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Macroevolutionary and Coevolutionary Models in Biogeography

A Dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in

Biology

by

Emma Elizabeth Goldberg

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2007

The dissertation of Emma Elizabeth Goldberg is approved, and it is acceptable in quality and form for publication on microfilm:

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Chair

University of California, San Diego

2007

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

FIGURES

TABLES

ACKNOWLEDGEMENTS

gradients. The American Naturalist. The dissertation author was an equal contributor to the analysis and writing of this paper.

Chapter 3, in full, is a reprint of the material as it appears in Goldberg, Emma E, and Russell Lande. 2006. Ecological and reproductive character displacement on an environmental gradient. Evolution 60:1344–1357. The dissertation author was the primary investigator and author of this paper.

Chapter 4, in full, will appear as Goldberg, Emma E, and Russell Lande. (in press). Species' borders and dispersal barriers. The American Naturalist. The dissertation author was the primary investigator and author of this paper.

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PUBLICATIONS

Goldberg, Emma E, Kaustuv Roy, Russell Lande, and David Jablonski. 2005. Diversity, endemism, and age distributions in macroevolutionary sources and sinks. The American Naturalist 165:623–633.

Goldberg, Emma E, and Russell Lande. 2006. Ecological and reproductive character displacement on an environmental gradient. Evolution 60:1344–1357.

Roy, Kaustuv and Emma E Goldberg. (in press). Origination, extinction and dispersal: integrative models for understanding present-day diversity gradients. The American Naturalist.

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FIELDS OF STUDY

Major Field: Ecology and Evolution

Studies in Evolutionary Ecology.
Professor Russell Lande

Studies in Macroevolution.
Professors Russell Lande and Kaustuv Roy

ABSTRACT OF THE DISSERTATION

Macroevolutionary and Coevolutionary Models in Biogeography

by

Emma Elizabeth Goldberg

Doctor of Philosophy in Biology

University of California, San Diego, 2007

Professor Russell Lande

Understanding the processes that have given rise to observed patterns of species distributions is a central question in biogeography. These patterns include spatial distributions of species richness, phylogenetic relatedness, phenotypic similarities and differences, and the geographic ranges of species. Much work in inferring process from pattern is based on qualitative expectations, but by modeling processes that are of interest, one can test such expectations and generate a firmer intuitive foundation. Dynamic models can also lead to more powerful methods of data analysis, allowing stronger inferences from available data. This dissertation brings quantitative methods to bear on topics in biogeography at two scales.

First, I develop neutral macroevolutionary models to address questions of regional diversity, endemism, and lineage ages with the goal of estimating region-specific rates of lineage origination, extinction, and dispersal. In Chapter 1, I introduce a model and show that a region with high diversity or high endemism need not have a rapid rate of taxon origination, as is often assumed, but that estimation of regional rates is possible when the ages of extant lineages are known. In Chapter 2, I emphasize that dispersal must be explicitly included in attempts to estimate origination and extinction rates of different regions. Comparing model results with empirical data suggests that the nature of macroevolutionary and biogeographic processes may differ substantially between marine and terrestrial groups.

Second, I employ more detailed coevolutionary models to investigate the formation of geographic borders between species, thus connecting ecological and evolutionary processes with observable patterns of species distributions and phenotypic variation. In Chapter 3, I find that character displacement may be common on an environmental gradient, but that it would often not be recognized by the customary methods of looking for greater difference in sympatry than allopatry. In Chapter 4, I find that species borders maintained by hybrid inviability or interspecific competition may be attracted to regions of reduced dispersal, while those maintained by local adaptation and gene flow are repelled from dispersal barriers. These results show that species interactions may be quite important in limiting geographic ranges and potentially in forming biotic provinces.

Part I

Macroevolutionary Models

Chapter 1

Diversity, endemism, and age distributions in macroevolutionary sources and sinks

Diversity, Endemism, and Age Distributions in Macroevolutionary Sources and Sinks

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ABSTRACT: Quantitative tests of historical hypotheses are necessary to advance our understanding of biogeographic patterns of species distributions, but direct tests are often hampered by incomplete fossil or historical records. Here we present an alternative approach in which we develop a dynamic model that allows us to test hypotheses about regional rates of taxon origination, extinction, and dispersal using information on ages and current distributions of taxa. With this model, we test two assumptions traditionally made in the context of identifying regions as "centers of origin"—that regions with high origination rates will have high diversity and high endemism. We find that these assumptions are not necessarily valid. We also develop expressions for the regional age distributions of extant taxa and show that these may yield better insight into regional evolutionary rates. We then apply our model to data on the biogeography and ages of extant genera of marine bivalves and conclude that diversity in polar regions predominantly reflects dispersal of taxa that evolved elsewhere rather than in situ origination-extinction dynamics.

Keywords: biogeography, paleontology, macroevolution, biodiversity, endemism, marine bivalve.

The processes that produce large-scale spatial patterns of taxonomic diversity remain poorly understood despite the existence of many competing hypotheses. In particular, the role of historical processes in shaping present-day biogeo-

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graphic patterns has been a subject of considerable debate (Francis and Currie 1998, 2003; Currie and Francis 2004; Qian and Ricklefs 2004; Ricklefs 2004). Historical hypotheses are considered to be essentially untestable by some (Francis and Currie 1998), while others maintain that past episodes of speciation, extinction, and range expansion or dispersal are major determinants of present-day biogeographic patterns (Qian and Ricklefs 2004; Ricklefs 2004). The fundamental problem here is that direct tests of historical hypotheses require a fossil or historical record with excellent temporal and spatial resolution, information that is not available for most taxa. On the other hand, information about the current spatial distributions of species and higher taxa is readily available for many groups and potentially obtainable for all living taxa. The challenge therefore is to develop a theoretical framework that allows us to use present-day biogeographic data to test hypotheses about historical processes underlying global biodiversity patterns.

The problems inherent in inferring past processes from present observations about the geographic distributions of taxa are perhaps best illustrated in attempts to identify regions as "centers of origin" or "cradles of diversity," or as their counterparts, "centers of accumulation" or "museums of diversity." The identification of such regions may aid explanation of spatial diversity patterns and could also guide conservation priorities. The terms "center of origin" and "cradle of diversity" designate regions with a high rate of taxon origination but do not specify relative rates of local extinction, immigration, or emigration (Chown and Gaston 2000; Mora et al. 2003; Briggs 2004). The term "center of origin" has also been used to indicate the region in which a particular taxon first appeared (Darwin [1859] 1975; Ricklefs and Schluter 1993). This may or may not be the same as the region in which it underwent greatest diversification or as a region in which many other taxa originated, as designated by the first meaning of the phrase. A "center of accumulation" is a region that obtains taxa through immigration (Ladd 1960; Palumbi 1996; Mora et al. 2003; Briggs 2004), and a "museum of diversity" is a region with a low rate of local extinction (Stebbins 1974;

Chown and Gaston 2000). Fundamentally, then, these terms are defined by the rates of origination, extinction, and dispersal, but these labels are often assigned to regions on the basis of current taxon richness, the amount of endemism, or other information about extant taxa (reviewed by Ricklefs and Schluter [1993]; Brown and Lomolino [1998]; Briggs [2004]). Many studies have used the qualitative expectations that a region with a higher origination rate should have higher levels of diversity and greater endemism (Willis 1922; Rosenzweig and Sandlin 1997; Mora et al. 2003; reviews by McCoy and Heck [1976] and Ricklefs and Schluter [1993]), but few have explicitly tested this hypothesis (but see Pandolfi 1992). Others have used ages of taxa to distinguish differences in regional rates (e.g., Stehli et al. 1969; Stehli and Wells 1971; Gaston and Blackburn 1996; Briggs 1999). The use of age distributions of taxa living in an area today to infer past diversification rates in that region is also not without problems (Ricklefs and Schluter 1993; Gaston and Blackburn 1996; Chown and Gaston 2000).

The work we present was motivated by a lack of theory on how information about extant taxa can be used to distinguish a "center of origin" from a "center of accumulation." To draw a sharper distinction between these two types of regions, we use the term "macroevolutionary source" to refer to a region that is a "center of origin" by the first meaning (high rate of origination relative to other regions) and also that does not receive taxa through dispersal (zero immigration). We use the complementary term "macroevolutionary sink" to refer to a region that obtains taxa through immigration, as a "center of accumulation" does, but has no local origination. Under these definitions, the differences between source and sink regions will be maximized, and so the different effects of local origination and dispersal will be highlighted. We address the issue of how a source region can be distinguished from a sink region by considering the more general issue of how distributions of extant taxa are determined by regional rates of origination, extinction, and dispersal. We examine the problem by first developing a theoretical model and then applying the model to empirical data on marine bivalves. We find that high regional diversity and endemism cannot be used alone to infer a high regional rate of origination. We show, however, that age distributions of extant taxa can be used to estimate rates of origination, extinction, and dispersal. In addition, we use this model to show that the origination rate of marine bivalve genera is significantly lower in the polar regions than at lower latitudes and that the rate of movement of genera is greater into the polar regions than out of them, indicating that the poles represent a macroevolutionary sink.

The Model

We develop a dynamic model that describes distributions of diversity (taxon richness), endemism, and age in a system consisting of two regions. These regions may differ in their local rates of taxon origination and extinction, and the taxa of the system are able to disperse from each region to the other (i.e., expand their ranges). The two regions are denoted R_α and R_β. Origination occurs through a branching process at a rate s_α per taxon in region R_α and s_β in region R_β. Extinction occurs at per-taxon rates x_α and x_β. Dispersal occurs at per-taxon rates d_α from R_α to R_β and d_β from R_β to R_α. All rates are nonnegative. We emphasize that extinction of a taxon is independent in the two regions and that some time may pass before a taxon present in one region appears in the other; the expected value of this lag time is the reciprocal of the dispersal rate. A schematic diagram of this system is shown in figure 1*A*, and a mathematical description is given below.

This general system can be specialized to represent a system consisting of a source region and a sink region by setting $s_\beta = 0$ and $d_\beta = 0$ as illustrated in figure 1*B*. We should clarify that we do not use these terms in the demographic sense; that is, we do not assume that a taxon can persist in a sink region only if it is being continually supplied from the source region. We mean only that all taxa in the system originated in the source region and that taxa do not move from the sink to the source.

We assume that all processes affecting taxa occur independently and that all taxa in a given region are subject to the same rates of origination, extinction, and dispersal, which are constant in time. These are significant assumptions and are addressed in "Discussion." The model is formulated deterministically in continuous time. Similar results were obtained with discrete time models (not presented here) and stochastic simulations (discussed in the appendix in the online edition of the *American Naturalist*).

Total Diversity and Endemism

We employ a matrix formulation to express the expected dynamics of the system. Define the column vector $\mathbf{n}(t) = (n_1, n_2, n_3)^T$ (the superscript T indicates matrix transposition), where $n_1(t)$ is the expected number of taxa present in both R_α and R_β at time t, $n_2(t)$ is the expected number of taxa present only in R_α (R_α endemics), and $n_3(t)$ is the expected number of taxa present only in R_β (R_β endemics). The total number of taxa expected in R_α is thus $n_1(t) + n_2(t)$, and the total number of taxa expected in R_β is $n_1(t) + n_3(t)$. With this notation, transition rates between these three states by origination, dispersal, and extinction can be written, respectively, as
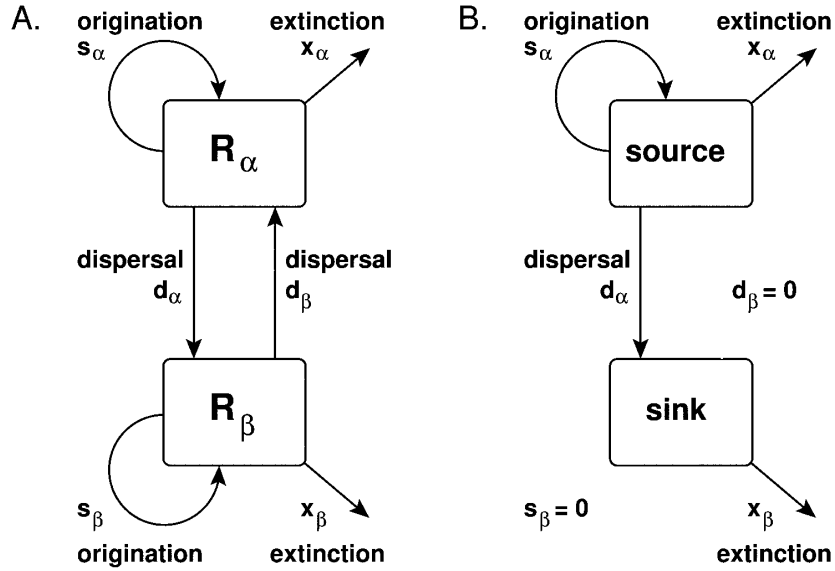
Figure 1: Schematic representation of the model. *A*, In the general case of the model, each region (R_α and R_β) has its own rate of taxon origination (s_α and s_β) and extinction (x_α and x_β), and dispersal (at rates d_α and d_β) occurs between the regions. All rates are per taxon and are constant in time and across taxa. *B*, In a special case of the model, one region is a macroevolutionary source and obtains taxa only through local origination, not immigration. The other region is a macroevolutionary sink and obtains taxa only through immigration, not local origination. Our results are for the general case of the model, *A*, except where explicitly stated otherwise. We emphasize that the special case, *B*, is used in the discussion of relative endemism (including eq. [3]; fig. 2) and that the general case, *A*, is used when fitting data.

$$S = \begin{pmatrix} 0 & 0 & 0 \\ s_\alpha & s_\alpha & 0 \\ s_\beta & 0 & s_\beta \end{pmatrix},$$

$$D = \begin{pmatrix} 0 & d_\alpha & d_\beta \\ 0 & -d_\alpha & 0 \\ 0 & 0 & -d_\beta \end{pmatrix},$$

$$E = \begin{pmatrix} -x_\beta - x_\alpha & 0 & 0 \\ x_\beta & -x_\alpha & 0 \\ x_\alpha & 0 & -x_\beta \end{pmatrix},$$

such that the system changes with time according to

$$\frac{d\mathbf{n}(t)}{dt} = (S + D + E)\mathbf{n}(t). \tag{1}$$

The general solution to equation (1) is

$$\mathbf{n}(t) = e^{(S+D+E)(t-t_0)}\mathbf{n}(t_0), \tag{2}$$

where t_0 is a time at which the state of the system is known and the matrix exponential is defined by its Taylor expansion (Apostol 1969).

