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EVOLUTIONARY SPEED OF SPECIES INVASIONS

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Abstract.—Successful invasion may depend of the capacity of a species to adjust genetically to a spatially varying environment. This research modeled a species invasion by examining the interaction between a quantitative genetic trait and population density. It assumed: (1) a quantitative genetic trait describes the adaptation of an individual to its local ecological conditions; (2) populations far from the local optimum grow more slowly than those near the optimum; and (3) the evolution of a trait depends on local population density, because differences in local population densities cause asymmetrical gene flow. This genetics-density interaction determined the propagation speed of populations. Numerical simulations showed that populations spread by advancing as two synchronic traveling waves, one for population density and one for trait adaptation. The form of the density wave was a step front that advances homogenizing populations at their carrying capacity; the adaptation wave was a curve with finite slope that homogenizes populations at full adaptation. The largest speed of population expansion, for a dimensionless analysis, corresponded to an almost homogeneous spatial environment when this model approached an ecological description such as the Fisher-Skellam's model. A large genetic response also favored faster speeds. Evolutionary speeds, in a natural scale, showed a wide range of rates that were also slower compared to models that only consider demographics. This evolutionary speed increased with high heritability, strong stabilizing selection, and high intrinsic growth rate. It decreased for steeper environmental gradients. Also indicated was an optimal dispersal rate over which evolutionary speed declined. This is expected because dispersal moves individuals further, but homogenizes populations genetically, making them maladapted. The evolutionary speed was compared to observed data. Furthermore, a moderate increase in the speed of expansion was predicted for ecological changes related to global warming.

Key words.—Genetic spatial model, invasions, local adaptation, quantitative trait, rapid evolution, species range, waves.

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The invasion of a species into a new habitat is a common event in the dynamics of a landscape. Invasions begin with the introduction of a species, and this is usually a naturally occurring event (Logde 1993). Humans may also contribute to species introductions, and data from the last four centuries indicate that most of these introduced species become invaders, species that successfully establish and spread geographically (Logde 1993; Williamson 1996). Species invasion has been commonly studied by ecological models of spatial population dynamics (Skellam 1951; Okubo 1980; Murray 1989; Andow et al. 1990; van den Bosch et al. 1990; Williamson 1996; Shigesada and Kawasaki 1997). Data indicate, however, that genetic aspects are important in determining the success of an invader (Williamson 1996). This success may involve a small proportion of the genome or a few quantitative genetic characters (Williamson 1996). Furthermore, invasions are frequently accompanied by a rapid morphological change (Huey et al. 2000; Reznick and Ghal-

ambor 2001) that suggests an important role for adaptation in the spread of a species. One explanation for the role of adaptation is that an invader rapidly adapting to a new environment may transform its sink populations into source populations, thus allowing the sustaining of the invader's spatial propagation. Moreover, this adaptiveness may regulate the speed of the expansion. However, a general theoretical study of the interaction between genetics and invasion ecology in determining species invasion has not been conducted.

A spreading invasion has been compared to a wave from a stone dropped on a lake. This spatial propagation was studied by Fisher (1937) to describe gene diffusion in population genetics. In his model, the spatial expansion for an advantageous gene was characterized by a profile from low to high gene frequency that moves forward, homogenizing the populations for that gene. This profile, or front, that propagates in a constant shape and at a constant speed is called a traveling

wave (Britton 1985). Traveling waves have also been modeled for expanding populations, and the simplest formalization is similar to the spread of a gene (Fisher 1937; Skellam 1951). The expansion of genes or populations may depend on interactions with other factors instead of being determined by a single process (Aoki 1987; Pease et al. 1989; Feldman and Laland 1996). Genes may spread due to the interaction with population density. An example is Pease et al. (1989), who used a quantitative genetics model to study how a species may shift its geographical range to track a changing environment.

The present research used a quantitative genetics model to study the success of a species invasion by examining the interaction between a quantitative genetic trait and population density. This model differs from Pease et al.'s (1989) in that it considers density-dependent populations and a temporally constant environment. It is based on the work of Kirkpatrick and Barton (1997), who modeled the geographic distribution of a species. The model used here involved local adaptation and gene flow (Antonovics 1976; Antonovics and Via 1988; Carter and Price 1988; Parsons 1991; Lawton 1993; Hoffmann and Blows 1994; Brown et al. 1996; Galston 1996). The mechanism considered that the borders of species may occur because phenotypes favored in marginal populations are swamped by gene flow from higher-density central populations. Phenotypes favorably selected in central areas will be maladapted to different environmental conditions near their borders. Consequently, peripheral populations will exhibit low growth rates that will restrict their expansion into new areas. For some conditions, however, the borders can be well adapted, resulting in a continual expansion of the margin of the species range. This situation describes the dynamics of an invading species.

