagged effects of density are termed "inherited environmental effects" (Ergon et al. 2001). However, the concept of spatial inheritance has not been operationally defined.

For phenotypic traits, inheritance of traits affecting fitness allows for evolution by natural selection, producing a shift in phenotypic distribution of a population and a tendency for mean fitness to increase. Therefore, recognizing that an organism's location affects its fitness and is inheritable raises the tantalizing possibility that the concepts and models of evolutionary theory could be brought to bear in understanding population dynamics in heterogeneous space. To wit, individuals in highly suitable sites generally leave more offspring, which can inherit relatively high suitability if they do not disperse far. Thus, spatial heterogeneity and limited dispersal interact to cause a passive spatial shift of the population toward suitable locations and to elevate population mean fitness (which is equivalent to per capita population growth rate) above the mean suitability of the landscape (Bolker 2003, Snyder and Chesson 2003, Goodwin et al. 2005). This phenomenon has been termed "habitat correlation" (Wiens 1976), "habitat association" (Bolker 2003), and "positive growth-density covariance" (Snyder and Chesson 2004), all of which describe the resultant pattern but not the process responsible. Here, we explicitly address process by making operational the conceptual analogy between spatial population dynamics and natural selection and by defining spatial inheritability and spatial selective differential. We explore the population dynamic consequences using a variant of the breeder's equation (Walsh and Lynch 1999), derived from fundamental models of locally exponential population

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[4] E-mail: schauber@siu.edu

growth in heterogeneous space. From this equation, we identify a conservative criterion for deterministic persistence of a population in hostile environments. Finally, we assess the utility of this simple modeling framework by comparing its analytic predictions with output of a spatially explicit, individual-based simulation of gypsy moths (*Lymantria dispar*) in areas with abundant predators (white-footed mice, *Peromyscus leucopus*).

## Genetic Heritability, Natural Selection, and the Breeder's Equation

Heritability ($h^2$) is the ratio of the additive genetic variance in a phenotypic trait to the phenotypic variance (Fisher 1930). If genetic effects on a trait are additive, $h^2$ can be measured by the regression of offspring phenotype ($z_o$) on parental phenotype ($z_p$): $h^2 = \mathrm{Cov}(z_o, z_p)/\mathrm{Var}(z_p)$, where $\mathrm{Var}(z_p)$ is phenotypic variance among parents. This regression is assumed to be calculated in the absence of selection; i.e., with a representative sample of the parental population, uniform contribution of offspring, and a uniform environment (Fernandez and Miller 1985). The relationship between parental phenotype and fitness ($w_p$) is described by the selective differential ($S$). Often, $S$ is explained in the context of artificial selection, where organisms failing to meet phenotypic criteria are not allowed to breed ($w_p = 0$). In such a case, $S$ is the difference in mean phenotype between parents allowed to breed $\bar{z}'_p$ and all potential parents including non-breeders ($\bar{z}_p$). More generally (e.g., when $w_p$ varies continuously), $\bar{z}'_p$ is the fitness-weighted mean phenotype of potential parents (i.e., $\bar{z}'_p = E(z_p w_p/\bar{w}_p)$ where $\bar{w}_p$ is the mean fitness of potential parents) and $S = \bar{z}'_p - \bar{z}_p = \mathrm{Cov}(z_p, w_p)/\bar{w}_p$ (Price 1970). The intergenerational change in mean phenotype due to selection follows the familiar breeder's equation: $R = \bar{z}_o - \bar{z}_p = h^2 S$, where $\bar{z}_o$ is the mean phenotype of offspring. If the trait of interest is fitness itself, (i.e., $z_p = w_p$), then $S = \mathrm{Var}(w_p)/\bar{w}_p$ and the breeder's equation yields Fisher's (1930) fundamental theorem of natural selection, which states that (absent countering forces) the increase in population mean fitness between generations is equal to the additive genetic variance in fitness divided by mean fitness. In general, $h^2 < 1$ so the breeder's equation implies that $|\bar{z}_o - \bar{z}_p| < |\bar{z}'_p - \bar{z}_p|$, so relative to $\bar{z}'_p$, $\bar{z}_o$ regresses toward $\bar{z}_p$ by an amount determined by $1 - h^2$. If selection were to cease $E(\bar{z}_o - \bar{z}_p) = 0$.