We can now assess the general validity of the claim that a source region will have higher diversity or endemism than a sink region. The equilibrium behavior of equation (2) can be obtained by considering the eigenvector corresponding to the dominant eigenvalue of $S + D + E$; we call this dominant eigenvector $\mathbf{u} = (u_1, u_2, u_3)^T$. Since we are interested in the case of a source and a sink, we set $s_\beta = d_\beta = 0$ to make R_α a pure source and R_β a pure sink. The proportions of taxa in each region that are endemic there are then

$$\frac{u_2}{u_1 + u_2} = \frac{s_\alpha + x_\beta}{s_\alpha + d_\alpha + x_\beta} \quad \text{at } R_\alpha, \tag{3a}$$

$$\frac{u_3}{u_1 + u_3} = \frac{x_\alpha}{s_\alpha + x_\beta} \quad \text{at } R_\beta. \tag{3b}$$

Some numerical experimentation reveals that proportional endemism can be greater either at a source or at a sink, depending on the relative values of s_α, x_α, x_β, and d_α. An example is shown graphically in figure 2. The number of endemic taxa (u_2 and u_3) and the total number of taxa ($u_1 + u_2$ and $u_1 + u_3$) can also be greater in either of the
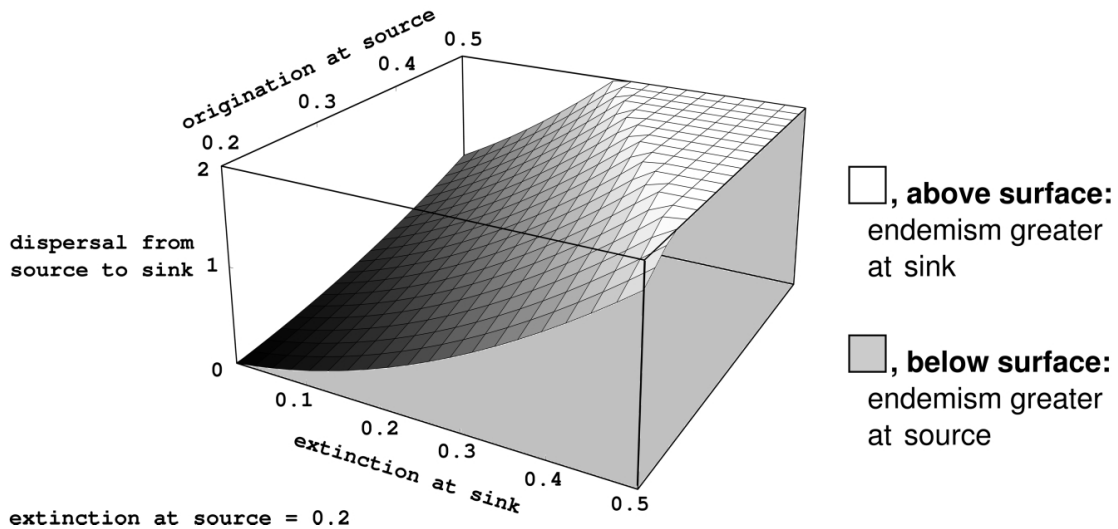
Figure 2: Relative proportions of endemism. The surface is that of equal proportional endemism at the source and the sink, defined as $u_2/(u_1 + u_2) = u_3/(u_1 + u_3)$ (see eq. [3]). This illustrates that there is a substantial portion of parameter space in which endemism is greater at the sink than at the source, demonstrating that high levels of endemism in a region do not necessarily indicate high levels of taxon origination there. (The back right corner is not really flat; it has been truncated for the plot.)

two regions. Total diversity and endemism at a single time therefore cannot be used alone to distinguish a source from a sink.

Age Distributions

In addition to the expression for the number of taxa in each location as a function of time (eq. [2]), we are interested in the age distribution of taxa in each region at a particular time. Define the vector $\mathbf{n}'(t, t')$ to describe the number of taxa alive at time t that survive until a later time t'. The survival of taxa is described by

$$\frac{d\mathbf{n}'(t, t')}{dt'} = (\mathbf{D} + \mathbf{E})\mathbf{n}'(t, t'), \tag{4}$$

which has the solution

$$\mathbf{n}'(t, t') = e^{(\mathbf{D}+\mathbf{E})(t'-t)}\mathbf{n}'(t, t). \tag{5}$$

To form the age distribution of taxa, first define $\tau = t' - t$ to be the age of taxa created at time t, as observed at time t'. The rate at which new taxa are created at time t is $\mathbf{Sn}(t)$; equation (2) gives an expression for $\mathbf{n}(t)$; equation (5) describes the survival of these new taxa. The age distribution of extant taxa, $\mathbf{f}(\tau)$, can thus be written as

$$\mathbf{f}(\tau) = e^{(\mathbf{D}+\mathbf{E})\tau}\mathbf{S}e^{(\mathbf{S}+\mathbf{D}+\mathbf{E})(t'-\tau-t_0)}\mathbf{n}(t_0). \tag{6}$$

Elements of the vector $\mathbf{f} = (f_1, f_2, f_3)^{\mathrm{T}}$ are such that $\int_0^\infty f_i(\tau)d\tau$ equals the total number of taxa in state i alive at time t'. The function $f_i(\tau)$ can therefore be normalized to become a probability density function by dividing by this integral.

Figure 3 shows the behavior of the normalized age distribution function for all taxa and for endemics at R_α and at R_β for three hypothetical sets of parameter values. It illustrates that the distributions of ages of extant taxa reflect differences in macroevolutionary rates between regions. In particular, there is a clear qualitative difference between the age distributions for source and sink regions (*solid lines*, fig. 3): most taxa in the source region are young, while most taxa in the sink region are of intermediate age. In this case, all taxa originate at the source, and none can disperse from the sink to the source. Young taxa are unlikely to have become extinct at the source and unlikely to have dispersed to the sink. Older taxa are more likely to have become extinct at the source than at the sink because they have been introduced to the source only once (when they were created) but have had many opportunities to disperse to the sink (until they become extinct at the source). Considering only endemic taxa makes
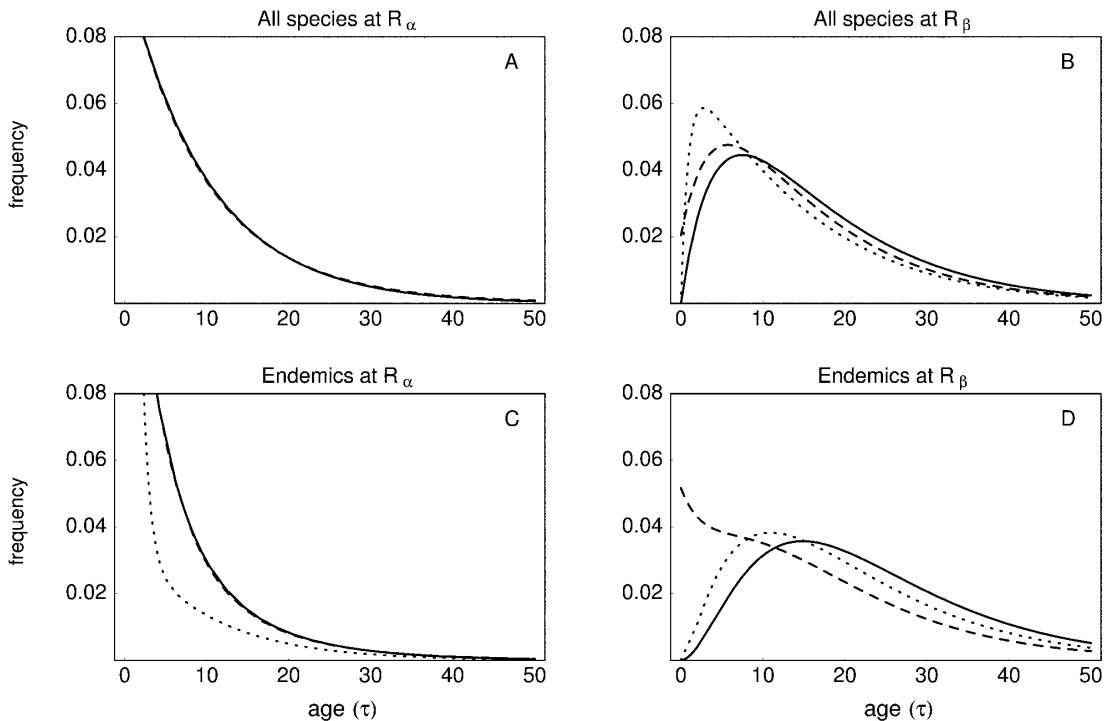
Figure 3: Normalized age distribution functions, equation (6). *A*, All taxa in R_α, $f_1(\tau) + f_2(\tau)$. *B*, All taxa in R_β, $f_1(\tau) + f_3(\tau)$. *C*, R_α endemics, $f_2(\tau)$. *D*, R_β endemics, $f_3(\tau)$. Solid lines are for parameter values $s_\alpha = d_\alpha = 0.1$, $s_\beta = d_\beta = 0$, $x_\alpha = x_\beta = 0.05$, illustrating the case when R_α is a pure source and R_β is a pure sink and demonstrating clear differences in the age distributions of the two regions. Dotted lines are for parameter values $s_\alpha = 0.1$, $d_\alpha = 1$, $s_\beta = d_\beta = 0$, $x_\alpha = x_\beta = 0.05$, illustrating the case of very high dispersal from the source, R_α, to the sink, R_β. Dashed lines are for parameter values $s_\alpha = d_\alpha = 0.1$, $s_\beta = d_\beta = 0.02$, $x_\alpha = x_\beta = 0.05$, illustrating a situation where the source-sink relationship is relaxed. In all cases the initial condition used is $\mathbf{n}(-50) = (1, 0, 0)^T$. With time units of millions of years, these origination and extinction rates are biologically reasonable (Van Valen 1973; Stanley 1985; Sepkoski 1998).

the differences between the source and sink regions more marked.

When there is no dispersal into a region, the shape of the age distribution is exponential with a rate constant equal to the local origination rate, independent of the extinction rate. This can be shown by writing the age distribution for an isolated region, $f(\tau)$, following the same reasoning as for the derivation of equation (6). With s as the origination rate and x as the extinction rate, $f(\tau) = e^{-x\tau}se^{(s-x)(t'-\tau-t_0)}n(t_0) = se^{(s-x)(t'-t_0)}n(t_0)e^{-s\tau}$. The only age dependence is in the last factor, so the age distribution normalized as after equation (6) is simply $se^{-s\tau}$ (see also Pease 1988; Foote 2001).

We also illustrate in figure 3 two situations in which the differences in age distributions between the regions are reduced. First, when dispersal from the source to the sink is very high, the sink region will better mirror the

contents of the source. The peak in the sink age distribution therefore shifts toward the left (*dotted lines*, fig. 3), and with an extremely high dispersal rate, the youngest taxa will dominate the sink age distribution as they do at the source. Note that this effect is less severe when considering only taxa endemic to the sink. Second, when the source-sink relationship is relaxed, the age distributions in the two regions become more similar (*dashed lines*, fig. 3). In particular, origination at the sink increases the proportion of young taxa at the sink, and this is especially so for endemics. The differences in age distributions between source and sink regions do, however, hold over a wide range of parameter values, demonstrating that such age distributions can be a robust means of inferring source or sink properties of a region.

Because our model gives a quantitative description of the expected ages of taxa, we can use it to estimate rates

of origination, extinction, and dispersal from data on taxon ages. Next we discuss the application of this model to biogeographic and paleontologic data on marine bivalves.

Application to Marine Bivalves

Polar regions of the world's oceans contain significantly fewer species and higher taxa than temperate or tropical areas. While many hypotheses have been proposed to explain why polar regions have so few taxa (Fischer 1960; Connell and Orias 1964; Crame 1992; Rohde 1992, 1999; Rosenzweig 1995; Blackburn and Gaston 1996; Willig et al. 2003; Currie et al. 2004), the evolutionary basis for this pattern remains poorly understood. Wallace (1878) was among the first to argue that the low diversity of the polar regions is largely a reflection of past episodes of glaciations and climatic change that repeatedly drove many high-latitude taxa to extinction, leaving little opportunity for diversity to recover, and this idea has had subsequent proponents (Fischer 1960; Skelton et al. 1990). However, empirical studies provide at best equivocal support for the idea that polar regions are characterized by significantly higher extinction rates compared with temperate or tropical areas (Raup and Jablonski 1993; Crame and Clarke 1997; Crame 2002). An alternative view is that the low diversity of polar regions results from low origination rates there, but again, empirical tests of this idea in the marine realm have produced inconclusive results (Crame and Clarke 1997; Crame 2002).

A central assumption of many previous attempts to explain the differences in diversity between high and low latitudes is that these differences reflect in situ differences in macroevolutionary rates. They either implicitly or explicitly exclude the possibility that such changes in diversity could result from past shifts in the geographic distributions of taxa (Fischer 1960; Stehli et al. 1969; Stenseth 1984; Flessa and Jablonski 1996; Cardillo 1999; Currie et al. 2004; but see Valentine 1968; Hecht and Agan 1972; Gaston and Blackburn 1996; Rosenzweig and Sandlin 1997). Yet there is overwhelming evidence for shifts in geographic distributions of species and higher taxa, not only in response to climate changes (Peters and Lovejoy 1992; Jackson and Overpeck 2000; Roy et al. 2001) but as invaders crossing climatic gradients (Vermeij 1991; Jablonski and Sepkoski 1996), and such shifts over geologic time may be an important determinant of large-scale biodiversity patterns (Wiens and Donoghue 2004). Using our model, we test the relative importances of origination, extinction, and dispersal in determining polar marine bivalve diversity.

The Data

Our analyses are based on 459 genera of marine bivalves living on the continental shelves (depth <200 m). These taxa belong to 14 of the 41 living superfamilies of bivalves and represent about half of the 958 living bivalve genera with a fossil record. We estimated the geological ages of individual genera using an existing database (Jablonski et al. 2003). Geographic distribution of each genus was obtained from an updated version of the data used by Flessa and Jablonski (1996). We then characterized each genus as being present only in the polar regions (defined as poleward of 60° north or south latitude), outside the polar regions, or in both areas. The superfamilies used here are less well represented in the Southern Hemisphere and so our polar data are predominantly from the Northern Hemisphere. Hence, instead of analyzing polar regions of the two hemispheres separately, we combined the data into one polar unit in our analyses. Previous studies have suggested interesting differences in evolutionary dynamics between the northern and southern polar regions (Clarke and Crame 1997, 2003), but the nature of our data prevents us from exploring these differences. We also used an updated version (Jablonski et al. 2003) of data from the Sepkoski (2002) compendium to determine an initial condition for the model as discussed in the next section.

Model Fit to Data

To estimate rates of dispersal, extinction, and origination of genera, we fit our model to these data using all genera of age 65 million years or less; older genera were not used because the end-Cretaceous mass extinction would severely violate the assumption of time-independent rates. We let R_β refer to the polar region above 60°N latitude and below 60°S latitude, and R_α refers to the tropical and midlatitude regions between 60°N and 60°S. We emphasize that we fit to the general version of the model (fig. 1*A*), and so we did not preassign source or sink characteristics to either region.

We used maximum likelihood to estimate the rates. The joint likelihood function and maximization procedure are described in the appendix in the online edition of the *American Naturalist*. We also used the method of least squares to estimate the rates as described in the appendix. Maximum likelihood and least squares emphasize different aspects of the data and make different assumptions, but they yielded nearly identical parameter estimates. We prefer the maximum likelihood approach because it does not require binning the data and therefore takes better advantage of the information available.

For the initial condition, $\boldsymbol{n}(t_0)$, we used data from Jablonski et al. (2003) and Sepkoski (2002) to determine the

number of genera that survived the end-Cretaceous mass extinction and belonged to families in the biogeographic data set. These genera are not included in the data set from which we estimate parameters, even if they are alive today, because they are older than 65 million years. Because biogeographic information for these genera was lacking and because there is evidence that the impact of the extinction on bivalves was globally uniform (Raup and Jablonski 1993), we assumed that they were distributed in the same proportions as present-day diversity. Setting $t' = 0$ and $t_0 = -65$ million years, the initial condition was thus $\mathbf{n}(-65) = (9, 54, 0)$. Reasonable deviations from this assumption, including the presence of four or five polar endemics (Marincovich 1993), were also considered. These gave parameter estimates within 10% of the nonzero parameter estimates or within the confidence intervals (CIs) of the zero estimates reported in table 1.

A parametric bootstrap was used to calculate a 95% CI for each parameter and to assess the bias and covariance of the parameter estimates (details in the appendix). The maximum likelihood parameter estimates and their CIs are given in table 1. Different widths of the CIs reflect differences in the sensitivity of the model to each parameter.

Significant differences exist between the two regions in the per-genus rates of origination, extinction, and dispersal, as shown in table 1. The rate of origination of new genera is significantly lower in the polar regions than at lower latitudes. The rate at which genera move from polar regions to lower latitudes is significantly lower than the rate of movement in the opposite direction. The rate of extinction of genera also appears higher in the polar regions than at lower latitudes.