The objective of this work was to characterize population spread resulting from interaction with local adaptation and to obtain the evolutionary speed of an expanding population. A continuous spatial model examined the effect of spatial variation, random dispersal, growth rates, and selection on the speed of a species invasion. In addition, the present model assessed changes in an ecological gradient related with global warming on the velocity of invasions. The study first used a dimensional analysis (Gurney and Nisbet 1975; Segel 1980). This mathematical simplification reduced the number of parameters and facilitated determination of the main behaviors of the model. Second, the results were translated to a natural scale for easier interpretation.

MODEL

Description

The model describes the spatio-temporal dynamics for population density, n , and for a quantitative genetic trait, z , which is related to the adaptation of individuals to their environment. It considers a species distributed continuously across a one-dimensional spatial domain. This species is subjected to a pattern of selection on the quantitative trait that varies spatially. The trait z , such as body size, follows standard quantitative genetic theory, and so it is amenable to description by its population trait mean alone (Barton and Turelli 1989; Falconer 1989; Roff 1997). Also, population growth

is considered to be regulated logistically, and individuals disperse randomly. The present genetics-density model is based on Kirkpatrick and Barton (1997; Appendix 1). To study wave of expansion using their model, their equations were transformed to eliminate the explicit space dependence (Appendix 2). The transformation enabled traveling wave solutions that advance with constant shape along the space. Also, they were nondimensionalized to study the full behavior of the model with few parameters.

Following transformation, this model represents the spatial-temporal dynamics for population density, $N(X, T)$, and for trait adaptation, $Z(X, T)$, at locality X at time T . The model has two parameters, A and B . They are clusters of biological parameters, some of them shared. By considering their distinctive biological parameters, A describes the potential for a genetic response and B indicates the actual spatial heterogeneity. B is high due to a rapid change with distance of the ecological conditions and to an extensive dispersal. Adaptation, Z , is defined as the distance between the mean for the quantitative genetic trait and its ecological optimum at each locality, $\tilde{Z} - BX$. Z can be interpreted as a spatially scaled trait mean. It has a maximum at $Z = 0$, otherwise $|Z| > 0$. The equations are thus given by

$$\frac{\partial N}{\partial T} = \frac{\partial^2 N}{\partial X^2} + N(1 - N) - \frac{NZ^2}{2} \quad \text{and} \quad (1)$$

$$\frac{\partial Z}{\partial T} = \frac{\partial^2 Z}{\partial X^2} + \frac{2}{N} \frac{\partial N}{\partial X} \left(B + \frac{\partial Z}{\partial X} \right) - AZ. \quad (2)$$

The first term on right side of equation (1) describes the redistribution of individuals caused by random dispersal. For an extended interpretation of this macroscopic dispersal term, see Okubo (1980) and Turchin (1998). The second term represents logistic population growth, which incorporates a density-dependent regulation. The third term ($-NZ^2/2$) shows the interaction between population density and adaptation. The form $Z^2/2$ in the interaction was obtained by considering a stabilizing selection toward an optimum trait that changes linearly over space. This term is negative because it is assumed that any maladaptation ($|Z| > 0$) reduces the growth potential. This means that the population growth at a given locality is reduced whenever the phenotypic trait mean deviates from the local ecological optimum. For equation (2), the first two terms on the right side reflect the effect of dispersal on the rate of adaptation of the trait: The first term describes random dispersal, and the second term describes the relative contribution to changes in adaptation by localities with higher densities. In this second term, as originally derived (Nagylaki 1975), density affects adaptation by the logarithmic change in population density. The third term represents the impact of selection on the local adaptation. Dimensionless parameters and variables are defined in Appendix 2.

Analysis

The model was studied using numerical simulations. Equations (1) and (2) were solved numerically by approximating the differential equations by a set of finite difference equations (John 1978; Ames 1992). The nonlinearities in the set

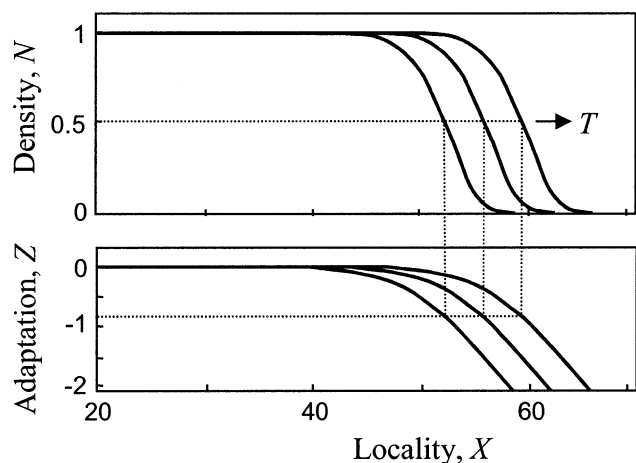


FIG. 1. Spatial expansion of a species advancing as synchronic traveling waves for population density (N) and for adaptation of a quantitative trait (Z). Parameters were $A = 0.25$ and $B = 0.4$. Time between each front was 10 units, and dimensionless speed of invasion was $\nu = 0.35$. Initial conditions were $N(X, 0) = 1$ and $Z(X, 0) = 0$ to $X \leq 6$, for other X , $N(X, 0) = 0$.

of equations made it difficult to search for analytical traveling wave solutions. Furthermore, theoretical techniques to determine wave existence were not simple to apply. The reason is that equations (1) and (2) were transformed to four ordinary differential equations for the analysis, resulting in a four-dimensional phase portrait (Segel 1980; Britton 1985; Grindrod 1996). The singularity that appears in equation (2) when it is evaluated at the equilibrium $N = 0$ is not a problem for that analysis, and it can be removed by introducing a new parameter.