## Spatial Inheritability and Spatial Selection

Here, we consider a scenario where organisms are genetically identical but inhabit locations of differing suitability. The average suitability ($w$) over all locations (occupied or not) yields the landscape mean suitability, $\bar{w}_l$. One can also average $w$ over all locations occupied by organisms to yield the mean fitness of the population of potential parents, $\bar{w}_p$, which determines the overall rate of population increase ($\lambda$). Similar to genetic heritability, we can define spatial inheritability ($I_S^2$) as the slope of the offspring–parent regression of environmental suitability when spatial selection is absent; i.e., parental locations are random and fitnesses are equal:

$$I_S^2 = \frac{\mathrm{Cov}(w_o, w_p)}{\mathrm{Var}(w_p)}. \quad (1)$$

If fitness were unaffected by location, the population would converge to a random spatial distribution over time due to diffusion. Thus, spatial selection differs from natural selection because in its absence $\bar{w}_o$ tends to regress not toward $\bar{w}_p$ but toward $\bar{w}_l$. We therefore define spatial selective differential ($S_S$) as the difference between fitness-weighted mean suitability experienced by parents ($\bar{w}'_p = E(w_p^2/\bar{w}_p)$) and $\bar{w}_l$, which can be calculated as

$$S_S = \bar{w}'_p - \bar{w}_l = \frac{\mathrm{Var}(w_p)}{\bar{w}_p} + \bar{w}_p - \bar{w}_l. \quad (2)$$

Recognizing that $E(w_o - \bar{w}_l) = I_S^2(w_p - \bar{w}_l)$, we find that the deviation of $\bar{w}_o$ from $\bar{w}_l$ provides an analogue of the breeder's equation:

$$R_S = \bar{w}_o - \bar{w}_l = I_S^2 S_S. \quad (3)$$

To obtain the intergenerational change in mean fitness, the spatial analogue of Fisher's fundamental equation, we combine Eqs. 2–3 and rearrange:

$$\Delta\bar{w} = \bar{w}_o - \bar{w}_p = I_S^2 \frac{\mathrm{Var}(w_p)}{\bar{w}_p} - (1 - I_S^2)(\bar{w}_p - \bar{w}_l). \quad (4)$$

From Chesson (2000), we note that $\bar{w}_p - \bar{w}_l$ is equal to the spatial covariance between local abundance and suitability. Therefore, Eq. 4 describes the dynamics of both mean fitness and spatial distribution of organisms. Because $\Delta\bar{w}$ is negatively related to $\bar{w}_p - \bar{w}_l$, the population ultimately converges to an asymptotic mean fitness and a stationary spatial distribution. Eqs. 2–4 are functions of $\mathrm{Var}(w_p)$, which itself changes over time depending on $\bar{w}_l$, $\mathrm{Var}(w_l)$, and higher moments of $w_l$. Therefore, finding exact solutions for asymptotic conditions (i.e., $\Delta\bar{w} = 0$) may not be straightforward. However, setting $\bar{w}_p = \bar{w}_l$ and $\mathrm{Var}(w_p) = \mathrm{Var}(w_l)$ in Eq. 4 provides solutions for the change in growth rate when the initial distribution of organisms is independent of local suitability. Thus, this framework can describe the expected dynamics in cases where aggregation in suitable sites has not yet developed or has been disrupted, as in a population colonizing a new area or experiencing a sudden shift in the spatial pattern of suitability.

## Analytical Population Models

Population mean fitness is equivalent to the per capita rate of population increase, so $\bar{w}_p = \lambda_t = N_{t+1}/N_t$ (where $N_t$ is the regional population size in generation $t$) and $\bar{w}_o = \lambda_{t+1}$. We derived expressions for $\Delta\lambda = \lambda_{t+1} - \lambda_t$ in spatially implicit models of genetically invariant populations with non-overlapping generations. The first model considers two discrete patches of different (but static) suitability ($w_1 \neq w_2$), with a constant and

symmetrical per capita probability ($b$) of newborns dispersing to the other patch. The second model considers a continuous two-dimensional universe in which dispersal is described by an arbitrary dispersal kernel ($k(x)$, where $x$ indicates distance) and environmental suitability varies in space and time according to an arbitrary spatiotemporal autocorrelation function ($\rho(x)$, i.e., correlation between suitability at a given location in generation $t$ and suitability at locations distance $x$ away in generation $t+1$). That $k(x)$ and $\rho(x)$ are functions of $x$ alone reflects our simplifying assumption that dispersal distance and environmental autocorrelation were independent of direction and starting location (i.e., isotropic [Cressie 1993]). We further assumed that local abundance did not affect suitability and that dispersal was unaffected by local density or environmental suitability. These assumptions are unrealistic in many cases, but our objective was to strip the process down to its fundamentals.