To help visualize the fit, figure 4 presents age distributions of the data and of the model with the estimated parameter values. We assembled the data into two age distribution histograms, one for all genera in the polar regions, R_β, and one for all genera at lower latitudes, R_α. Each of these age distributions is shown with 12 bins of equal width spanning ages from 0 to 65 million years. Using the parameter estimates, we formed age distributions from equation (6). These were in continuous time, so the integral of $\mathbf{f}(\tau)$ over each bin was computed for comparison with the binned data.

In figure 4, the data showed considerable scatter around the model, raising potential concerns about the applicability of this model to these data and especially bringing into question the assumption of constant rates over time. However, the CIs produced by the parametric bootstrap (*dotted lines*, fig. 4; methods in the appendix) show that much of this scatter can be explained by the stochastic nature of the origination-extinction-dispersal process. We cannot, however, entirely rule out the possibility that some

Table 1: Parameter estimates

Parameter	ML estimate (genus^{-1} Ma^{-1})	95% CI (genus^{-1} Ma^{-1})
s_α	.03049	(.02886, .03564)
s_β	.00088	(.00042, .00252)
x_α	.00000	(.00000, .00022)
x_β	.02956	(.00030, .12212)
d_α	.01069	(.00633, .02421)
d_β	.00000	(.00000, .00004)

Note: ML = maximum likelihood; CI = confidence interval. Using the CI of the difference between parameters, we find significant differences between s_α and s_β ($P < .005$) and between d_α and d_β ($P < .001$) and a marginally significant difference between x_α and x_β ($P = .03$). The methods used for calculating CIs and P values are described in the appendix in the online edition of the *American Naturalist*.

of the variation is caused by rate heterogeneity or possible sampling effects, and future work could explore the effects of such heterogeneities on the model's predictions.

Discussion

Identifying the role of historical processes in shaping biogeographic patterns of species diversity seen today remains a challenging problem. Direct quantitative tests of historical hypotheses require a complete fossil or historical record that is absent for the vast majority of living taxa. In addition, there is little quantitative theory relating historical processes to present-day biogeographic patterns. The model we present here is an attempt to formulate such a theoretical framework. Our model connects the processes of taxon origination, extinction, and dispersal with present-day regional diversity, endemism, and age distributions. Our results question some widely held assumptions regarding the relationship between endemism, diversity, and origination rates. In particular, we use this model to show that a region that is a macroevolutionary source or "center of origin" need not necessarily have high levels of diversity and endemism, as is often assumed (Willis 1922; Rosenzweig and Sandlin 1997; Mora et al. 2003; reviews by McCoy and Heck [1976]; Ricklefs and Schluter [1993]), but that it must have a high proportion of young taxa. Conversely, a macroevolutionary sink or "center of accumulation" need not necessarily have low levels of diversity and endemism, but its age distribution often will have a single intermediate peak. Our conclusion is therefore that regional measures of diversity and endemism are not sufficient to estimate average regional evolutionary rates but that age distributions often are. By fitting this model to data on extant marine bivalves, we are able to estimate regional rates of origination, extinction, and dispersal, and we show that polar regions have on average a
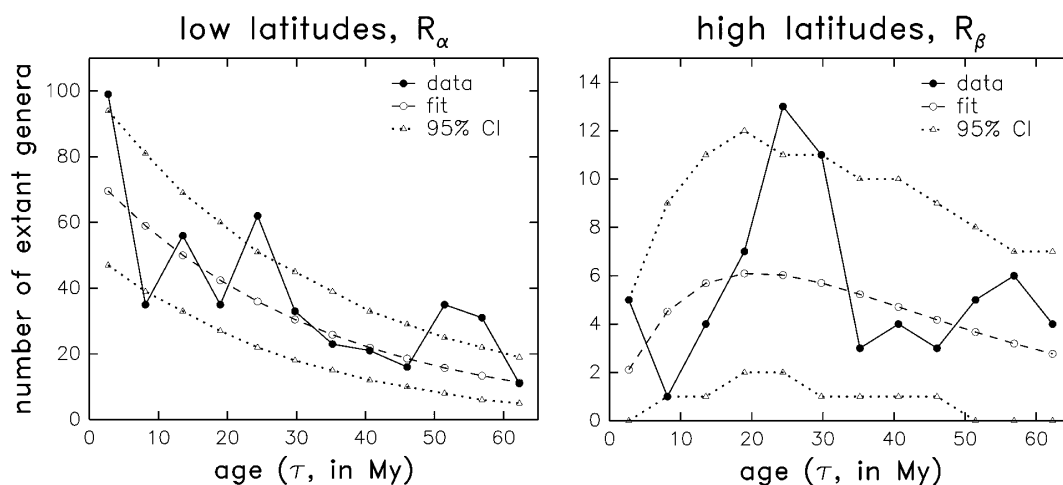
Figure 4: Age distributions of marine bivalve genera and the model fit, using the maximum likelihood parameter estimates given in table 1. Left panel shows all genera in R_α; right panel shows all genera in R_β. Filled circles are the data, and open circles are the model, which is $\int_{\text{bin}} [f_1(\tau) + f_2(\tau)] d\tau$ for R_α and $\int_{\text{bin}} [f_1(\tau) + f_3(\tau)] d\tau$ for R_β. The open triangles show approximate 95% confidence intervals on the data determined by the parametric bootstrap, as described in the appendix in the online edition of the *American Naturalist*. The quality of the fit is discussed in the text. The maximum likelihood fitting procedure did not require binning the data; these histograms are used only to display the results.

lower rate of origination, a higher rate of extinction, and a higher rate of immigration of genera than do the lower latitudes.

Our model is in the same spirit as other "neutral" models of biogeography and diversity, notably MacArthur and Wilson's theory of island biogeography (MacArthur and Wilson 1967) and Hubbell's unified neutral theory (Hubbell 2001). These share the assumption that the "units" that are considered (species or higher taxonomic units in our case, species in the case of island biogeography, and individuals of all species in the case of unified neutral theory) are all equivalent: there are no intrinsic individual or species differences. Hubbell describes his theory as an extension of MacArthur and Wilson's theory because he considers not only extinction and immigration of species from a "mainland" pool or "metacommunity" but also speciation in the metacommunity and relative abundances of species. Our model can also be seen as an extension of the theory of island biogeography but in a different direction. Like it, we consider only presence or absence of taxa, not abundances, and like unified neutral theory, we include origination of new taxa. We differ in considering our two regions to be functionally symmetric (though perhaps with different parameter values) rather than designating one area as a mainland pool or metacommunity and one as an island or local community. This enables us to consider relative levels of diversity and endemism be-

tween the regions as functions of regional rates. Unlike previous work, we use the ages of taxa to infer regional rates.

In addition to our "neutral" assumption that all taxa behave equally, our model makes the significant assumption that regional rates of origination, extinction, and dispersal do not change over time. This restriction is not quite as strong as it seems because the requirement is only that the average rates over an entire region remain constant. If, however, the rate parameters were explicit functions of time, equation (1) would still hold but equation (2) would not be its solution, and the subsequent equations for diversity and age distributions would not be valid. To our knowledge, an analytic form of this model cannot be obtained for general time-dependent rates, but specific situations of interest could be investigated numerically or through simulations.

The validity of the assumptions of taxon equivalence and constant rates can be addressed on two levels. The model was developed to identify criteria, based on extant taxa, that can or cannot be used to infer the magnitudes of evolutionary rates. For questions like what the indications are that a region has a high rate of origination, our assumptions are appropriate because the issue is one of average rates over time and over taxa.

It is when we apply our model to data that the validity of the assumptions becomes more important. We took

the obvious precaution of restricting the data set to the last 65 million years to avoid the end-Cretaceous mass extinction, which would be a serious violation of the constant-rates assumption. Inspection of figure 4 indicates that the period 50–60 million years ago may have had higher origination rates, perhaps reflecting a rebound from the end-Cretaceous extinction (Flessa and Jablonski 1996; Jablonski 1998), and 25 million years ago also may have been a time of greater origination. An important observation here is that these anomalies are present in both regions. Given that the average origination rate is two orders of magnitude greater in the lower latitudes (table 1), the anomalous peaks in the polar regions most likely resulted from subsequent dispersal of taxa that originated in the lower latitudes. This highlights the importance of taking into account past dispersal patterns in interpreting present-day regional age distributions: if we assumed that the current distributions of taxa reflected their places of origin, as is commonly done, we would have concluded that both regions had high in situ origination rates during these times.

It is possible that geographic differences in the nature of the fossil record to underestimate taxon ages could introduce a bias into our results. The poorer quality of the fossil record in the tropics (Van Valen 1969; Johnson 2003) could lead to greater underestimation of ages for lower-latitude taxa; this bias could therefore add false support to our conclusion of higher origination rates at lower latitudes. This is unlikely to produce a large effect here, since we defined our "low-latitude" region as both the tropics and also the well-sampled temperate region to take into account such sampling problems. In principle, our approach can be used to compare tropical versus extratropical regions, as many previous studies have done (Stehli et al. 1969; Jablonski 1993; Flessa and Jablonski 1996; Gaston and Blackburn 1996; among many others). However, more work is needed to improve sampling and taxonomic standardization of the tropical fossil record before rigorous analyses are feasible. Similarly, a more complete data set of the ages of taxa living in high-latitude southern oceans would be useful for exploring the differences in the evolutionary dynamics between the two polar oceans (Clarke and Crame 1997, 2003).

The excellent fossil record for marine bivalves makes it possible to determine regional macroevolutionary rates and range shifts explicitly, and some of this has been done (Vermeij 2001). Such analyses, however, are not possible for many other taxa, and we hope that the approach taken by our model may be useful for cases in which only more limited information about extant taxa is available. In particular, it would be quite useful if this method could be applied to the rapidly increasing number of taxa for which phylogenetic trees and estimates of branching times are available. There is a large body of work (Nee et al. 1994; Pybus and Harvey 2000; among others) on estimating rates of origination and extinction from branching times, but this does not allow consideration of differences in rates between regions. Our model does not require an explicit phylogeny, but we assume that an origination event creates one daughter taxon and leaves the age of the parent taxon unaffected, as is the convention with phylogenies determined from the fossil record. In phylogenies determined from molecular data, taxa do not have absolute ages and the most recent branching time of a lineage therefore depends on the survival of potential sister taxa (Gaston and Blackburn 1996). Because of this difference, modification of our model would be necessary in order to apply it to lineage ages from this second kind of phylogeny, but simulations (not shown) do suggest that similar patterns in age distributions will hold.

The spatial extent of our system was the entire globe and our data were at the level of genera, but the model presented here could be applied to closed systems of two regions on any spatial or taxonomic scale. This model could also be extended in a straightforward manner to multiple regions. This could allow, for example, quantitative description of expected age distributions in a region where diversity is elevated by the overlap of biogeographic provinces, or it could lead to a model for expected distributions of range sizes.

In general, findings for marine bivalve genera clearly show that shifts in geographic ranges can play an important role in determining global patterns of biodiversity. Future attempts to estimate regional origination and extinction rates for any taxon therefore should not be based explicitly on the assumption of in situ origination, and the possible effects of dispersal between regions should be evaluated. Spatially explicit models, in which in situ processes interact with biotic interchanges, should prove important for our understanding of past and future dynamics of biological diversity.

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Appendix from E. E. Goldberg et al., "Diversity, Endemism, and Age Distributions in Macroevolutionary Sources and Sinks"

(Am. Nat., vol. 165, no. 6, p. 623)

Data Analysis

Maximum Likelihood

The likelihood of observing the data given our model is $L(\mathbf{x}, m|\boldsymbol{\theta})$, where $\mathbf{x}$ is the data vector, m is the number of taxa in the data set (459 genera for our data), and $\boldsymbol{\theta}$ is the parameter vector. Each element of $\mathbf{x}$ corresponds to a taxon and contains the age and present location of that taxon. The elements of $\boldsymbol{\theta}$ are the six macroevolutionary rates: s_α, s_β, x_α, x_β, d_α, and d_β.

Although there are m elements in $\mathbf{x}$, the probability of observing m taxa can be considered independent of the ages and geographic distributions observed. This is because each set of parameter values yields a stable distribution of taxa (i.e., the dominant eigenvector $\mathbf{u}$, defined in the text, has its direction independent of its magnitude). The elements of $\mathbf{x}$ are nearly independent; although they are all connected by a phylogeny, the survival of each taxon, once it is created, is independent of all the others. Using these independence assumptions, we write the likelihood function as

$$L(\mathbf{x}, m|\boldsymbol{\theta}) = L(m|\boldsymbol{\theta})L(\mathbf{x}|\boldsymbol{\theta}) = L(m|\boldsymbol{\theta})\prod_{j=1}^{m} L_j(x_j|\boldsymbol{\theta}), \tag{A1}$$

where $L_j(x_j|\boldsymbol{\theta})$ is the likelihood of observing the jth taxon.

To compute $L(m|\boldsymbol{\theta})$, we begin with the crude assumption that this has a Poisson distribution because the survival of each cohort is Poisson distributed. The mean of this distribution is the expected total number of genera at the time of observation, t': $n_T(\boldsymbol{\theta}) = n_1(t') + n_2(t') + n_3(t')$, where $\mathbf{n}(t')$ is defined by equation (2). From the Poisson assumption, the variance is also $n_T(\boldsymbol{\theta})$. Because $n_T(\boldsymbol{\theta})$ is large, we then approximate this distribution with a normal distribution, yielding $L(m|\boldsymbol{\theta}) = N[n_T(\boldsymbol{\theta}), n_T(\boldsymbol{\theta})]$. Using this functional form, with the rest of the likelihood function described below, we estimate the parameters, and then we use these parameter estimates in simulations to check the validity of the Poisson assumption. We find that the assumption of normality is justified but that the variance is underestimated by a factor of about six. Repeating the likelihood maximization using this general normal distribution, we find parameter estimates identical to before. We therefore retain $L(m|\boldsymbol{\theta}) = N[n_T(\boldsymbol{\theta}), 6n_T(\boldsymbol{\theta})]$ and are confident that this is a reasonable approximation.

Now consider $L_j(x_j|\boldsymbol{\theta})$. The likelihood of observing the jth taxon is determined by its age, τ_j, and current geographic location, γ_j, which can take a value of 1 (if it is present in R_α and in R_β), 2 (if it is present only in R_α), or 3 (if it is present only in R_β). If we knew the location in which this taxon originated (call this δ_j, taking values in the same manner as γ_j), the likelihood of observing this taxon, $L_j(x_j|\boldsymbol{\theta})$, would equal the probability of transitioning from δ_j to γ_j in time τ_j. Because δ_j is unknown, we define a vector describing the initial state: $\mathbf{v}_j = [0, Pr(\delta_j = 2), Pr(\delta_j = 3)]^T$, where $Pr(\delta_j = i)$ is the probability that $\delta_j = i$, and we know that $Pr(\delta_j = 1) = 0$ because a taxon cannot arise in both locations simultaneously. This initial state vector can be found from the model:

$$\mathbf{v}_j = \left(0, \frac{w_2}{w_2 + w_3}, \frac{w_3}{w_2 + w_3}\right)^{\mathrm{T}}, \tag{A2}$$

where

$$\mathbf{w} = \mathbf{S}\mathbf{n}(t' - \tau_j) = \mathbf{S}e^{(\mathbf{S}+\mathbf{D}+\mathbf{E})(t'-\tau_j-t_0)}\mathbf{n}(t_0). \tag{A3}$$

The matrix of transition probabilities between δ and γ, $\mathbf{T}(\tau, \boldsymbol{\theta})$, can also be determined from the model:

$$\mathbf{T}(\tau, \boldsymbol{\theta}) = e^{(\mathbf{D}+\mathbf{E})(\tau)}. \tag{A4}$$

The likelihood of observing the jth taxon, $L_j(x_j|\boldsymbol{\theta})$, is the γ_jth element of the vector $\mathbf{T}(\tau, \boldsymbol{\theta})\mathbf{v}_j$. This completes the terms necessary to compute the likelihood function in equation (A1). Maximization of this likelihood is described in the next section.