In the present model, populations were initially restricted around the center of the domain ($X = 0$), and once the central population reached its carrying capacity ($N = 1$) waves were originated moving left and right over time. Simultaneously, trait adaptation gained its maximum ($Z = 0$) and developed two similar fronts, one advancing to the right and the other to the left. Waves are described in detail below. The analysis only addresses the half of the domain for $X \geq 0$ and for this region $Z \leq 0$. The left boundary of this region located at $X = 0$ shows symmetry for the values of N at each side of that locality, whereas Z shows diagonal symmetry with the same values but different signs. The right boundary of the region was considered reflecting, and waves were studied far from this border. The waves rapidly approached a constant speed as invasion progressed. Wave speed was estimated using the displacement of the inflection point at the front of the population density wave, the position for $N = 0.5$. Wave speed was also estimated by applying to equation (1) a method for calculating asymptotic speed (Murray 1977). This speed resulted in $\nu = \Delta X \sum_i N_i (1 - N_i - Z_i^2/2)$ (Appendix 3). The index i identified the spatial points, and ΔX the space increments. For the simulations the time increment was $\Delta T = 0.05 \Delta X^2$, and $\Delta X = 0.25$. The basic initial condition used was $N = 1$ and $Z = 0$ for $X \leq 6$, and $N = 0$ elsewhere. This condition represents the situation in which the populations are in their carrying capacity and fully adapted for the first 24 localities. To test the stability of the waves, several initial conditions

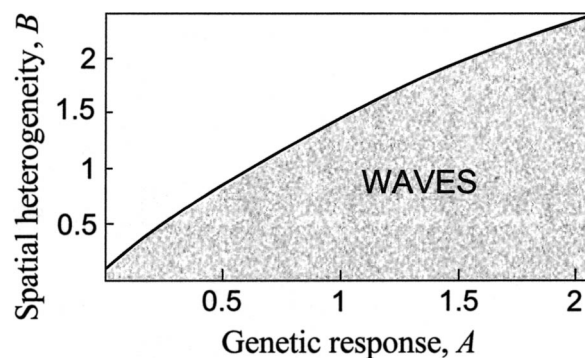


FIG. 2. Values of the parameters that allow for the spatial expansion of populations. A is the genetic response, and B is the spatial heterogeneity. Waves of population expansion existed under the curve $B = 0.11 + 1.55A - 0.22A^2$.

were used. First, the populations were fully adapted ($Z(X, 0) = 0$) with varying population densities: $N(X, 0) = 1$, $N(X, 0) = 0.9 \exp(-X^2/2)$, and $N(X, 0) = 1 - 0.1X^2$ for $X \leq 3$. Second, maladapted populations were tested based on $Z(X, 0) = -0.5$, for the following densities: $N(X, 0) = 1 - 0.1X^2$ for $X \leq 3$; and $N(X, 0) = 0.3$ for $X \leq 6$. All of them assumed $N(X, 0) = 0$ for the rest of the region. The size of the region required that the variables did not change at the origin ($X = 0$) and at the right border. This was assumed when $\partial \ln N / \partial T$ was lower than 10^{-12} for these localities.

RESULTS

The model has an equilibrium with the species exhibiting an infinite range and is fully adapted everywhere ($\hat{N} = 1$ and $\hat{Z} = 0$). Simulations showed that populations reached this equilibrium by advancing as two synchronic traveling waves for population density and for trait adaptation. Typical traveling waves are illustrated in Figure 1. The form for the density wave was a step front as in Fisher's model, which approaches its maximal value $N = 1$ at $X = 0$ and decays to $N = 0$ as X goes to $+\infty$. The form for wave adaptation is an open curve. This approaches $Z = 0$ at $X = 0$ and grows negatively in a linear fashion as X goes to $+\infty$. The advancing parts of both waves show different slopes depending of the

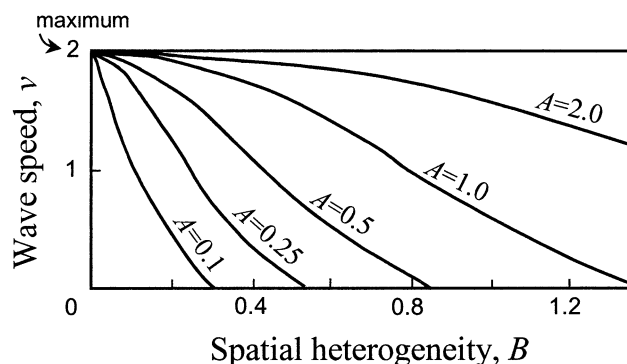


FIG. 3. Range of speed of the expansion as a function of the parameters A and B . A is the genetic response, and B is the spatial heterogeneity. The dimensionless speeds showed a maximal value at $\nu \sim 2.0$.