Eq. 4 can be derived from both models, differing only by the expression for $I_S^2$ (Appendix A). In the two-patch model $I_S^2 = 1 - 2b$, whereas in the continuous-space model,

$$I_S^2 = \int_{x=0}^{\infty} k(x)\rho(x)dx. \tag{5}$$

Thus, Eq. 4 applies regardless of the treatment of space as discrete or continuous. If $k(x)$ and $\rho(x)$ can both be approximated by exponential functions ($k(x) \approx \beta e^{-\beta x}$ and $\rho(x) \approx \rho(0)e^{-\gamma x}$) then

$$I_S^2 \approx \frac{\beta\rho(0)}{\beta+\gamma} \tag{6}$$

where $\beta$ and $\gamma$ are, respectively, the rates at which dispersal probability and spatiotemporal autocorrelation of suitability decay with distance, and $\rho(0)$ is the temporal autocorrelation of suitability across generations at lag distance 0. If patch suitability is static, the asymptotic value of $\lambda$ and the stable spatial distribution in the two-patch model (or generally $n$-patch models) can be determined by eigenanalysis (Rogers 1966, Lebreton and Gonzalez-Davila 1993). For continuous space, Snyder and Chesson (2003) presented a framework for deriving asymptotic $\lambda$ and the stable spatial distribution in the special case of a static environment ($\rho(0) = 1$).

The spatial distribution of a population colonizing a new area or experiencing a sudden change in the spatial pattern of suitability may be independent of environmental suitability, so $E(\lambda_0) = \overline{w}_1$. In hostile environments ($\overline{w}_1 < 1$), parameter values resulting in $E(\lambda_1) > 1$ provide a conservative criterion for deterministic population persistence. To find this criterion, we set $\overline{w}_p = \overline{w}_1$ and $\overline{w}_o > 1$ in Eq. 4. Rearranging yields

$$I_S^2 CV^2(w_1) > (1 - \overline{w}_1)/\overline{w}_1 \tag{7}$$

where $CV^2(w_1)$ is the squared spatial coefficient of variation in environmental suitability. This criterion can provide a useful gauge for the level of dispersal limitation and the magnitude and scale of spatial heterogeneity necessary to ensure population persistence.

## Comparison with a Spatially Explicit Individual-Based Simulation (SEIS)

We have studied predation by white-footed mice on gypsy moths (see Plate 1) for over a decade (Ostfeld et al. 1996, Jones et al. 1998), and have been intrigued by the persistence of gypsy moths in areas of abundant mice, despite empirically parameterized mean-field models suggesting that the moths could be driven locally extinct (Schauber 2000, Schauber et al. 2004, Goodwin et al. 2005). Gypsy moths are univoltine, adult females cannot fly (Elkinton and Liebhold 1990), and larvae typically disperse less than 100 m (Weseloh 1987). Predation by white-footed mice on gypsy moth pupae can substantially affect low-density gypsy moth populations (Elkinton et al. 1996, Jones et al. 1998), yet the mice show no numerical or aggregative response to local densities of pupae (Elkinton and Liebhold 1990, Schauber et al. 2004). Local risk of predation by mice varies substantially in space, is spatially autocorrelated at scales of 10 to >100 m, and is temporally autocorrelated between years (Connors 2005, Schmidt et al. 2006). Goodwin et al. (2005) developed an empirically parameterized SEIS of this system, and found that the synergistic effects of spatial heterogeneity in risk and limited dispersal of moths greatly enhanced moth persistence. To assess the utility of the concepts of spatial selection and inheritance in understanding this system, we compared predictions of Eq. 4 with output of the Goodwin et al. (2005) SEIS, modified to remove the ability of pupae to locally satiate the mice (Appendix B).