Optimization

To maximize the likelihood function described in the previous section with respect to the parameter values, we used the downhill simplex algorithm (Nelder and Mead 1965; also called Nelder-Mead or Amoeba [Press 1992]) to minimize the negative of the logarithm of the likelihood. To avoid negative estimates of rate parameters, the minimization was constrained (Nelder and Mead 1965): when a proposed set of parameters (a vertex of the simplex) contained a negative parameter, a large value was returned instead of the actual value of the negative log likelihood for that vertex, ensuring that the vertex was rejected.

Least Squares

We also estimated parameters by using a least squares fit to the empirical age distribution histograms in figure 4. This consisted of minimizing the sum of squared differences of the data for each bin from the model prediction for that bin, which was $\int_{\text{bin}}[f_1(\tau) + f_2(\tau)]d\tau$ for R_α bins and $\int_{\text{bin}}[f_1(\tau) + f_3(\tau)]d\tau$ for R_β bins. The minimization was also done with the downhill simplex algorithm, and when a negative value was proposed for a parameter, the sum-of-squares value returned was multiplied by a large value.

We applied the bootstrap procedure described below, and the parameter estimates and their 95% confidence intervals (CIs) are: $s_\alpha = 0.0318$ (0.0269, 0.0359), $s_\beta = 0.0000$ (0.0000, 0.0114), $x_\alpha = 0.0000$ (0.0000, 0.0095), $x_\beta = 0.0149$ (0.0000, 0.0839), $d_\alpha = 0.0101$ (0.0062, 0.0220), $d_\beta = 0.5758$ (0.0000, 2.7199), with a significant difference between s_α and s_β. There was strong correlation between d_α and x_β ($\rho = 0.81$) and between s_α and x_α ($\rho = 0.74$).

The close agreement between parameter estimates from these two methods lends confidence that assumptions we made in computing the likelihood function did not unduly influence our results. (An exception to this agreement is d_β, although the modal value was 0; the least squares method is quite insensitive to this parameter.) Because the least squares procedure required binning the data before fitting and because appropriate weighting of each resulting bin could not be calculated, this method did not extract information from the data as appropriately as did maximum likelihood. This is reflected in the CIs, which are generally broader under the least squares method.

Bootstrap Methods

We used a parametric bootstrap to form CIs for the parameter estimates, to test for differences between parameter estimates, to assess bias and covariance in the parameter estimates, and to construct CIs on the amount of scatter expected in the data under this model.

Each bootstrap iteration used a simulation of the origination-extinction-dispersal process described by the fitted model; parameter values were set equal to their estimates, the initial condition was $\mathbf{n}(-65) = (9, 54, 0)$ (see text), and the simulation ran for the equivalent of 65 million years. The resulting simulated list of extant taxa and their ages was then fit in the same manner as the real data, yielding a set of bootstrap parameter estimates. This was repeated 10,000 times.

To estimate bias in the parameter estimates, we compared the mean of the bootstrap estimates of each parameter (call this $\hat{\theta}_i^*$ for the ith parameter) with the estimate of that parameter (call this $\hat{\theta}_i$). The bias is equal to $\hat{\theta}_i^* - \hat{\theta}_i$. We found the bias to be -0.00250 for s_α, -0.00044 for s_β, 0.00000 for x_α, -0.00224 for x_β, -0.00020 for d_α, and 0.00013 for d_β. Although it may not be appropriate to perform bias correction by subtracting this bias from $\hat{\theta}_i$ (Efron and Tibshirani 1986), this analysis gives an indication of the approximate level of bias.

We used the bootstrap iterations to form the variance-covariance matrix for the parameters. Correlation between pairs of parameter estimates in the bootstrap samples was low ($|\rho| < 0.21$), except for x_β and d_α ($\rho = 0.91$).

We constructed CIs for the parameters as described by Efron and Tibshirani (1986) and summarized briefly here. First the cumulative distribution function of the bootstrap estimates is formed for each parameter, $\hat{G}(\theta_i)$. The 95% CI is then $(\hat{G}^{-1}[0.025], \hat{G}^{-1}[0.975])$, where the exponent denotes the inverse of a function. Bias is introduced with this method when the median of the bootstrap estimates is not equal to the parameter estimate, that is, when $\hat{G}(\hat{\theta}_i) \neq 0.5$. To correct these CIs for this bias, we use the cumulative distribution function of the standard normal, $\Phi(z)$. Let $z_\alpha = \Phi^{-1}(1 - \alpha/2)$ ($z_\alpha = 1.96$ for $\alpha = 0.05$) and define $z_0 = \Phi^{-1}[\hat{G}(\theta_i)]$. The bias-corrected CI is then $(\hat{G}^{-1}[\Phi(2z_0 - z_\alpha)], \hat{G}^{-1}[\Phi(2z_0 + z_\alpha)])$. This is the CI we report for each parameter in table 1.

To test for significant differences between parameter values θ_i and θ_j (particularly between s_α and s_β, between x_α and x_β, and between d_α and d_β), we tested whether 0 was contained in the 95% CIs of $\theta_j - \theta_i$ (Lo 1994), constructed as in the previous paragraph. To obtain probability levels for the differences between parameter estimates (the P values reported in table 1), we identified the α-levels at which the CIs just contained 0 (Forney and Barlow 1998).

To construct CIs on the amount of scatter expected in the data, we formed age distribution histograms of the model predictions for each set of bootstrap parameter estimates, using the same bin widths as were applied to the data. We then calculated the 95% CIs of each bin, using the method described above. The results are shown with the dotted lines in figure 4.

Chapter 1, in full, is a reprint of the material as it appears in Goldberg, Emma E, Kaustuv Roy, Russell Lande, and David Jablonski. 2005. Diversity, endemism, and age distributions in macroevolutionary sources and sinks. The American Naturalist 165:623–633. The dissertation author was the primary investigator and author of this paper.

Chapter 2

Origination, extinction and dispersal: integrative models for understanding present-day diversity gradients

Abstract

Species diversity gradients seen today are, to a large degree, a product of history. Spatially non-random originations, extinctions and changes in geographic distributions can create gradients in species and higher taxon richness, but the relative roles of each of these processes remain poorly documented. Existing explanations of diversity gradients have tended to focus on either macroevolutionary or biogeographic processes; integrative models that include both are largely lacking. We used simple models that incorporate origination and extinction rates along with dispersal of taxa between regions to show that dispersal not only affects regional richness patterns but also has a strong influence on the average age of taxa present in a region. Failure to take into account the effects of dispersal can, in principle, lead to biased estimates of diversification rates and potentially wrong conclusions regarding processes driving latitudinal and other gradients in diversity. Thus it is critical to include the effects of dispersal when formulating and testing hypotheses about the causes of large-scale gradients in diversity. Finally, the model results, in conjunction with the results of existing empirical studies, suggest that the nature of macroevolutionary and biogeographic processes may differ between terrestrial and marine diversity gradients.

Introduction

With human footprints covering every habitat on the planet and the resulting threats to biodiversity, the need to understand the processes that determine why some regions have many species while others have relatively few has never been greater. Yet despite many hypotheses and a considerable literature, we still know relatively little about what causes large-scale gradients in diversity (Currie et al. 2004; Mittelbach et al. 2007). Recent work has largely focused on the role of the present-day environment in regulating regional diversity, and while such analyses have revealed much about the diversity-environment relationship, process-based explanations of these patterns remain elusive (Currie et al. 2004). Climate clearly has an influence on large-scale patterns of species diversity, and numerous studies have demonstrated strong correlations between diversity and present-day environmental variables such as temperature and productivity (e.g. Currie 1991; Roy et al. 1998; Mittelbach et al. 2001; Hawkins et al. 2003; Currie et al. 2004). But as Ricklefs (2004) pointed out, it is not straightforward to interpret these correlations or to demonstrate that they reflect causality. Present-day environmental variables could regulate spatial patterns of species diversity by influencing geographic range limits of individual species, the carrying capacity of a particular place, or both (Allen et al. 2002; Currie et al. 2004). Thus

one possible explanation of the correlations between present-day climatic variables and diversity gradients is that the latter simply reflect how environmental conditions influence spatial patterns of species distributions or how they constrain interactions between species that determine local coexistence. Under this view, historical factors such as speciation and extinction either do not show strong spatial biases or such signals are secondary. Alternatively, the correlations between present-day climate and diversity may predominantly reflect a historical signal of speciation and extinction along with phylogenetic conservatism of ecological, life history and physiological traits (Ricklefs 2004; Wiens and Donoghue 2004; Ricklefs 2006a). Note that in the latter case, climate can still have a role in regulating diversity patterns through its influence on speciation and extinction, but the emphasis is shifted to the roles of past environments as well as other factors such as biotic interactions that promote speciation and extinction (Schemske 2002). In general, present-day diversity gradients reflect the influences of spatially non-random originations and extinctions as well as changes in the geographic distributions of taxa over time (see Jablonski et al. 2006). The challenge then is to untangle the relative roles of macroevolutionary dynamics and biogeographic processes. Here we build on some recent studies and use integrative models that incorporate dispersal between regions along with spatially variable origination and extinction rates to explore how dispersal affects the nature of diversity gradients. In particular, we ask whether ignoring dispersal dynamics is likely to affect our estimates of macroevolutionary rates and our ability to separate the relative contributions of macroevolutionary and biogeographic dynamics in generating diversity gradients. We address this issue in the context of the latitudinal diversity gradient primarily because of the large body of work associated with that gradient, but the general results presented here should be applicable to other gradients such as those along longitude, bathymetry and elevation. We also use these models to explore whether latitudinal diversity gradients in marine and terrestrial systems are likely to result from different dynamics.

Untangling patterns and processes

Existing attempts to understand the causes of the latitudinal diversity gradient have either focused on the roles of current environmental variables (e.g. Currie 1991; Roy et al. 1998; Mittelbach et al. 2001; Hawkins et al. 2003; Currie et al. 2004) or on geographic patterns of origination, extinction and diversification (see Jablonski et al. 2006). Except for a few studies (e.g. Hawkins et al. 2005; Harrison et al. 2006; Jablonski et al. 2006; Wiens et al. 2006), integrative analyses of diversity gradients that include macroevolutionary as well as biogeographic and ecological processes are largely lacking. This makes it difficult, if not impossible, to evaluate the relative roles of these processes in shaping present-day diversity gradients.

The idea that contemporary climate plays an important role in determining global diversity gradients goes back almost two centuries (Clarke and Gaston 2006). However, there are still very few process-based models relating past or present environmental conditions to large-scale patterns of species diversity, and hence quantitative predictions about diversity-environment or diversity-energy relationships are lacking (Rosenzweig 1995). Support for a strong influence of the present-day environment on diversity gradients is almost exclusively based on significant positive relationships between measurements of various climatic or environmental variables (e.g. temperature, productivity, water availability) and species or higher taxon richness (see Currie et al. 2004 for a review). But the slopes of these regressions vary widely across taxa and/or regions, and the empirical data are largely inconsistent with the commonly cited explanations of such relationships (Currie et al. 2004). In cases where specific predictions about the slopes of relationships are available, such as the link between diversity and temperature predicted by Allen et al. (2002), results of empirical tests have been mixed (Allen et al. 2002; Roy et al. 2004; Hunt et al. 2005). Some authors have even argued that a general species-energy relationship that applies to both plants and animals is unlikely to exist and that the effect of temperature on diversity is likely to be indirect and complex (Clarke and Gaston 2006; also see Currie et al. 2004). Thus it is not straightforward to interpret the observed correlations between contemporary environmental variables and diversity and to demonstrate that they reflect causality (see Ricklefs 2004).

The hypothesis that present-day diversity gradients bear a strong imprint of history is also not new. Wallace (1878) was among the first to argue that parts of the world with a longer and more stable geological and climatic history have had a chance to accumulate more species compared to areas, such as high latitudes, that have seen large environmental fluctuations in the geological past. This general idea, in various forms, has had proponents ever since, as have other macroevolutionary hypotheses about the origin and maintenance of the latitudinal diversity gradient (Jablonski et al. 2006; Mittelbach et al. 2007). However, most analyses of historical influences on the present-day latitudinal diversity gradient have focused on how origination and/or diversification rates vary with latitude (patterns of extinction remain poorly known) and have ignored the effects of post-origination changes in the distribution of taxa (Jablonski et al. 2006). Yet large-scale gradients in species richness today almost certainly reflect the interactions between how originations and extinctions vary in space and changes in geographic distributions of taxa in response to changes in the ambient environment (Wiens and Donoghue 2004; Jablonski et al. 2006; Ricklefs 2006). Equally importantly, even though there is increasing recognition that history can be an important determinant of present-day diversity gradients, the effects of historical processes are still studied largely using descriptive and retrospective analyses rather

than tests of specific models incorporating speciation, extinction and dispersal dynamics (but see Goldberg et al. 2005; Jablonski et al. 2006; Wiens et al. 2006).

We argue that the first step towards a better understanding of the processes underlying the contemporary latitudinal diversity gradient should be to evaluate the relative roles of macroevolutionary dynamics (i.e. origination and extinction) and biogeographic dynamics (i.e. patterns of immigration, local extinctions and distributions of geographic range limits) using general models that relate spatial patterns of speciation, extinction and changes in geographic distributions of individual taxa to large-scale gradients in diversity. Understanding the relative contributions of macroevolutionary versus biogeographic or paleobiogeographic dynamics in determining the present-day latitudinal diversity gradient would allow us to focus better on potential mechanisms that are likely to be important. It would also allow us to explore whether the contemporary latitudinal diversity gradient in some groups largely reflects macroevolutionary processes (i.e. differential originations and/or extinctions) while in others is more a function of how past and present environments influence biogeographic dynamics. Historical processes are often somewhat idiosyncratic and have therefore been deemed essentially untestable by some authors (Francis and Currie 1998), but model-based approaches can form the basis for developing a general framework for analyzing their role in producing diversity gradients.

Models of diversity gradients

The models discussed here are special cases of the two-region model of Goldberg et al (2005). These dynamic models track the number of taxa and their ages in each of two regions, R_a and R_b, over time. The regions can have different per-taxon rates of origination (s_a and s_b), extinction (x_a and x_b), and dispersal or range expansion (d_a from R_a to R_b and d_b from R_b to R_a). These rates are assumed to be constant over time and across taxa, and the macroevolutionary process is modeled as a multi-state branching process. For taxa present in both regions at any particular time, extinctions in each region are independent events and represent range contractions (i.e. they are local extinctions); for taxa present in only one region, extinctions are global. In each model used here, we chose R_a to be the region of greater expected richness. Using this framework, we explored the relationship between taxon richness and the average age of taxa in each of the two regions under different scenarios of origination, extinction and dispersal. We focused on taxon ages because they are widely used for calculating diversification rates using molecular phylogenies (Nee et al. 1994; Gaston and Blackburn 1996; Magallón and Sanderson 2001; Cardillo et al. 2005; Nee 2006; Ricklefs 2006b; Weir and Schluter in press) or data from the fossil record (Flessa and Jablonski 1996; Foote 2001; Goldberg et al. 2005; Allen et al. 2006;

Jablonski et al. 2006).

For each model described below we calculated average ages, a commonly used metric (e.g. Gaston and Blackburn 1996; Weir and Schluter in press), using three different approaches (Fig. 2.1). First we used absolute ages of taxa such as those derived from the fossil record, where the age of a lineage is simply its first stratigraphic occurrence. Next, we used tip lengths, as would be obtained from a molecular phylogeny, where the most recent branching point of a lineage depends on the time of an origination event and on the survival of its sister taxon (see Chown and Gaston 2000). Finally, we used root distance, obtained by counting the number of nodes between each tip and the root of a phylogenetic tree; this metric has been used in lieu of tip length when branch lengths are not available on a phylogeny (Kerr and Currie 1999; Hawkins et al. 2006). For all the models presented below, tip lengths and root distances yielded qualitatively similar results, so we only show the results for the absolute ages and tip lengths.