TABLE 1. Estimation of evolutionary speeds of expansion of a species v_{EVOL} . Biological parameters are heritability, h^2 ; intensity of stabilizing selection, P/ω ; intrinsic growth rate, r ; standard deviation of dispersal, σ ; and spatial change in ecological optimum, b . Genetic response, A , and spatial variation, B , are dimensionless parameters, and their definitions are $A = h^2 (P/\omega)/(r - P/2\omega)$ and $B = b\sigma\sqrt{(P/2\omega)(1/P)/(r - P/2\omega)}$. v is the dimensionless speed from simulations. Rows s1–9 show values for r and σ from the muskrat, *Ondatra zibethicus* (Williamson and Brown 1986; Andow et al. 1990).

Row	h^2	P/ω (year ⁻¹)	r (year ⁻¹)	σ (km year ^{-1/2})	b (PSD/km)	A	B	v	v_{EVOL} (km year ⁻¹)	
a	0.5	0.10	0.4	10.0	0.030	0.14	0.192	0.67	4.18v	2.80
b	0.3	0.10	0.4	10.0	0.030	0.09	0.192	0.35	4.18v	1.46
c	0.7	0.10	0.4	10.0	0.030	0.20	0.192	0.99	4.18v	4.14
d	0.5	0.07	0.4	10.0	0.030	0.10	0.156	0.60	4.27v	2.56
e	0.5	0.14	0.4	10.0	0.030	0.21	0.244	0.78	4.05v	3.16
f	0.5	0.30	0.4	10.0	0.030	0.61	0.470	1.10	3.54v	3.89
g	0.5	0.10	0.2	10.0	0.030	0.33	0.447	0.47	2.74v	1.29
h	0.5	0.10	1.0	10.0	0.030	0.05	0.071	0.82	6.89v	5.65
i	0.5	0.10	2.0	10.0	0.030	0.03	0.034	1.00	9.87v	9.87
j	0.5	0.10	0.4	2.0	0.030	0.14	0.038	1.84	0.84v	1.55
k	0.5	0.10	0.4	7.0	0.030	0.14	0.134	1.03	2.93v	3.02
l	0.5	0.10	0.4	14.1	0.030	0.14	0.270	0.33	5.89v	1.94
m	0.5	0.10	0.4	18.0	0.030	0.14	0.345	0.10	7.53v	0.75
n	0.5	0.10	0.4	10.0	0.009	0.14	0.058	1.78	4.18v	7.44
o	0.5	0.10	0.4	10.0	0.010	0.14	0.064	1.65	4.18v	6.90
p	0.5	0.10	0.4	10.0	0.027	0.14	0.173	0.77	4.18v	3.23
q	0.5	0.10	0.4	10.0	0.046	0.14	0.294	0.25	4.18v	1.03
r	0.5	0.10	0.4	10.0	0.050	0.14	0.319	0.17	4.18v	0.71
s1	0.5	0.10	0.8	10.0	0.030	0.07	0.089	0.84	6.12v	5.14
s2	0.3	0.10	0.8	10.0	0.030	0.04	0.089	0.45	6.12v	2.80
s3	0.3	0.10	0.8	10.0	0.010	0.04	0.030	1.30	6.12v	7.96
s4	0.5	0.10	1.4	10.0	0.030	0.04	0.050	0.90	8.22v	7.40
s5	0.3	0.10	1.4	10.0	0.030	0.03	0.050	0.45	8.22v	3.70
s6	0.5	0.14	1.4	10.0	0.015	0.05	0.028	1.60	8.18v	13.01
s7	0.5	0.14	1.4	10.0	0.020	0.05	0.040	1.27	8.18v	10.39
s8	0.5	0.10	0.8	20.0	0.030	0.07	0.179	0.26	12.25v	3.19
s9	0.5	0.10	1.4	20.0	0.030	0.04	0.099	0.51	16.43v	8.38

values of the parameters. The shallower slopes corresponded to the faster waves. The outcome of the waves was to homogenize spatially both density and adaptation.

Figure 2 showed a region of the space of parameters for A and B that originated population expansion waves. This region was defined by the condition $B \leq 0.11 + 1.55A - 0.22A^2$, that indicates the combination of parameters for a species invasion. Figure 2 showed that a larger genetic response, A , and a smaller spatial heterogeneity, B , favored the appearance of waves. The condition for wave appearance was obtained by sampling a biological range of values, $A[0, \sim 1]$ and $B[0, \sim 2]$ from $A \geq 0.003$ and $B \geq 0.06$. The points with low speeds, $v < 0.006$, were fitted to a quadratic function. Approximations for this region have been provided by Kirkpatrick and Barton (1997) and Case and Taper (2000).