Initial $\Delta\lambda$ of the simulated populations, starting from a random spatial distribution, showed a nearly 1:1 relationship with predictions from the breeder's equation (Fig. 1A), and after several generations $\lambda$ approached an asymptotic value that was inversely related to median dispersal distance (Fig. 1B). For certain parameter values, spatial selection and inheritance caused $\lambda$ to reach an asymptotic value >1.1 even when $\overline{w}_1$ was below 0.8 (Fig. 1B). Also, observed spatial inheritability closely followed the hyperbolic relationship predicted by Eq. 6. Thus, several important outputs of our computationally intensive simulations could be obtained from Eq. 4.

## Discussion

We propose that, at its most fundamental, population growth in heterogeneous space can be usefully thought of as a process analogous to natural selection. The results are increasing per capita growth rate of the population coupled with increasing aggregation of organisms in sites of high suitability, paralleling the increase in mean fitness and phenotypic change predicted by Fisher's (1930) fundamental theorem of natural selection. This analogy enables explicit and a priori

predictions about the change in per capita growth rates and the spatial distribution of populations in heterogeneous space, and focuses empirical efforts on critical parameters estimable from field data. In addition, it highlights the generality of selection and inheritance as mechanisms of ecological as well as evolutionary change and provides opportunities to borrow from the well-developed quantitative framework of quantitative genetics in addressing difficult problems of modeling spatial population dynamics.

Most population dynamic models are rooted in the assumption that density-independent population growth is exponential, an assumption so fundamental that it has been proposed as a natural law (Ginzburg 1986, Turchin 2001). However, the analogy between spatial population dynamics and natural selection means that $\lambda$, absent countering forces, has a fundamental tendency to increase over time (i.e., hyper-exponential growth) when the spatial pattern of the environment is correlated between generations and dispersal distances are limited. This change in $\lambda$ may explain the delay in achieving high per capita growth sometimes observed between introduction and eruption of invasive species (Sakai et al. 2001) or between crash and increase of cyclic populations (Boonstra et al. 1998). In the former case, colonizing propagules can be expected to arrive at locations independent of local habitat suitability, so more often than not initial per capita growth rate can be expected to increase over generations as spatial selection and inheritance cause the population to shift toward more suitable locations. In the case of cyclic populations, sites offering high relative fitness during the crash (e.g., refuges) may not offer high fitness during the increase phase (e.g., rich food patches; Ylönen et al. 2003). Thus, the spatial distribution of organisms after the crash may be independent of or even negatively related to local suitability for increase, and the time required for a new spatial distribution to emerge through spatial selection and inheritance may extend the low phase of the cycle.

Although the model we derive here is simplistic, it circumvents some limitations of existing modeling frameworks. Previous approaches to incorporating both spatial heterogeneity and limited movement include spatially explicit simulations (Goodwin et al. 2005) and analytical approximations derived from simulations (Bolker 2003), which explicitly model changes in population distribution and $\lambda$, and simpler analytical models (Snyder and Chesson 2003) that focus on asymptotic conditions (i.e., covariance with suitability has already equilibrated). The framework we initiate here is analytically tractable yet explicitly describes the process whereby $\lambda$ and the covariance between local abundance and suitability increase toward maxima. Perhaps more importantly, spatial inheritability explicitly accounts for inconstant but autocorrelated environments and unifies dispersal characteristics and the spatiotemporal pattern of suitability into a single