For each set of parameter values, determined by the models described below, we calculated the proportional difference in richness between the regions, (R_a richness − R_b richness) / (R_a richness + R_b richness), and the difference in average age, as measured by each metric. Because R_a is always the more diverse region, the proportional richness difference varies between zero (when R_a and R_b have equal numbers of species) and one (when R_b has no species). It does not, however, vary linearly with the ratio of R_b to R_a richness; when R_b has half as many species as R_a, the proportional richness difference is one-third. These calculations were based on a continuous-time branching process in which origination, extinction, and dispersal proceed under the assumptions of the two-region model. The initial condition of this process was taken to be a single lineage present in both regions, and the process was run for ten time units. In some cases this did not provide sufficient time for the relative proportions of taxa in each geographic region to reach equilibrium, but fixing the time elapsed seemed more analogous to the empirical situations we are trying to model than insisting on effectively-infinite intervals. For the absolute age metric, richness and average age were calculated analytically following the methods of Goldberg et al. (2005). For the tip length and root distance metrics, analytical solutions are not available, so we calculated richness and average age differences for each of 10,000 simulated trees and then averaged the results. Note that all simulated trees used here are global phylogenies (i.e. they include species in both regions).

Each of the models described below (and summarized in Table 2.1) was designed to represent an existing hypothesis about the causes of the present-day latitudinal diversity gradient, and in the discussion we have attempted to relate the insights derived from these models to results of previous empirical studies. The primary difference between these models and most

previous work is that here, in each case, we evaluated the effects of origination and extinction in conjunction with dispersal rather than separately looking at evolutionary and biogeographic processes.

Model 1 – Pure dispersal model

If shifts in geographic range limits due to the environment are the main driver of diversity gradients then such gradients should result from preferential movement of taxa into regions that can support more species and not from spatial gradients in macroevolutionary rates. Such high diversity areas could represent those that have higher energy (e.g. the species-energy hypothesis, Currie (1991)) or some other attribute of the environment allowing many taxa to co-exist (e.g. Allen et al. 2002). From a macroevolutionary perspective this is the null hypothesis where diversification rates do not show a spatial bias (Ricklefs 2006). In fact, the implicit assumption of most regression studies relating diversity gradients to gradients in present-day environmental variables (see Currie et al. 2004 for a review) as well as some null models used in analyses of diversity gradients (Colwell and Lees 2000; Jetz and Rahbek 2002; Storch et al. 2006) is that originations and extinctions are not spatially biased. In the model used here, R_a and R_b have identical origination and extinction rates ($s_a = s_b$, $x_a = x_b$), but after origination species are more likely to disperse into R_a than R_b ($d_a < d_b$). Thus the diversity gradient, in this case, should result not from differences in evolutionary rates between R_a and R_b but solely from higher dispersal of taxa into R_a.

Model 2 – Macroevolutionary source-sink model

Biogeographers have long postulated that certain regions of the world represent "centers of origin"—areas where species and higher taxa preferentially originate—and that these areas are generally situated in lower latitudes (see Ricklefs and Schluter 1993; Brown and Lomolino 1998). Over time taxa spread outwards from these centers of origin into regions with much lower origination rates, or macroevolutionary sinks (Goldberg et al. 2005). Thus the rate of spread and the difference in origination rates between the regions determine the strength of the diversity gradient. In the case of a pure source-sink system there would be no originations in the sink, but in reality this extreme is unlikely. Under our model, a source-sink system has $s_a > s_b$, $x_a = x_b$ and $d_a > d_b$. Note that this characterization of a macroevolutionary sink follows Goldberg et al. (2005) but is somewhat different from a demographic sink, in which the death rate is high (e.g. Pulliam 1988).

Model 3 – Out of the tropics model

Analyses using taxon ages derived from the fossil record (Flessa and Jablonski 1996; Goldberg et al. 2005), paleontological data on the time and place of origin of individual taxa (Jablonski 1993; Jablonski et al. 2006) and phylogenetic relationships of taxa (Judd et al. 1994; McKenna and Farrell 2006) all suggest that the latitudinal diversity gradient results from taxa preferentially originating in lower latitudes, persisting there over geological time and expanding their geographic distributions into high latitudes. This dynamic of tropical origination followed by expansion into higher latitudes, called the Out of the Tropics (OTT) model (Jablonski et al. 2006, also see Ricklefs 2006), is a variant of the source-sink model with a lower extinction rate in the source region. In our case, this means $s_a > s_b$, $x_a < x_b$ and $d_a > d_b$.

Model 4 – Wallace model

Wallace (1878) was among the first to argue that present-day diversity gradients bear a legacy of past changes in climate. This general idea, in various forms, has had proponents ever since (see Jablonski et al. 2006; Weir and Schluter, in press) and postulates that parts of the world with a longer and more stable geological and climatic history have had a chance to accumulate more species compared to areas, such as high latitudes, that have seen large environmental fluctuations (and hence higher extinctions) in the geological past. Thus, in this case, the main driver of the diversity gradient is higher extinction in the region with fewer species. In terms of dispersal, empirical tests of this hypothesis done at the level of clades and higher taxa argue that the gradient is partially driven by dispersal of taxa from low to high latitudes (i.e. from the regions that are more stable to those rebounding from extinctions; e.g. Hawkins et al. (2006)). Others focusing on species-level gradients highlight the importance of differential speciation and extinction rather than dispersal (e.g. Weir and Schluter, in press). We therefore modeled this hypothesis in two different ways to reflect these views: first, we took dispersal to be greater from the region with low extinction to the one with high extinction (i.e. from low to high latitudes), and second, we took dispersal to be equal in both directions. In our model, this translates to $s_a = s_b$, $x_a < x_b$ and either $d_a > d_b$ or $d_a = d_b$. The main conceptual difference between the Out of the Tropics model and the Wallace model is that in the former origination is higher in low latitudes while in the latter it is the same across latitudes.

Results

The results of all the models clearly show that the average age of the lineages present in a region depends not only on origination and extinction rates but also on the magnitude and direction of dispersal. Of the four models considered here (summarized in Table 2.1), perhaps the most surprising result comes from the pure dispersal model (Model 1), the null model in terms of macroevolutionary rates. In this case, dispersal into one region (R_a) not only creates a difference in diversity between the two regions but also affects the average age of taxa in each region. Thus, greater dispersal into R_a leads to greater differences in taxon richness and in average age between the regions even though the actual diversification rates do not differ (Fig. 2.2). Moreover, the sign of the difference in average age (and to a smaller extent its magnitude) depends on whether we use absolute ages of taxa, such as those derived from the fossil record, or tip lengths, as estimated from a phylogeny. For absolute ages, the more diverse region (R_a) has the younger average age (Fig. 2.2A) but for tip lengths, the less diverse region has the younger average age (Fig. 2.2B).

To understand the observed differences between the regions and why the two metrics behave so differently, it is useful to consider a single tree generated under this model with the added simplification of no extinction (i.e. a pure birth model, Fig. 2.3). The higher richness in R_a not only results from direct immigration but is also magnified by the origination of descendants from those immigrants; descendants in R_b may become immigrants themselves, but descendants in R_a remain endemic to R_a. As for the average ages, when dispersal is high, there are few R_b endemics (because these rapidly become cosmopolitans, i.e. present in both regions) and many R_a endemics (because these arise from both R_a endemics and cosmopolitans). The average age of R_b taxa is, therefore, largely determined by cosmopolitans, and that of R_a taxa by R_a endemics. With the absolute age metric, cosmopolitan lineages are older, on average, than R_a endemics because sufficient time must have elapsed not only for their origination but also for their dispersal: R_a are thus younger on average than R_b taxa. For the tip length metric, on the other hand, cosmopolitan lineages are younger on average than R_a endemics because the time to the most recent branching point in the reconstructed phylogeny is inversely related to the effective speciation rate. Cosmopolitan lineages have a higher effective origination rate because they can speciate in either region, while R_a endemics can speciate only in R_a. Cosmopolitan lineages are therefore younger, making the average for R_a older than R_b. Adding extinction (as in Fig. 2.2) decreases the age difference between the regions under the absolute age metric but increases it under the tip length metric. This is because extinction decreases expected absolute ages but increases expected tip lengths (Chown and Gaston 2000), and the effective global extinction rate

is lower for cosmopolitans than for endemics.

For the macroevolutionary source-sink model (Model 2) the results shown here are consistent with those of Goldberg et al. (2005). In this model, the sink region (R_b) serves as a region of accumulation of older taxa, since older lineages have a greater time-integrated probability of dispersal, and hence R_b has an older average age than the source region (R_a) (Fig. 2.4). Larger per capita dispersal rates increase the probability of younger taxa dispersing from R_a to R_b, thereby reducing the difference in average age, but the sink can never be younger than the source. Similarly, the difference in diversity between the two regions also depends on the rate of dispersal; when dispersal is high it is possible for the two regions to have similar levels of diversity even though the underlying diversification rates are very different. Note that unlike in Model 1, the results are qualitatively the same whether one uses absolute ages (Fig. 2.4A) or tip lengths (Fig. 2.4B).

Our exploration of the OTT model (Model 3) of Jablonski et al. (2006) reveals that when taxa preferentially originate in region R_a and expand their distributions to R_b, R_a always has a younger average age than R_b (Fig. 2.5). The magnitude of the difference in average ages decreases with increasing dispersal into R_b or increasing extinction in R_b. These results are similar to that of Model 2 since the OTT model is a variant of the source-sink model, and they are consistent with the findings of previous empirical analyses (Goldberg et al. 2005; Jablonski et al. 2006). However, our results also show that when extinction is very high in the recipient region (large x_b) or dispersal from R_a to R_b is rapid (large d_a), it is possible for the regional differences in average age or diversity to virtually disappear even though the OTT dynamic still operates (Fig. 2.5). Thus once again, dispersal may cause the two regions to look very similar even when they differ greatly in diversification rates. The qualitative results in this case are the same whether we use absolute ages (Fig. 2.5A) or tip lengths (Fig. 2.5B).

Of our four models, the Wallace model (Model 4) is the only one where the gradient in diversity is driven primarily by the difference in extinction rates between the two regions. In this case, the average age is generally younger in R_b, the region with higher extinction and lower diversity (Fig. 2.6). While this result is intuitively obvious, what is interesting is that under such a scenario, where origination rates do not differ between the regions, the age difference in relatively insensitive to dispersal—there are only small differences between results from balanced dispersal between the two regions or preferential dispersal from R_a to R_b. The maximum difference is observed at moderate extinction rates in R_b; as x_b increases, surviving lineages in R_b get younger, but when extinction in R_b exceeds origination there, immigrant lineages, which tend to be older, contribute relatively more to richness in R_b. Again the qualitative results hold irrespective of

which age estimate we use (Fig. 2.6A & B).

Discussion

Why we should not ignore dispersal

The model results shown above reveal that dispersal not only influences the steepness (i.e. relative differences in richness) of diversity gradients but that movement of taxa between regions can affect our ability to estimate regional origination and extinction rates retroactively. Thus they once again underscore the need to consider the effects of dispersal, in conjunction with origination and extinction, in order to understand the processes that shape spatial patterns of diversity. Our results are consistent with previous empirical analyses that have demonstrated a strong influence of post-origination changes in taxon distributions on the strength of the latitudinal diversity gradient (Goldberg et al. 2005; Jablonski et al. 2006; Wiens et al. 2006), but they also show that failure to include dispersal effects while testing various hypotheses about the drivers of the latitudinal diversity gradient can potentially lead to wrong conclusions.

The clearest example of this comes from Model 1 where two regions with identical origination and extinction rates show a difference in diversity and average age simply due to asymmetric dispersal from one region to another (Fig. 2.2). Thus in this case, retroactive calculations of evolutionary rates based on species richness and taxon age (e.g. using lineage-through-time plots or other methods that rely on ages of living taxa) could lend support to the hypothesis that the difference in diversity is a direct result of differences in diversification rates between the two regions even though in reality the per capita origination and extinction rates are exactly the same. The situation is further complicated by the fact that which region is younger could depend on the age metric used. As shown in Fig. 2.2, if we use the average absolute ages of regions to test whether the region with higher diversity is a cradle or a museum in a macroevolutionary sense (e.g. Gaston and Blackburn 1996), we would conclude that region R_a is a cradle (sensu Stebbins 1974; see Jablonski et al. 2006) using paleontological data (Fig. 2.2A) but a museum using ages derived from molecular phylogenies (Fig. 2.2B). Obviously neither is true given the real model. Conversely, as seen in the out of the tropics model, it is possible for the average ages of two regions or their diversities not to differ substantially even when the origination rate in one is considerably higher than in the other (Fig. 2.5).

The effect of dispersal on regional differences in average age is greater under some models than others, but whether it is measurable in real-world data would depend on the true parameter values, the time resolution of the dataset, and the importance of any other confounding

processes that may be acting. We are therefore certainly not claiming that all previous empirical tests of hypotheses about the latitudinal diversity gradient using taxon ages but without taking into account the effects of dispersal have reached wrong conclusions regarding macroevolutionary dynamics. But our results clearly show that, in principle, dispersal by itself can lead to biased estimates of diversification rates and hence to potentially wrong conclusions about underlying processes. This issue is analogous to the biases that occur when estimating rates of character change without accounting for character-dependent diversification (Maddison 2006). Also, because of these complex interactions between origination, extinction and dispersal and, potentially, the types of age estimates used, we strongly caution against using qualitative predictions about how taxon ages (or evolutionary rate estimates based on such ages) would vary among regions when testing hypotheses about the macroevolutionary dynamics underlying diversity gradients (e.g. Stevens 2006).

To avoid misinterpretations, it is essential to analyze real data using models that account for all three processes rather than separately testing macroevolutionary and biogeographic dynamics as is currently the norm (but see Xiang et al. 2004; Goldberg et al. 2005; Hawkins et al. 2006; Jablonski et al. 2006; Wiens et al. 2006). Analyses that explicitly account for the effects of dispersal either using direct evidence (Jablonski et al. 2006) or through model fitting (Goldberg et al. 2005; Wiens et al. 2006) can separate the contributions of ecological and evolutionary processes in generating spatial gradients in diversity. This approach also allows us to focus better on the actual mechanisms that produce diversity gradients. For example, climate can affect diversity gradients either through its influence on originations and extinctions or through its effects on dispersal and the geographic distributions of taxa. Obviously the actual mechanisms involved in each case are different, and the relative importance of each would depend on whether the diversity gradient seen in a clade is primarily due to differences in macroevolutionary rates or due to biogeographic processes such as dispersal of taxa from one region to another.

Since our focus in this paper was on general models of diversity gradients that integrate macroevolutionary and biogeographic dynamics, we have assumed that all six rates in our models are stochastically constant over time. While this is a widely used approach in macroevolutionary analyses, it does not allow us to explore the effects of time-dependent changes in origination, extinction and dispersal or the effects of phylogenetic selectivities in any of these parameters. Some existing hypotheses about the latitudinal diversity gradient (e.g. the niche conservatism hypothesis of Wiens and Donoghue, 2004) invoke non-random extinctions and dispersals (Hawkins et al. 2006; Wiens et al. 2006), and we certainly do not deny that such processes may play important roles in determining regional diversity levels. However, evaluating such non-neutral or

time-dependent hypotheses requires tests beyond simply comparing average differences in ages or rates. Modeling these more complex dynamics would require specific information about the nature, timing and magnitude of the changes as well as phylogenetic conservatism of ecological and physiological traits, information currently unavailable for most taxa. In addition, those specifics are likely to vary from one clade to another and between different regions. Our results are, therefore, best viewed as quantitative explorations of general and long-standing ideas about the processes structuring diversity gradients, where the neutral assumption is helpful and widely used in empirical analyses (e.g. Flessa and Jablonski 1996; Gaston and Blackburn 1996; Cardillo et al. 2005; Ricklefs 2006b; Weir and Schluter in press).