The results showed a range of speeds of expansion that also depended on the values of the parameters A and B . These dimensionless speeds exhibited a maximum value of $v_{\text{max}} \sim 2.0$ (Fig. 3). Speeds increased as the spatial variation declined until the maximal speed that corresponded to an almost homogeneous spatial environment, $B \sim 0$. The genetic response, A , also affected dimensionless speed, and high speeds resulted from a large A . Figure 3 shows that when A and B are small, the speed of the wave increased rapidly with a small increment in B . Many species appear to have small values for both parameters (Case and Taper 2000), and their speeds may respond greatly to changes in the spatial heterogeneity. This model also showed that the speed was not affected by changes in initial conditions. For the same set of parameter

values, all the different conditions considered showed similar wave speeds. This suggested that waves are stable. The inflection point and the Murray method showed similar speeds.

To apply the model it was necessary to estimate dimensioned speeds. This required a return to natural space and time based on $\Delta X/\Delta T = v$, $X = \sqrt{2r^*/\sigma^2}x$ and $T = r^*t$ (Appendix 1, 2). This resulted in the evolutionary speed predicted in a natural scale, $\Delta x/\Delta t = v_{\text{EVOL}}$,

$$v_{\text{EVOL}} = \sigma v \sqrt{(r - P/2\omega)/2}. \quad (3)$$

This speed has a maximum value determined by replacing the largest dimensionless speed $v_{\text{max}} \sim 2.0$ into equation (3), this is $v_{\text{EVOL-MAX}} \sim 2\sigma\sqrt{(r - P/2\omega)/2}$. Notice that this maximal speed is always lower than an ecological speed of expansion, $v_{\text{EC}} = 2\sigma\sqrt{r/2}$ (Fisher's model; Murray 1989). Typical biological values were chosen to evaluate the evolutionary speed. Heritability was considered around its average value for morphological traits of $h^2 = G/P = 0.5$ (Mousseau and Roff 1987). For convenience, the trait z was scaled so that the phenotypic variance P was one. Also, z and x were scaled such that the value of the trait mean was equal to the optimum at spatial point $x = 0$, making $\tilde{z} = 0$ and $Z = 0$. Values used for stabilizing selection in relation to phenotypic variance were around the average $P/\omega = 0.1$ (Turelli 1984; Endler 1986) and $P/\omega = 0.12$ (the quadratic selection gradient $\gamma = -[1/(\omega + P)][\omega/(\omega + P)]^{1/2}$ [R. Lande and S. Arnold, pers. comm; from Lande and Arnold 1983, eq. 14b], was standardized $\gamma' = \gamma P$, equalized to $\gamma' = -0.1$ [Kingsolver et al. 2001], and solved for P/ω). The analysis used inter-

TABLE 2. Data from the muskrat, *Ondatra zibethicus*, during its invasion in Europe in the past century. Estimations of observed, v_{OB} , and predicted speeds of expansion from different ecological models, v_{EC} , are shown. D , diffusion coefficient; $\sigma = \sqrt{2D}$.

r (year ⁻¹)	D (km ² year ⁻¹)	v_{OB} (km year ⁻¹)	v_{EC} (km year ⁻¹)	Reference
		11.3		Williamson (1996)
1.39	23.0		3.9–7.0	van den Bosch et al. (1990)
0.2–1.1	51.2–230	0.9–25.4	6–32	Williamson and Brown (1986) Andow et al. (1990, 1993)

mediate values for the intrinsic rate of growth, $r = 0.2 - 2.0 \text{ year}^{-1}$ (Pianka 1988). Dispersal was quantified by σ , this is the standard deviation of the distance moved by individuals from their natal site to the breeding site. Values of σ ranging from 10 to 100 km year^{-1/2} have been reported for owls (Barrowclough and Coats 1985), and from 10 to 21 km year^{-1/2} for the muskrat (Andow et al. 1990, 1993). This analysis considered a range of 1–20 km year^{-1/2} for σ . The rate of change in the ecological optimum over space, b , was discussed by García-Ramos and Kirkpatrick (1997). They suggested that a cline for trait mean will be shallower than the gradient in the ecological optimum. A linear cline for wing size for the downy woodpecker showed a slope of 0.003 phenotypic standard deviation (PSD) km⁻¹ (26–40°N, 80°W; James 1970). This gives a minimum value for b , and the model used a range from 0.009 to 0.050. These parameter values were replaced in A and B to obtain v , and then used to evaluate equation (3). Table 1 shows the response of the wave speed to the biological parameters. These data indicated that high heritability (rows a–c), strong stabilizing selection (P/ω large, rows d–f), and high intrinsic growth rate (rows g–i) increase evolutionary wave speeds. They also showed that steeper environmental gradients reduce the speed (rows n–p). Furthermore, dispersal affects the wave speed in a non-linear fashion: For low values of dispersal, dispersal increases will increase speed (rows j–k). For large values, dispersal increases will reduce wave speed (rows k–m). This indicates the contrary effects of individual dispersal and gene flow on the spread of species. Dispersal moves individuals further but homogenizes populations, making them maladapted. For high dispersal, the combination of these effects will reduce wave speeds. Table 1 (last column) also shows that for this set of parameters values speed may vary by a few orders of magnitude. Table 2 describes biological parameters and observed speeds for the muskrat, *Ondatra zibethicus*, during its expansion in Europe. This example was chosen to evaluate the model because it has become a standard for studying invasions. Therefore, it has been analyzed with considerable detail, providing estimations for ecological parameters, and comparing theoretical predictions with data. Table 3 com-