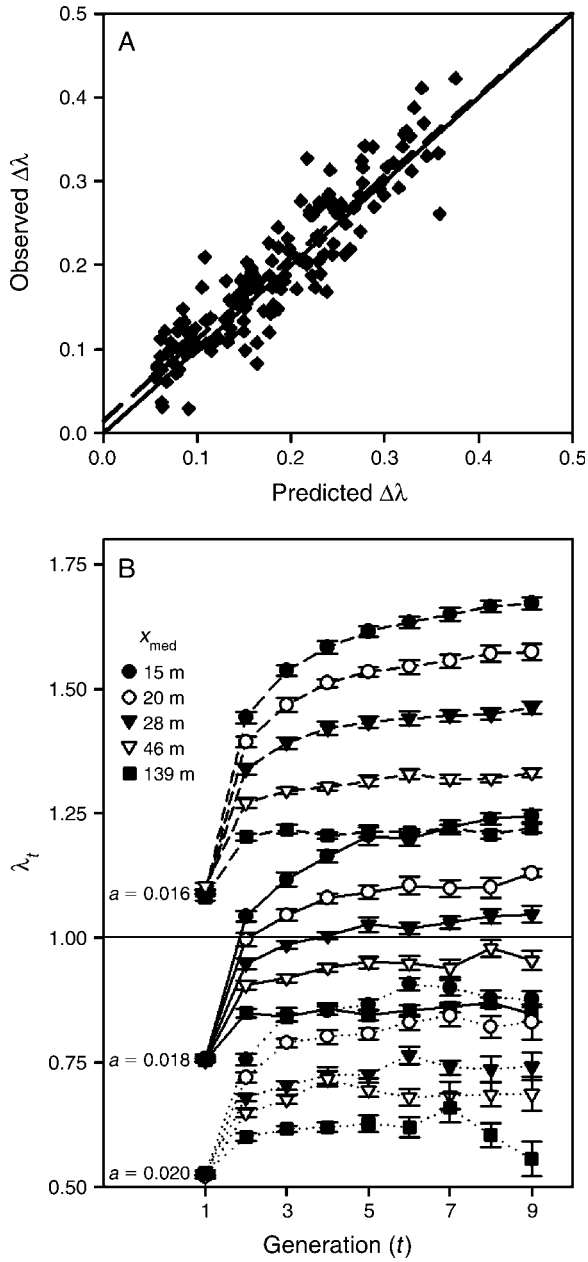


FIG. 1. Output of gypsy moth SEIS (spatially explicit individual-based simulation) model. (A) Concordance between observed initial increase in per capita population growth rate ($\Delta\lambda$) and predictions from the breeder's equation (Walsh and Lynch 1999), with 1:1 (solid) and least-squares regression (dashed) lines. Each point represents the average $\Delta\lambda$ from 1000 replicate simulations. (B) Trajectories of mean $\lambda$ ($\pm$SE, $n$ = 10 000) over generations ($t$) with the initial generation distributed randomly in space (i.e., $\lambda_1 \approx \overline{w}_1$), for various values of attack rate by mice ($a$) and median dispersal distance of gypsy moth larvae ($x_{med}$). With the modeled spatial scale of variations in mouse density, spatial inheritability ($I_S^2$) ranges from 0.04 ($x_{med}$ = 139 m) to 0.25 ($x_{med}$ = 15 m).

PLATE 1. Larval gypsy moth (*Lymantria dispar*). Limited larval dispersal and flightlessness of adult female gypsy moths may act in combination to allow the vulnerable pupal stage to nongenetically "inherit" areas of low predation risk, where their mothers survived to lay eggs. Photo credit: E. Schauber.



parameter. Previous analytical frameworks for modeling population dynamics in heterogeneous space have typically been restricted to situations in which the environmental pattern is constant over time (Muko and Iwasa 2000, Bolker 2003, Snyder and Chesson 2003, Goodwin et al. 2005) or is redistributed completely between generations (May 1978). Although some fitness-related factors (e.g., topography) are essentially fixed, others (e.g., local weather) have little continuity over time, others may be autoregressive, and still others, like the home ranges of long-lived predators, may themselves move in space at a characteristic rate. Incorporating such a complex suite of factors on the distribution of suitability in a spatially explicit model would require many parameters, each of which is likely to be weakly supported by data. In the framework we describe here, temporal change in the spatial pattern of environmental suitability simply reduces spatiotemporal autocorrelation (especially at short distances), thereby reducing $I_S^2$.

The parameters involved in $I_S^2$ (Eq. 6) are amenable to estimation from empirical studies. Because $\rho(0)$ and $\gamma$ can be estimated from measurements over relatively small scales and $\beta$ is easily estimated from median dispersal distance, researchers may readily generate rough estimates of $I_S^2$. Identifying these three parameters as critical to $I_S^2$ underlies our current field research to estimate the median dispersal distance of gypsy moth larvae and the spatial and temporal autocorrelation of mouse predation risk, to test the hypothesis that spatial selection and inheritance can explain gypsy moth persistence. $S_S$ can be estimated through spatial monitoring of survival and reproduction and estimating their spatial mean and variance. For example, a beta-binomial model can estimate the mean and variance of survival among individuals monitored at multiple sites (Kendall 1998). Combining empirical estimates of $I_S^2$ and $CV^2(w)$, Eq. 7 can indicate whether a population is likely to persist in a hostile environment.