Are marine and terrestrial diversity gradients driven by different processes?

A number of studies have now quantified how macroevolutionary rates of taxa vary along latitude, and although the results are difficult to compare directly given the variety of methods and types of data used (see Jablonski et al. 2006), they reveal a potentially interesting difference between marine and terrestrial clades. For marine mollusks, paleontological data show that taxa not only preferentially originate in lower latitudes but also tend to persist there over geological time while spreading to higher latitudes (Jablonski 1993; Flessa and Jablonski 1996; Crame 2002; Goldberg et al. 2005; Jablonski et al. 2006). This dynamic, combined with higher extinctions in high latitudes, leads to a latitudinal gradient in diversity (Crame 2002; Jablonski et al. 2006). Under this hypothesis, called the Out of the Tropics (OTT) model by Jablonski et al. (2006), high latitudes represent a macroevolutionary sink and average ages of taxa should increase with latitude (Goldberg et al. 2005. also see Fig. 2.5A). In contrast to marine mollusks, analyses of age distributions of avian taxa, derived from molecular phylogenies, have painted a somewhat different picture with high latitudes harboring more recently derived and hence younger species and clades of birds compared to the tropics (Hawkins et al. 2006; Weir and Schluter in press). This shift towards younger taxa in extratropical latitudes is interesting given that diversification rates of birds appear to be higher in low latitudes (Cardillo et al. 2005; Hawkins et al. 2006; Ricklefs 2006b; Weir and Schluter in press) although whether this is due to higher origination or lower extinction rates remain unclear (Ricklefs 2006). A recent study of North American birds provides evidence that speciation and extinction rates increase with latitude (Weir and Schluter in press) while other more global analyses of bird clades suggest potentially higher origination rates in low latitudes (Hawkins et al. 2006; Ricklefs 2006b).

Since diversity gradients in all taxa, including birds and mollusks, are driven by interactions between the three processes in our models, the first step towards understanding why

latitudinal patterns of taxon ages differ in the two groups would be to simply ask under what combinations of origination, extinction and dispersal would one expect high latitude, low diversity assemblages to be younger than low latitude, high diversity assemblages. Of the models presented here, the source-sink, out of the tropics and Wallace (Models 2–4) all invoke higher diversification rates in one region (R_a) than the other (R_b), analogous to the tropical-extratropical case. Of these three, the only model that can yield a younger average age in the low diversity region (R_b) is the Wallace model where the origination rates are similar in the two regions (Fig. 2.6). Neither the source-sink model nor the OTT model, both with higher origination rates in the source region, mimics the empirical trend seen in New World birds where temperate latitudes are enriched in younger clades and species compared to the tropics (Hawkins et al. 2006; Weir and Schluter in press). In the OTT model, increasing dispersal or the extinction rate in the region with the lower diversification rate makes the average ages of the two regions more similar, but it cannot make the lower diversity region younger (Fig. 2.5). Unlike in the pure dispersal model (Model 1), the qualitative results in these cases do not change whether one uses absolute or relative age estimates (Figs. 2.4–2.6), so the observed difference between birds and marine mollusks is unlikely to be due to the use of phylogenetic age estimates for birds and fossil-based absolute ages for marine mollusks.

In combination, these results suggest that for birds, the observed latitudinal difference in taxon ages and/or diversification rates either reflects higher extinction in the extra-tropical regions rather than higher origination in lower latitudes (Weir and Schluter in press) or it reflects time inhomogeneous processes including selective extinctions and dispersal of taxa into the extra-tropics (Hawkins et al. 2006). In either case, the situation appears to be different from that in marine mollusks where the hypothesis of a latitudinal gradient in origination rates is supported by analyses of taxon age distributions using time-homogenous models such as those discussed here (Goldberg et al. 2005) or direct evidence from the fossil record (Jablonski 1993; Jablonski et al. 2006). Furthermore, in marine mollusks, most taxa show preferential origination in the tropics followed by the expansion of geographic ranges into high latitudes (Goldberg et al. 2005; Jablonski et al. 2006) while in birds, such northward expansion of geographic ranges apparently only involves select clades (Hawkins et al. 2006). In fact, the current data are even consistent with the possibility that the latitudinal gradient in diversification rates in birds, at least at the species level, is driven solely by high extinctions in temperate and polar regions, with no latitudinal difference in origination rates and no spatial bias in dispersal (Fig. 2.6, also see Weir and Schluter in press).

Given that most of our existing insights about the macroevolutionary and biogeographic

dynamics underlying the latitudinal diversity gradient come from terrestrial birds and mammals and marine mollusks (see Jablonski et al. 2006 for review), it is obviously premature to conclude that such dynamics differ in important ways between the land and the sea; the differences discussed above could simply reflect clade-specific differences. However, other independent observations also suggest that there could be interesting land-sea differences in macroevolutionary and biogeographic dynamics.

Extinctions of species in extratropical regions due to Pleistocene glacial cycles, featured so prominently in discussions of the latitudinal diversity gradient on land (e.g. Wallace 1878; Svenning 2003; Hawkins et al. 2006; Weir and Schluter in press), may be far less important for marine taxa. While local extinctions and range expansions of marine mollusks in response to glacial-interglacial cycles are well documented (Valentine and Jablonski 1993), there is little evidence for widespread global extinctions of species during the middle or late Pleistocene (see Roy et al. 1996; Roy and Pandolfi 2005 for review). Pliocene and early Pleistocene extinctions are well documented in many marine groups, but the timing and spatial patterns of these extinctions are complex and they involved both tropical and extra-tropical assemblages (see Smith and Roy 2006). This difference between marine and terrestrial groups in the timing, magnitude and nature of putative extinctions (evidence for extinctions driven by Pleistocene glacial cycles in many terrestrial groups is indirect due to the lack of a well preserved fossil record) could reflect the difference in the nature of the two habitats. On land, Pleistocene glaciers completely covered large areas making them uninhabitable, and it is reasonable to assume that species that were restricted to those areas went extinct. The oceans, on the other hand, are three dimensional and except for some very shallow basins, the effects of Pleistocene glaciations would have been manifested largely as changes in temperature and ocean circulations rather than total habitat destruction. So it may be reasonable to postulate that, on average, marine species would have been less likely to go globally extinct due to the Pleistocene glaciations than would terrestrial species. This is particularly true given the wide geographic distributions of many marine taxa and the observed correlation between bathymetric range and geographic range in marine species (Harley et al. 2003).

Both the magnitude and pace of environmental variability also differ between land and sea. Long term measurements have revealed that in the ocean, variance in sea surface temperature increases with the temporal scale of observation (i.e. it is red-shifted) while on land the variance stays relatively stable over time (Steele 1985; Vasseur and Yodzis 2004; Halley 2005). This implies that terrestrial organisms have to adapt to a different rhythm of environmental variation than their marine counterparts (Steele 1985, Halley 2005), which could lead to differences in

population-level responses to environmental change. Similarly, long distance larval dispersal and recruitment dynamics, so critical for marine population biology, has virtually no analog in terrestrial animal ecology (Paine 2005). So it is not surprising that marine ecologists tend to view physical oceanographic processes as being important drivers of many ecological and biogeographic patterns, from geographic distributions of species (Gaylord and Gaines 2000) to the structure and composition of communities (Gaines and Roughgarden 1985; Connolly and Roughgarden 1998). Thus for marine organisms, traits such as larval mode that determine the ability of an organism to disperse, often passively taking advantage of oceanographic flows, play an important role in macroevolution (Jablonski 1986; Jablonski and Hunt 2006). Again, analogs of this among terrestrial animals appear to be few.

Of course, it remains an open question whether any of these differences are relevant for understanding the observed differences in macroevolutionary dynamics underlying the latitudinal diversity gradient in marine versus terrestrial clades. But the first step towards resolving the issue would be to analyze latitudinal trends in origination, extinction and dispersal rates in marine versus terrestrial clades using the same models and similar types of data (i.e. paleontological or phylogenetic age estimates). Only such standardized comparative analyses can reveal the parameter or combination of parameters that leads to the observed differences, thereby facilitating the search for the underlying processes.

Challenges that remain

While the models presented here highlight the role of dispersal in generating spatial gradients in diversity, estimating past trajectories and rates of dispersal for real taxa remains a major challenge. Even for clades with a good fossil record, quantifying how distributions of taxa change over time poses a difficult problem because of uneven sampling (Jablonski et al. 2006). For clades without a good fossil record, quantifying biogeographic histories of taxa generally involves reconstructing ancestral states using phylogenies (e.g. Ronquist 1997; Ree et al. 2005; Wiens et al. 2006), a potentially useful approach but not immune to the general problems inherent in reconstructions of ancestral states (e.g. Cunningham et al. 1998). Furthermore, estimating the effects of dispersal requires comprehensive phylogenies that include taxa from multiple regions rather than region-specific phylogenies. Obviously the former presents a much larger analytical and logistical challenge although such global phylogenies are increasingly becoming available for smaller clades (e.g. Xiang et al. 2004; Wiens et al. 2006). Similarly, estimating parameters by applying dynamic, spatial models to data on extant taxa is possible for simple models and fossil-based phylogenies that use absolute ages (Goldberg et al. 2005), but it is much harder for more

detailed, parameter-rich models and molecular phylogenies.

Extinction is another critical component of many hypotheses about present-day diversity gradients (e.g. Wallace 1878, Latham and Ricklefs 1993; Svenning 2003; Hawkins et al. 2006), and our results again underscore the importance of extinction. Yet robust estimates of extinction rates remain scarce for most groups of living organisms. Even for groups such as marine invertebrates where global extinction rates of higher taxa are well known (see Jablonski 1995, 2005), relatively few studies have quantified how regional extinction rates vary over time, especially at the species level (see Smith and Roy 2006). Obviously, hypotheses about diversity gradients cannot be properly tested without reliable estimates of how extinction rates of species and/or lineages have changed along latitude. Generating reliable estimates of past extinction rates for groups with a fossil record remains a challenge, again because of spatial biases in sampling and preservation (Jablonski et al. 2006; Valentine et al. 2006), and it is even more difficult for groups without a fossil record unless one assumes that extinction rates have been stochastically constant (Nee et al. 1994). This assumption may be violated by empirical data showing not only temporal variations in rates but also direct and indirect evidence for taxonomic and ecological selectivity (e.g. Todd et al. 2002; Paradis 2004; Smith and Roy 2006, Latham and Ricklefs 1993; Svenning 2003). Whether such variations are large enough to invalidate the assumption of stochastically constant extinction rates over long periods of time or across large regions inherent in many empirical analyses (e.g. Flessa and Jablonski 1996; Gaston and Blackburn 1996; Cardillo et al. 2005; Ricklefs 2006b; Weir and Schluter in press) or in models such as ours remains to be seen.

Finally, it remains an open question whether there are general rules that determine latitudinal and other diversity gradients in all taxa. Given the complex interactions between origination, extinction and dispersal seen in the models presented here, we suspect that the relative importance of macroevolutionary versus ecological and/or biogeographic processes in generating diversity gradients is likely to be different for different clades and perhaps for terrestrial and marine organisms. However, the issue cannot even be addressed unless future studies of diversity gradients are based on consistent metrics and analytical methods. Unlike many questions in ecology and evolution, at present there are no standard models or statistical methods that are widely used for analyses of diversity gradients (see Jablonski et al. 2006, for a review), making it impossible to compare the results of individual studies. Furthermore, some of the existing analyses of diversity gradients focus on the species level while others emphasize clade-level dynamics (see Jablonski et al. 2006; Mittelbach et al. 2007). Given the different time scales involved, we think it is unlikely that the macroevolutionary and biogeographic dynamics are the

same across different levels of the phylogenetic hierarchy. Species-level trends are more likely to bear a signature of Plio-Pleistocene environmental changes while the higher taxon-level patterns have origins in deeper geological times under very different climate regimes.

Biologists and naturalists have wondered about the causes of latitudinal and other gradients in diversity for close to two centuries, but the explanations still elude us, despite increasing availability of phylogenetic and paleontological data and advances in analytical methods in recent decades. Solving the problem will require using this information and analytical methods in a consistent manner across different clades within the framework of quantitative models that include both macroevolutionary and biogeographic processes.

Acknowledgements
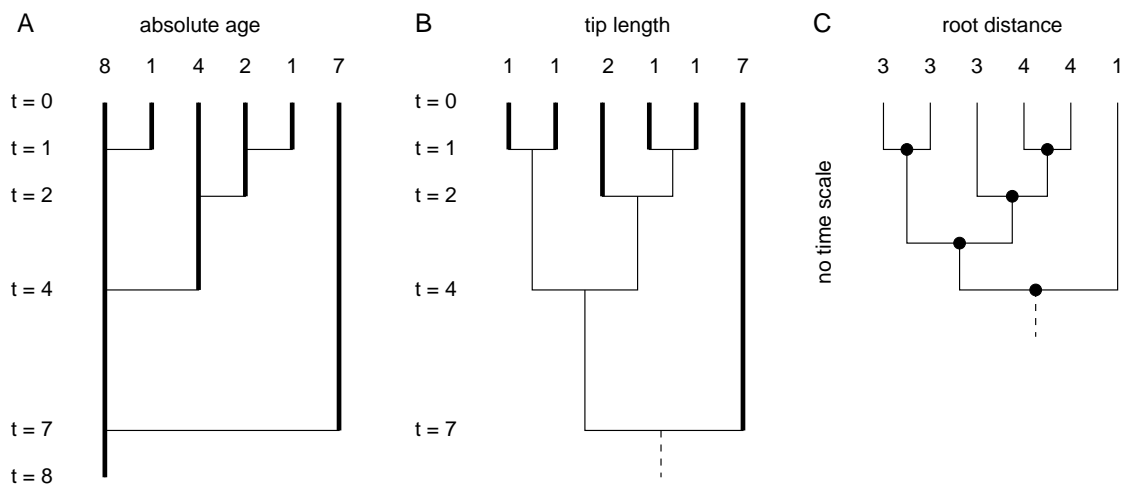
Figure 2.1: Illustrations of the three age metrics on a simple hypothetical tree. The number above each tip denotes the age of that taxon. (A) Absolute age is the duration from the present time to the time of origination of a lineage. A good fossil record is required to obtain the time of origination. The absolute age of a taxon is not affected by origination or extinction events of other taxa so sister taxa can have different absolute ages. (B) Tip length is the duration from the present time to the most recent node (i.e. origination event that appears in the reconstructed phylogeny) of the lineage. Tip lengths (and lengths of internal branches) can be obtained from molecular phylogenies, but the length of any one branch can be affected by origination and extinction of other taxa. (C) Root distance is simply the number of nodes between a tip and the root of a tree. Shorter tip lengths generally (but not perfectly) correspond to greater root distances. Note that the tree representations used for these metrics, from left to right, contain decreasing amounts of information.