pares muskrat speeds predicted for this model with those using only ecological dynamics. This example illustrates that, depending on the ecological and genetic parameter values, the interaction between population density and adaptation in this model may greatly reduce evolutionary wave speeds compared with those expected from ecological modeling.

The rapid speed of population expansion shown above suggests the following question: What is the rate of adaptation and morphological evolution, using a natural scale, that may sustain an invasion? The advance of the adaptation wave shows larger adaptation changes in localities toward the front of the invasion (Fig. 1). It indicates that local adaptation rates are larger following the invasion, but then rapidly decays as time progresses. In natural scale, the correspondent change in the trait mean in a locality is given by $\Delta\bar{z}/\Delta t = r^* \sqrt{\omega r^*} (\Delta Z/\Delta T)$. At the front of the wave, typical values for $\Delta Z/\Delta T$ ranged from 0.10 to 0.02 for slow to rapid waves respectively (Table 1, rows a, g–i). For fast evolutionary speeds such as $v_{EVOL} = 9.87$, and $7.44 \text{ km year}^{-1}$ (Table 1, rows i, n), the concurrent rates of morphological evolution in a locality following invasion are $\Delta\bar{z}/\Delta t = 0.19$, and $0.03 \text{ PSD year}^{-1}$. These rates have the same order of magnitude as the observed rates of morphological change measured over short time intervals (Barton and Turelli 1989; Hendry and Kinnison 1999).

In the logistic model of Fisher, waves are always generated independent of the magnitude of dispersal and growth rate. In the present model, waves arose only when the condition of invasion was satisfied. In natural scale, this condition was $b\sigma/\sqrt{P} \leq (0.16/\sqrt{P/\omega})(r - P/2\omega) + 2.19h^2\sqrt{P/\omega}$ (neglecting the A^2 term and reordering). This indicated that invasions are favored for low dispersal and ecological gradient and for high growth rate and heritability. Notice that a low dispersal may reduce maladapted gene flow, allowing high local population densities that may sustain the spread. Furthermore, a low dispersal makes B small, producing fast dimensionless speeds; however, returning to natural scale these speeds are reduced by multiplying by the low dispersal (eq. 3). Therefore, low dispersal favors invasions but with slow speeds of spread.

Invasion Speed under Climatic Changes

An average increase in global temperature of 2.5°C is predicted for the present century. Moreover, this increase will be unevenly distributed, with temperature increasing more toward the poles (Graves and Reavey 1996; Santer et al. 1996). These two changes, elevation in temperatures and a decrease in the temperature gradient, may have different consequences on species distributions. First, the elevation in tem-

TABLE 3. A comparison of ecological, v_{EC} , and evolutionary speeds, v_{EVOL} . Ecological speed comes from Fisher's model, $v_{EC} = 2\sqrt{rD}$ (Murray 1989). Ecological parameters correspond to the muskrat (Table 2). Other parameters for v_{EVOL} are in Table 1, rows s1–9.

r (year ⁻¹)	D (km ² year ⁻¹)	v_{EC} (km year ⁻¹)	v_{EVOL} (km year ⁻¹)	v_{EVOL}/v_{EC}
0.8–1.4	50 ($\sigma = 10$)	12.6–16.7	2.8–8.0/3.7–13.4	0.22–0.80
0.8–1.4	200 ($\sigma = 20$)	25.3–33.5	3.2–8.4	0.13–0.25