The analogy between spatial dynamics and natural selection opens the possibility of harnessing the well-developed conceptual and quantitative framework of evolutionary theory in understanding purely ecological processes. For example, local density dependence can be thought of as a form of frequency-dependent selection, causing the relative suitability of a site to depend on the locations of other individuals. Thus, evolutionary game theory (Lewontin 1961, Maynard Smith 1982) may be usefully applied in understanding how the growth and distribution of populations with local feedback change over time. Also, continuous temporal variability in the spatial distribution of suitability can produce a spatial analogue to Red Queen dynamics (Jaenike 1978, Hamilton 1980), in that spatial selection and inheritance force the distribution of organisms to continually "chase" that of suitability for mean fitness to remain constant.

### *Assumptions and generality*

It is important to reiterate that we are considering a problem of population dynamics, not evolution (genetic or phenotypic). Therefore, as with nearly all models of population dynamics, we started from the assumption that variations in fitness among individuals have no

genetic component. This assumption is false for real populations, but it is approximately true when variance in fitness among individuals due to their environment is much greater than the genetic variance in fitness and genotype × environment covariance. Demographic traits most strongly tied to fitness tend to have low genetic heritability and strong environmental influence (Kruuk et al. 2000, McCleery et al. 2004), bolstering the applicability of this assumption.

Spatial selection and inheritance can be opposed or accelerated by local density dependence (direct or inverse). Exact spatially implicit models incorporating spatial heterogeneity, limited dispersal, and local density dependence are not currently available, although moment-closure can provide useful approximations (Bolker 2003). Incorporating local density dependence represents a crucial next step in the development of this analogy. As individuals aggregate in suitable areas they can degrade local suitability, reducing the variance of fitness among individuals and therefore $S_S$, whereas Allee effects are expected to have the opposite effect. However, the assumption of density independence is applicable to transient dynamics of populations that are newly invading, recovering from disturbance, or otherwise well below equilibrium densities.

Further complications arise when organisms can select sites or alter their dispersal tendency or distance in response to local population density or environmental suitability (Clobert et al. 2001, Dwyer and Morris 2006), behavioral responses to local conditions that constitute active habitat selection. However, most organisms (bacteria, plants, fungi) have little or no ability to assess the suitability of current or prospective environments and alter movements in response. Even organisms capable of making such assessments can do so only within their perceptual range (Zollner 2000, Shochat et al. 2002), so spatial selection and inheritance may overwhelm habitat selection if typical dispersal distances greatly exceed the perceptual range.

The existence of active habitat selection is often inferred from observed patterns, e.g., positive covariance between local density and habitat quality. However, spatial selection and inheritance can produce the same patterns without any behavioral responses whatsoever. Therefore, it provides a more appropriate null model in studies of habitat selection than a model in which organisms are distributed randomly with respect to habitat suitability. Similarly, spatial selection and inheritance with local density dependence are likely to homogenize the fitness of organisms in heterogeneous space, providing an alternative explanation for patterns often attributed to habitat selection under the Ideal Free Distribution (Fretwell and Lucas 1970). Thus, we argue that active habitat selection cannot be demonstrated on the basis of pattern alone but requires demonstration of an active behavioral response to habitat suitability.

Incorporating spatial heterogeneity and limited movements into population dynamic theory is an important challenge for ecologists. We propose that the concepts of spatial selection and inheritance provide a novel, empirically convenient, and conceptually familiar foundation for modeling spatial population dynamics, and open avenues for applying the well-developed conceptual and quantitative foundations of evolutionary theory to purely ecological problems.

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## APPENDIX A

Derivation of spatial inheritability, spatial selective differential, and change in per capita population growth rate (*Ecological Archives* E088-069-A1).

## APPENDIX B

Spatially explicit, individual-based simulation (SEIS) of gypsy moth populations (*Ecological Archives* E088-069-A2).