Model 1: pure dispersal
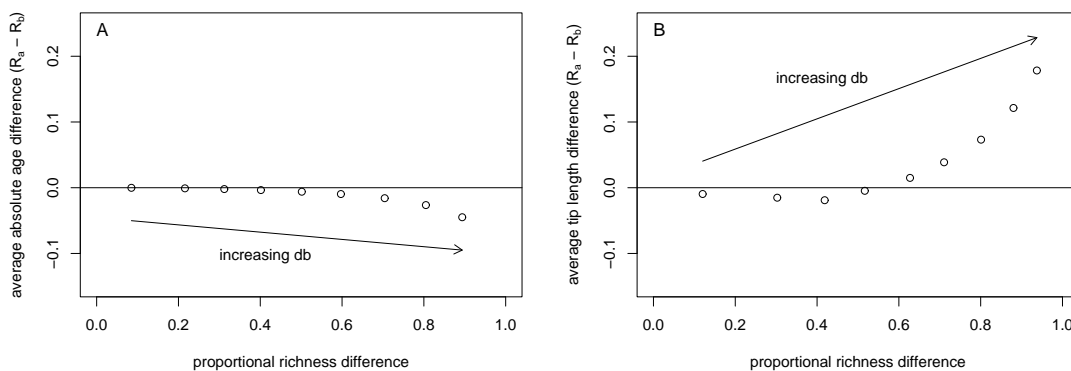
Figure 2.2: Differences in average age between the two regions under Model 1, the pure dispersal model. The x-axis shows the proportional difference in taxon richness (R_a richness $-$ R_b richness) / (R_a richness $+$ R_b richness): R_a is always the more diverse region, so x values can range from 0 to 1. The y-axis shows the difference in age between the regions (R_a average age - R_b average age): when this is positive, R_a is older, and when it is negative, R_a is younger. The left panel (A) shows age differences using the absolute age metric, and the right panel (B) shows age differences using the tip length metric (see Fig. 2.1). Parameter values for all points are $s_a = s_b = 1.0$, $x_a = x_b = 0.5$, $d_a = $ 1e-6. In each panel, from left to right, the points show values for $d_b = 0.02$, 0.06, 0.10, 0.15, 0.23, 0.35, 0.60, 1.20, 4.00; these values were chosen for roughly equal spacing in proportional richness difference. With either age metric, higher dispersal causes large diversity differences and moderate average age differences between the regions, but the two age metrics give age differences of opposite sign (see Fig. 2.3 and the text for explanation).

		by geographic state			by region	
		AB	A	B	A+AB	B+AB
number of tip species:		6	10	3	16	9
average absolute age (left tree):		0.863	0.385	0.179	0.564	0.635
average tip length (right tree):		0.151	0.321	0.113	0.257	0.138
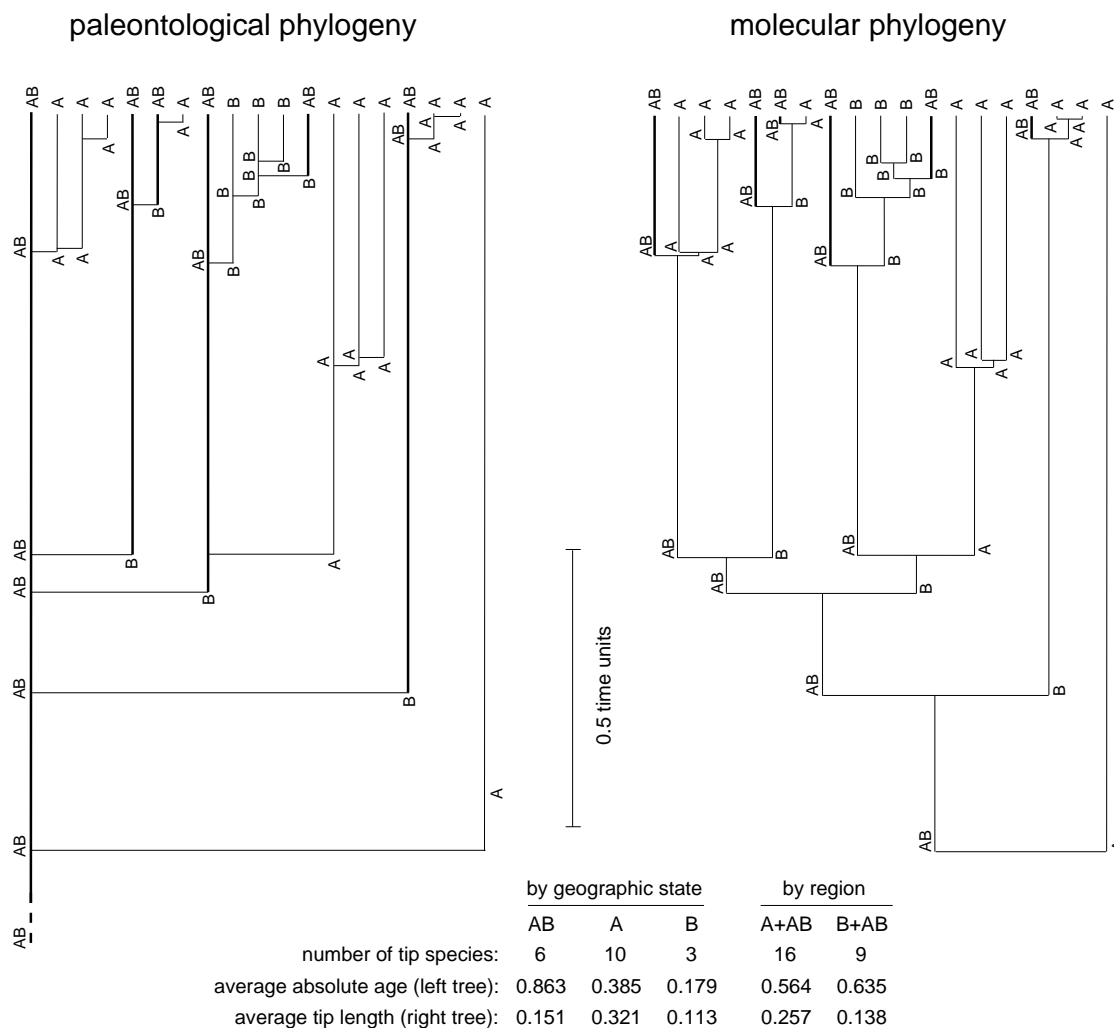
Figure 2.3: A tree simulated under Model 1 ($s_a = s_b = 1.0$, $x_a = x_b = 0$, $d_a = 0$, $d_b = 4$, elapsed time $= 2$) illustrating the richness differences between regions and the opposite sign of the difference in average age under the two different age metrics (Fig. 2.2). This particular tree is reasonably representative of these parameter values; the expected number of species (accounting for dispersal, which increases the effective overall speciation rate) is 5.9 cosmopolitans, 12.1 R_a endemics and 1.5 R_b endemics, totaling 19.5 species. Much of the diversity in R_a results from lineages that originated in R_b and then immigrated to and left descendants in R_a. As shown in the simple calculations below the tree, the average age in R_b is dominated by cosmopolitan lineages (present in both R_a and R_b and shown in bold) while the average age in R_a is influenced more by endemics. With the absolute age metric (left), cosmopolitan taxa are older, on average, than R_a endemics, whereas with the tip length metric (right), cosmopolitan taxa are younger than R_a endemics.

Figure 2.4: Differences in average age between the two regions under Model 2, the source-sink model. Axes and panel layout are the same as in Fig. 2.2. Parameter values are $s_a = 1.0$, $s_b = 1e-6$, $x_a = x_b = 0.5$, $d_b = 1e-6$, $d_a = 3.00, 2.05, 1.50, 1.10, 0.81, 0.60, 0.42, 0.29, 0.18, 0.08$. In this case both age metrics show similar behavior. The more diverse source region (R_a) is always younger than the sink region (R_b), though the diversity and age differences decrease with larger dispersal rates.
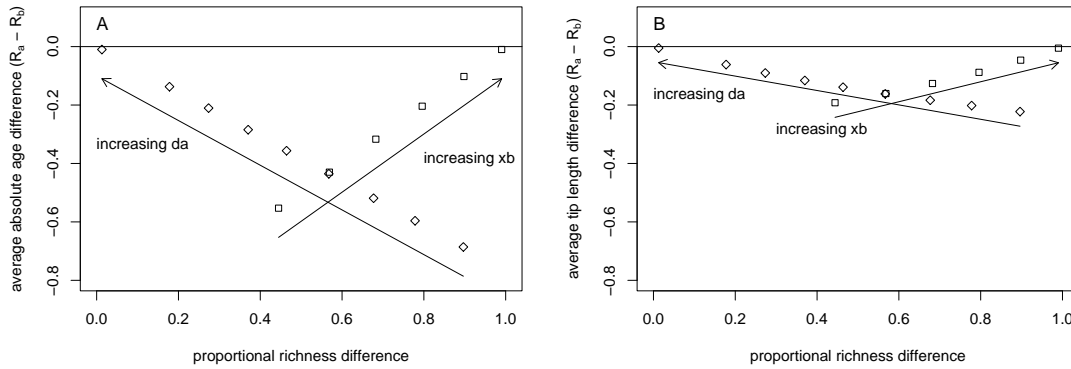
Figure 2.5: Differences in average age between the two regions under Model 3, the OTT model. Axes and panel layout are the same as in Fig. 2.2. Parameter values are $s_a = 0.8$, $s_b = x_a = d_b = 1e{-}6$. For the squares, $d_a = 1.00$, $x_b = 0.\ 001$, 0.52, 1.35, 3.10, 8.00, 100; for the diamonds, $x_b = 0.5$, $d_a = 100$, 6.00, 3. 45, 1.50, 0.99, 0.62, 0.37, 0.15. Both age metrics show similar behavior in this case. As in Model 2 (Fig. 2.4), the more diverse region is always younger, though diversity and age differences decrease with larger dispersal rates. Greater extinction in the recipient region increases the diversity difference and decreases the age difference because recent immigrants are younger and are more likely to survive there.
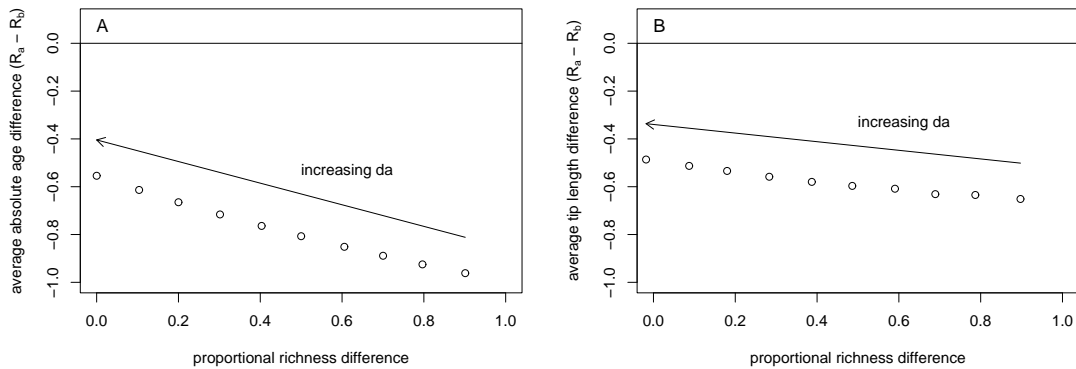
Model 4: Wallace hypothesis
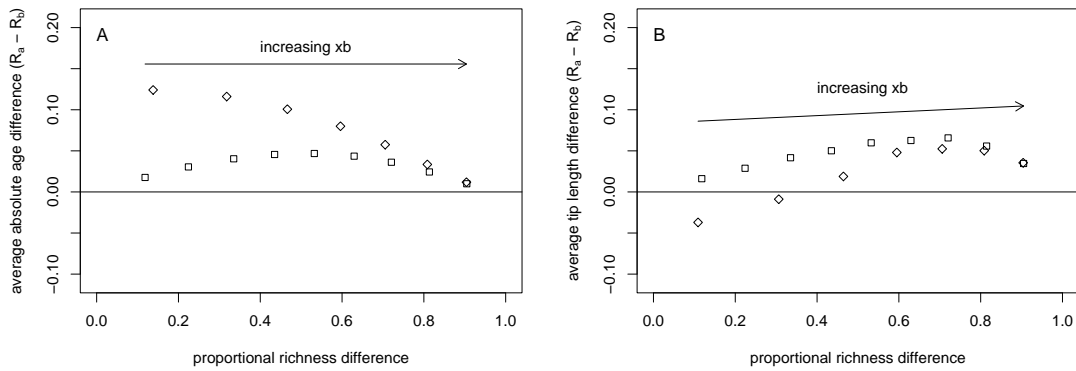
Figure 2.6: Differences in average age between the two regions under Model 4, the Wallace hypothesis model. Axes and panel layout are the same as in Fig. 2.2. Parameter values are $s_a = s_b = 0.6$, $x_a = 1e-6$, $d_a = 0.5$. For the squares, $d_b = 0.5$, $x_b = 0.13$, 0.26, 0.42, 0.60, 0.83, 1.16, 1.65, 2.60, 5.25; for the diamonds, $d_b = 1e-6$, $x_b = 0.42$, 0.60, 0.83, 1.16, 1.65, 2.60, 5.25. The age metrics show slightly different behavior, but for both, species are generally younger in the less diverse region. The magnitude of the age difference is relatively insensitive to the amount of extinction in R_b or dispersal from R_a to R_b.

Table 2.1: Summary of the parameters used in each model discussed here.

Model	Name	Origination	Extinction	Dispersal
Model 1	Pure dispersal	$s_a = s_b$	$x_a = x_b$	$d_a \ll d_b$
Model 2	Macroevolutionary source-sink	$s_a \gg s_b$	$x_a = x_b$	$d_a \gg d_b$
Model 3	Out of the tropics	$s_a \gg s_b$	$x_a \ll x_b$	$d_a \gg d_b$
Model 4	Wallace	$s_a = s_b$	$x_a \ll x_b$	$d_a \gg d_b$ or $d_a = d_b$

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Part II

Coevolutionary Models

Chapter 3

Ecological and reproductive character displacement on an environmental gradient

ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT ON AN ENVIRONMENTAL GRADIENT

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Abstract.—Character displacement, in which coevolution of similar species alters their phenotypes, can be difficult to identify on the basis of observational data alone. In two-species systems, the most commonly identified (i.e., classic) resulting pattern is greater phenotypic difference between species in sympatry than allopatry. We show that restricting studies to this pattern may exclude many instances of character displacement, particularly in the presence of spatial environmental gradients. We present four spatial models of character displacement in quantitative traits affecting competition and hybridization between the species. Our models highlight the connections between range limits and character displacement in continuous space. We conclude that the classic pattern is less likely to occur for a trait affecting resource acquisition than for a trait affecting mate choice. We also show that interspecific hybridization (when hybrids are inviable), even in very small amounts, has marked effects on the shape and stability of borders between species and the nature of character displacement. A survey of the empirical literature shows that character displacement studies often lack analysis of spatial phenotype and abundance data. We recommend more careful spatial sampling in character displacement studies, and we illustrate how comparison of clines in mean phenotype in sympatry and allopatry can be used to suggest the action of character displacement.

Key words.—Character displacement, competition, gene flow, hybridization, quantitative trait, spatial coevolution, species borders.

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Coevolution of interacting species can cause their phenotypes to diverge, because of either resource competition or mate choice and interspecific hybridization. Understanding the importance of and the conditions that facilitate such divergent coevolution will illuminate the role of competition in adaptive radiation (Schluter 2000a), the relative importance of species interactions versus neutral dynamics (Hubbell 2001) in determining community structure, and the role of selection in creating prezygotic isolation between newly formed species (Waage 1979; Geyer and Palumbi 2003; Coyne and Orr 2004). Considering coevolution of ecological and reproductive traits in the same context, as we do here, also emphasizes the potential importance of hybridization in shaping patterns traditionally seen as ecological rather than evolutionary.