perature may cause a shift in the species' range toward the poles, thus tracking their optimal temperature (Parmesan 1996); this situation was modeled by Pease et al. (1989). Second, a reduction in the gradient may reduce the spatial variation, and so influence the invasion speed of a species. To study this second scenario, the effect of warming on the rate of change in the ecological optimum over space b was determined for a character such as body size. Estimated below is the new gradient b and its effect on the invasion speed. The region between 25°N and 60°N in the past century showed an annual average temperature that changed almost linearly from 23°C to -1°C (Linacre 1992), and this gives a gradient of -0.69°C/°latitude. Climatic models predict a difference of about 2°C in temperature rise between these latitudes (Santer et al. 1996). This will diminish the temperature gradient by 9%. Optimal traits may follow the temperature changes where they are fitted, so the existing gradient b may decline following the temperature gradient by 9%. In general, any decrease in b , and by definition in B , will increase evolutionary speed, by increasing dimensionless speed ν within ν_{\max} (eq. 3, Table 1, Fig. 3). For a 9% decrease in b , the increment in ν is approximately 0.1 units (Table 1 rows n/o , p/a , q/r). In terms of the evolutionary speed, and for typical values of the parameters, this increment varies from 0.1 to 1.6 km year⁻¹ for speeds up to 13 km year⁻¹ (Table 1, column 10, for $\nu = 0.1$). Thus this model predicts a moderate increment in the speed of invasion caused by the reduction in an ecological gradient due to the expected global warming.

DISCUSSION

This study examined the interaction between local adaptation and population density on the spatial spread of a species. The model showed that the genetic and demographic interaction reduced the speed of expansion of a species compared to models that only consider demographics. The reduction in the evolutionary speed is the result of a limited rate of adaptation of the populations to new environments. Thus, the rate of adaptation will determine how rapidly a population is able to invade a new environment.

The dimensionless model showed that the largest speed of species expansion ($\nu_{\max} \sim 2$) occurred when the spatial domain is almost homogeneous ($B \sim 0$). For a spatial homogeneous domain, the model is reduced to an ecological equation that is identical to Fisher and Skellam's model of expansion (Fisher 1937; Skellam 1951). Studies of the Fisher equation have shown that it may exhibit many theoretical wave speeds; however, when the solution is computed numerically, it always evolves into a stable wave propagating at the speed $\nu = 2$ (Fisher 1937; Kolmogoroff et al. 1937; Murray 1977, 1989; Fife 1979). The faster speed of expansion in the present model approaches Fisher's speed. This means that for a spatially varying domain the interaction between trait adaptation and population density reduces the species propagation given by an ecological model.

How fast can the speed at the beginning of the invasion be when population growth is more exponential than logistic? From ecological studies, the simplest model to describe population spread is an exponential (Skellam 1951), and it assumes that density at each locality grows without limits. This

model does not develop a traveling wave with a wave front invariant in shape; therefore, population spread is defined by the constant speed at which new localities reach a threshold density. Interestingly, both models predict the same speed of expansion, and this results from a population growth at the edge front of the wave that is not dependent on density factors (Turchin 1998). From those results we suspect that the evolutionary expansion at the beginning of the invasion will not be affected by these growth functions. At that time, however, the effect of maladapted gene flow in reducing the expansion could be diminished because the range of the species is small. It could favor a faster speed than the evolutionary speed. The spatial evolutionary model of equations (1) and (2) predicts a second type of expansion—a transitory spread for a limited species range (Kirkpatrick and Barton 1997). This spread does not advance at a constant speed, instead it may slow and eventually stop, reaching the range limits of the species. In addition, their initial speeds could be moderated due to the strong effects of gene flow limiting these expansions.

Observed speeds for many invading species have been reported (muskrat 11.3 km year⁻¹, Williamson 1996; gray squirrel 7.7 km year⁻¹, Okubo et al. 1989; sea otter 1.4–3.1 km year⁻¹, Lubina and Levin 1988). Observed speeds appear to be faster or slower than expected speeds from ecological modeling (Okubo et al. 1989; van den Bosch et al. 1990; Williamson 1996). Several reasons may explain these differences. Common functions for the growth and diffusion terms may not apply for particular cases. For example, density-dependent dispersal or age structure may overcome Fisher's speed (Andow et al. 1993). Age structure or Allee effects may reduce the rate of population growth at the lowest density, making the advance slower (Williamson 1996). In addition, there is uncertainty regarding the parameter values used to apply these models. Data on the intrinsic rate of increase and diffusion coefficients show a wide variation for the same species. Also, dispersal rates seem to be underestimated in many cases because of the difficulty to register individual dispersers (Koenig et al. 1996). The present model may exhibit a significant reduction in speed compared to an ecological model. For some parameter values, the genetic-density interaction can be so strong that it may stop any population propagation. The bottom of Table 1 shows the range of evolutionary speed predicted using this model for the muskrat. The average speed observed during the invasion of this species in Europe (11.3 km year⁻¹, Williamson 1996), falls within the range predicted for this model. Because many observed speeds have been shown to be substantially lower than ecological speeds (Grosholz 1996), we also expect that for those invasions the observed speeds may fall within the range of the evolutionary speeds.

It is generally considered that genetic changes are undetectable in ecological time, that is, less than a century for many organisms (Williamson 1996). Artificial selection, however, has shown that morphological evolution can be fast, and populations may change their quantitative trait means up to a dozen standard deviations in 100 generations (Barton and Turelli 1989). Rates of morphological evolution in the wild can also be large, with changes up to 0.7 standard deviations per generation (Hendry and Kinnison 1999). According to this quick response to selection, invading species

may evolve rapidly following exposure to different environments. The present model showed that population invasion and evolution of a quantitative genetic trait are synchronized processes—they occur with identical rates of spatial expansion. The waves for these processes, however, differed in the shape of their advance fronts. The adaptation front was shallower than the population front. Because of this shallower adaptation front, several generations after both waves pass by a locality are required to observe a significant change in the level of adaptation (Fig. 1). The wave fronts also indicated that any main change in population density at a given locality is associated with a significant change in the evolution of the trait, illustrating the strong interaction between demographic and evolutionary processes. A possible example of this synchronous expansion for population density and trait adaptation is the rapid evolution of a geographic cline in the introduced fly *Drosophila subobscura* (Huey et al. 2000; Gilchrist et al. 2001). This fly is a native of the Old World, and there it shows clinal increases in body size with latitude. It was introduced two decades ago into western North America and spread rapidly. No cline was observed one decade after the introduction; however, it was evident after two decades.

One major prediction for the changes in global climate is the acceleration of species invasions (Logde 1993). This model predicts a moderate increment in the speed of invasion caused by the reduction in an ecological gradient due to global warming. However, speeds could be larger because other parameters in the model may change in the new climate. Warmer conditions favor longer growing seasons, earlier reproduction, and earlier migration for many species (Inouye et al. 2000) that may increase growth and dispersal rates and consequently may increase the speed of expansion. These effects can be evaluated with this model. The present model also may predict if the changes in these parameters could transform a species into an invader.

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APPENDIX 1

Description of Original Equations

The present model is based on Kirkpatrick and Barton's (1997). Their model has the following assumptions. First, the phenotypic value of an individual is denoted z ; z is a trait that follows the standard quantitative genetic theory (Falconer 1989), and it considers that the phenotypes and breeding values for the quantitative trait are Gaussian distributed. The phenotypic variance, P , and additive genetic variances, G , are assumed to be constant in time and space. Second, the ecological optimum for the trait θ varies as a linear function of space, $\theta(x) = bx$. The parameter b is the rate at which the ecological optimum changes spatially. Individuals whose phenotype z differs from their local optimum have reduced viability, and the probability of survival for a phenotype z at location x within a generation is given by $w(z, x) \propto \exp[-(bx - z)^2/2\omega]$. ω is the variance of the Gaussian fitness function, and a large value of ω corresponds to weak stabilizing selection towards the local optimum. Third, individuals disperse randomly with a dispersal variance σ^2 . Fourth, populations have a logistic regulation where r is the intrinsic growth of increase and K is the carrying capacity. Under these assumptions Kirkpatrick and Barton's (1997) equations to describe the dynamics of the population density, $n(x, t)$, and the trait mean, $\bar{z}(x, t)$, at position x and time t are,

$$\frac{\partial n}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 n}{\partial x^2} + rn \left(1 - \frac{n}{K}\right) - \frac{(bx - \bar{z})^2}{2\omega} n - \frac{P}{2\omega} n \quad \text{and} \quad (\text{A1})$$

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \frac{\sigma^2}{n} \frac{\partial n}{\partial x} \frac{\partial \bar{z}}{\partial x} + \frac{G}{\omega} (bx - \bar{z}). \quad (\text{A2})$$

APPENDIX 2

Dimensionless Variables and Parameters

To obtain equations (1) and (2), it was first necessary to make dimensionless equations (A1) and (A2). The dimensionless variables and parameters are as follows, and some are identical to Kirkpatrick and Barton (1997): $N = n/K^*$; $\bar{Z} = \bar{z}/\sqrt{\omega r^*}$; $T = r^* t$; $X = \sqrt{2r^*/\sigma^2} x$; $A = G/\omega r^*$; $B = b\sigma/r^*\sqrt{2\omega}$; $r^* = r - P/2\omega$; $K^* = (1 - P/2\omega r)K$. Secondly, the transformation $Z = \bar{Z} - BX$ was applied to the dimensionless equations to eliminate their explicit space dependence. Definitions of symbols are as in Appendix 1. For dimensionless techniques, see Gurney and Nisbet (1975) and Segel (1980).

APPENDIX 3

Estimation of the Asymptotic Wave Speed for Population Density

This procedure followed the approximation of Murray (1977, appendix 5.2) to estimate wave speed. The new variables considered were $s = X - \nu T$, $N(X, T) = F(s)$, and $Z(X, T) = H(s)$. Also considered was $\partial N/\partial T = -\nu \partial F/\partial s$, where ν is the wave speed. By replacing these variables into equation (1) and integrating this equation from zero to $+\infty$ for $F(0) = 1$ and $F(+\infty) = 0$, the asymptotic wave speed for the population density was obtained: $\nu = \int_0^\infty F(1 - F - H^2) ds$. For the simulations the discrete form of this speed was $\nu = \Delta X \sum_i N_i(1 - N_i - Z_i^2/2)$, where i describes the spatial points and ΔX is the space increments. The speed was measured for a large T .