We consider the coevolution of traits that affect resource competition and mate choice between species with complete postzygotic isolation. We use the term ''ecological character displacement'' to describe the process in which a trait affecting resource competition evolves due to the presence of a competing species, consistent with older and current definitions (e.g., Grant 1972; Schluter 2000b, ch. 4). We use the corresponding term ''reproductive character displacement'' to describe the same process for a trait affecting mate choice, and this definition has been used previously (Grant 1972; Butlin 1987). However, the term now more often describes the pattern of greater prezygotic isolation in sympatry than in allopatry that may result from this process or, if there is gene flow between the species, from the more general process of reinforcement of prezygotic isolation between species (Howard 1993; Noor 1999; Lemmon et al. 2004). This confusion of terminology in the literature is unfortunate, but we use a single term, ''character displacement,'' to describe the coevolutionary process in both ecological and reproductive traits to emphasize that different aspects of this process can be treated in the same context. We refer to the pattern of greater phenotypic difference between species where they occur in sympatry as the ''classic pattern'' of character displacement because it was Brown and Wilson's (1956) original definition of the term. The coevolutionary process itself is what is of interest, and the classic pattern is only one among many patterns that may result from this process (Lemmon et al. 2004).

The greatest challenge in studying character displacement is identifying its occurrence in nature. Direct identification of character displacement at a single locality is generally impossible because it requires simultaneously knowing the phenotype of a species both in the presence and in the absence of another species under otherwise identical conditions. Identifying character displacement by experimentally adding or removing species or changing environmental conditions is sometimes feasible (Pfennig and Murphy 2000; Schluter 2000a; Bolnick 2004) and can provide strong evidence that character displacement is occurring. Far more common, however, is using purely observational evidence to infer the action of character displacement. Such evidence often takes the form of exaggerated divergence in sympatry (the classic pattern) (e.g., Brown and Wilson 1956; Fjeldså 1983; Røskaft and Järvi 1992; Adams 2004) or trait overdispersion (also known as community-wide character displacement, in which a collection of species in sympatry have trait values that differ from each other more than is expected by chance, and connected to Hutchinson's [1959] size ratios; e.g., Pearson 1980; Dayan et al. 1990; Marchinko et al. 2004). Other observational methods include species-for-species matching (in which independently evolved species sets show similarities in their trait values; Schluter 1990; Losos et al. 1998); spatial analysis of phenotypic values (Dunham et al. 1979; Hansen
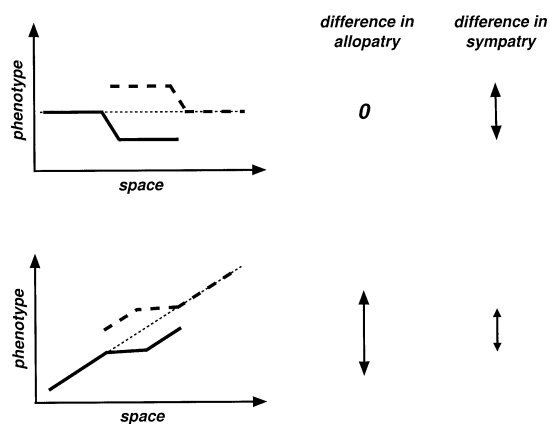
FIG. 1. Differences in sympatry and allopatry. When the optimum phenotype is constant over space, character displacement gives rise to the classic pattern of greater divergence in sympatry than in allopatry (top). When the optimum phenotype increases monotonically over space, phenotypes may differ more in allopatry than in sympatry even though character displacement is occurring (bottom). The thick solid lines show the phenotype of one species, the thick dashed lines show the phenotype of another species, and the thin dotted lines show the optimum phenotype.

et al. 2000); comparison of trait values with abundances (Tynkkynen et al. 2004); or the use of phylogenetic (Losos 1990; Radtkey et al. 1997), historical (Diamond et al. 1989), or fossil (Eldredge 1974; Kellogg 1975) information. Of these forms of observational evidence, the first is the most commonly used (see Theory and Practice below), probably because it requires only two species.

Simply observing one of these patterns, however, is not sufficient to conclude that character displacement is its cause, and Schluter and McPhail (1992) and Waage (1979) describe alternatives that must be considered and ruled out. Put briefly, the character must be relevant to the process being considered (competition or mate choice); displacement in sympatry must not be just an extension of conditions in allopatry; and chance, plasticity, species sorting, and environmental differences (in resource availability, mate perception, or other selective forces on the character) must be eliminated.

Finding systems that exhibit character displacement therefore consists of two steps. First, potential systems must be identified, typically based on observational evidence. Second, of such potential systems, those in which factors other than character displacement explain the observed patterns must be eliminated. Our focus here is on broadening the first of these two steps.

A common situation in which character displacement occurs in two species, but the classic pattern may not be observed, arises along a spatial environmental gradient. The classic pattern of character displacement occurs when the optimum phenotype of each species is constant across space, and one of the criteria for ruling out the effects of environmental differences is thus met. Character displacement on an environmental gradient is illustrated qualitatively in Figure 1, where it is compared with the classic pattern, and it is

clear that an environmental gradient can cause species to differ more in allopatry than in sympatry, even when character displacement is occurring. This outcome was obtained by Lemmon et al. (2004), who modeled the evolution of three single-locus traits (male trait, female preference, and hybrid incompatibility) and by Case and Taper (2000), who modeled a polygenic trait affecting resource acquisition.

We will discuss these models in more detail below (see The Models), but we emphasize here that in the model of Case and Taper (2000), a spatial environmental gradient appears to be essential for the formation of a stable border between the species in continuous space and, thus, to the possibility of observing character displacement. This result suggests that character displacement may be common on environmental gradients but that it would likely be missed by the standard methods of detection.

Discussing species borders and character displacement in the same context also emphasizes an important biogeographic aspect of observing character displacement in two-species systems. Its identification requires both areas of sympatry and allopatry for each species. In island systems or those where space is otherwise disjunct (including some famous examples of character displacement; Lack 1947; Schoener 1970; Schluter and McPhail 1992), this requirement may be met by different islands, some of which have only one of the species and one or more of which have both. In continental systems (or more generally, those where space is continuous rather than disjunct), the requirement of regions of both allopatry and sympatry becomes identical with the requirement of a stable border between the species. Studies of character displacement and range limits therefore become closely linked.

We expand on the earlier models of Case and Taper (2000) and Lemmon et al. (2004), by analyzing and comparing models of ecological and reproductive character displacement. We find that the qualitative behavior of these two processes can be quite different, and that a trait affecting assortative mating is much more likely to exhibit the classic pattern of character displacement than is a trait affecting resource acquisition. We also investigate how the formation of inviable hybrids can interact with resource competition to affect the patterns produced by character displacement. Both competition and hybridization may depend on phenotypic values, such that individuals of more similar phenotypes may compete more strongly and be more likely to mate with each other. Each process may thus generate frequency-dependent disruptive selection, but the nature of this selection differs. Under competition along a broad resource axis individuals with rarer phenotypes have higher fitness, while under hybridization (when interspecific hybrids are less fit) fitness is higher for individuals of the more common species. Coexistence is thus more likely under competition than under hybridization, and this will influence the shape and stability of borders between species and the pattern of character displacement. By considering the joint operation of ecological and reproductive character displacement, we also show how the processes may interact and illustrate how observations may be able to distinguish them.

Models are potentially useful for aiding the identification of character displacement, and they also can clarify how evo-

E. E. GOLDBERG AND R. LANDE

lution of phenotypes and changes in population size determine the feasibility and resulting patterns of character displacement. A review of the literature, however, shows that spatial data on population abundance and phenotype are not usually considered in studies of character displacement. Therefore, we suggest some general methods for collecting and analyzing data that may allow detection of many more systems exhibiting character displacement.

THE MODELS

We describe four different but related models for ecological and reproductive character displacement. The first deals only with ecological character displacement and is essentially the model of Case and Taper (2000), extended to include hybridization independent of phenotype. The second is a model of reproductive character displacement; it differs from Lemmon et al. (2004) by dealing with a single polygenic trait affecting assortative mating and in assuming complete inviability of hybrids. Because we consider only situations in which hybrids are completely inviable, our results relate to reinforcement of prezygotic isolation in the broad sense (Howard 1993; Servedio and Noor 2003) but not the strict sense (Butlin 1987). The third model considers the evolution of a character affecting both resource acquisition and mate choice. The fourth describes the simultaneous evolution of two genetically uncorrelated characters, one ecological and the other reproductive. We derive expressions for the dynamics of population size and the evolution of mean phenotype across space. Analytic solutions are not possible, so we illustrate the behavior of the models by iteratively evaluating the systems numerically. The results all concern stable equilibrium patterns, where the system does not change with further iteration.

Details Relevant to All Four Models

Each model consists of coupled difference equations describing the changes in population size and mean phenotype of two species across space. We assume that each species has discrete, nonoverlapping generations of the same length. Previous models upon which ours are based (Pease et al. 1989; Kirkpatrick and Barton 1997; Case and Taper 2000) treat time and space as continuous, but we use discrete time (in units of generations) and space to facilitate derivation of selection and hybridization formulas and their numerical analysis. We consider only one-dimensional space, although the methods are straightforward to generalize to two dimensions. We take the population size of species i ($i = 1$ or 2) at spatial location x and time t to be a continuous variable, $n_i(x, t)$, and we assume that each population grows logistically with intrinsic rate of increase r and nominal carrying capacity K. For simplicity, we take these and other parameters to be the same for each species (we do, however, briefly consider species differences in the Discussion) and constant over space and time. We assume a constant sex ratio at birth with no sexual dimorphism, and therefore we do not keep track of the number of males and females in each population.

We model the evolution of a phenotypic trait, z, in each species. (In model 4, we consider two traits, denoted y and

z.) We assume the trait is quantitative (polygenic) and has, in each species i, a Gaussian distribution of phenotypes (and breeding values), $p_i(z, x, t)$, with mean $\bar{z}_i(x, t)$ and variance $\sigma_{\bar{z}}^2$. The phenotypic variance may change as selection proceeds within a generation, but we assume it is maintained at a constant value at the start of each generation. These assumptions are reasonable if the genetic variance is maintained by a balance between mutation, recombination, and stabilizing selection, with dispersal having only a small effect (Slatkin 1978; Lande 1982; Barton 1999).

The phenotypic trait is subject to frequency-dependent selection arising from resource competition or hybridization. The environment imposes stabilizing natural selection toward an optimum value, $\theta(x)$, that may vary over space. The strength of stabilizing selection is determined by the parameter σ_s^2, such that natural selection decreases the Malthusian fitness of an individual of phenotype z by the amount $(\theta - z)^2/(2\sigma_s^2)$.

We employ the assumptions of each model to construct mean Wrightian fitness functions, $\bar{W}_i(x, t)$, for each species at each location at each time; these mean fitness functions are then used to determine changes in population size and mean phenotype.

We assume that dispersal occurs once per generation and that individuals move only to neighboring positions in space. Each generation, some fraction, δ, of individuals moves to each adjoining spatial cell. In the limit of infinitesimal temporal and spatial divisions, this discrete process becomes the diffusion process used in previous related models (Pease et al. 1989; Kirkpatrick and Barton 1997; Case and Taper 2000). The changes in population size and mean phenotype can be written, omitting the time dependence in $n_i(x, t)$ and using Δ to represent change per generation, as

$$\Delta n_{i,disp}(x) = (1 - 2\delta)n_i(x) + \delta n_i(x - 1) + \delta n_i(x + 1)$$
$$- n_i(x) \quad \text{and} \tag{1a}$$

$$\Delta \bar{z}_{i,disp}(x) = \frac{1}{n_i(x) + \Delta n_{i,disp}(x)}$$
$$\times [(1 - 2\delta)n_i(x)\bar{z}_i(x) + \delta n_i(x - 1)\bar{z}_i(x - 1)$$
$$+ \delta n_i(x + 1)\bar{z}_i(x + 1)] - \bar{z}_i(x). \tag{1b}$$

We consider here distinct but closely related species. Heterospecific individuals may mate with each other if they are in the same spatial location, but we assume that no hybrid offspring are produced; hybrid embryos are inviable. Such cryptic hybridization may go undetected in natural populations because hybrid phenotypes are not seen, but it often occurs between closely related species (Dobzhansky 1951; Coyne and Orr 1989; Arnold 1997; McCarthy 2006), and, as we will show, it may have a substantial impact on species' borders and character displacement.

When modeling the effects of survival, reproduction, and dispersal, we assume that the events in each time unit happen in sequence. First, competition and stabilizing selection occur, then reproduction (including mate choice and hybridization), and finally dispersal of the newly produced juveniles. The population is censused in the middle of each gen-

eration, after dispersal. We use asterisks on n_i and $\bar{z}_i$ to denote intermediate values of population size and mean phenotype: a single asterisk indicates that natural selection through competition and stabilizing selection has acted, and a double asterisk indicates that reproductive fitness through mating and hybridization has acted. After dispersal, the cycle repeats and the superscripts are dropped.

We will use the terms ''environmental gradient'' to refer to the change in environmental conditions and hence optimum phenotype over space, ''cline'' to refer to the pattern of mean phenotype of each species across space, and ''border'' to indicate a boundary of declining numerical abundance near the edges of the species' geographic ranges.

Each of the models we present can be reduced, by eliminating one of the species and thus interspecies interactions, to the single-species model of Kirkpatrick and Barton (1997) in which steep environmental gradients allow the range of the species to be limited solely by gene flow. Although it is possible that two such range limits could abut, we do not consider such steep gradients because we are interested in the coevolution of species at their borders. When gene flow alone (and therefore not species interactions) limits the ranges, character displacement is unlikely to be important.

Model 1: Ecological Character Displacement

In this model, resource acquisition depends on a phenotypic character, with individuals of more similar phenotypes competing more strongly. This model is based on that of Case and Taper (2000) but also includes hybridization independent of phenotype.

Formulation

Using the results of Case and Taper (2000, their eq. 7), we begin with their expression for the mean Malthusian fitness of species i, $\bar{m}_i^*(x, t)$ (using the subscript j to refer to the other species):

$$\bar{m}_i^* = r - \frac{r}{K}\sqrt{\frac{\sigma_u^2}{\sigma_u^2 + \sigma_z^2}}\left\{n_i + n_j\exp\left[\frac{-(\bar{z}_i - \bar{z}_j)^2}{4(\sigma_u^2 + \sigma_z^2)}\right]\right\}$$
$$- \frac{\sigma_z^2 + (\theta - \bar{z}_i)^2}{2\sigma_s^2}. \quad (2)$$

This function contains the effects of population growth (terms with r) with density dependence (n_i term for intraspecific competition, n_j term for interspecific competition) and stabilizing selection (terms with denominator σ_s^2). The Gaussian resource utilization function has width (analogous to the standard deviation) σ_u: smaller values indicate increased resource specialization of phenotypes (Roughgarden 1979; Taper and Case 1985; see also Slatkin 1980). In eq. (2) and subsequently, we do not write explicitly the dependences on x and t in order to improve readability.

We express our discrete-time model of population growth, density dependence, and stabilizing selection as

$$n_i^* = \exp(\bar{m}_i^*)n_i, \quad (3)$$

where we have approximated the mean Wrightian fitness as

$$\bar{W}_i^* = \exp(\bar{m}_i^*). \quad (4)$$

This approximation (Crow and Kimura 1970, ch. 1) is appropriate when the population growth rate is low enough that the dynamics are not cyclic or chaotic (May 1973).

The mean Wrightian fitness also can be used to find the altered values of mean phenotype after this first phase:

$$\bar{z}_i^* = \bar{z}_i + h^2\sigma_z^2\frac{\partial(\ln \bar{W}_i^*)}{\partial\bar{z}_i}$$
$$= \bar{z}_i + h^2\sigma_z^2\left\{\frac{rn_j\sigma_u(\bar{z}_i - \bar{z}_j)}{2K(\sigma_u^2 + \sigma_z^2)^{3/2}}\exp\left[\frac{-(\bar{z}_i - \bar{z}_j)^2}{4(\sigma_u^2 + \sigma_z^2)}\right] + \frac{\theta - \bar{z}_i}{\sigma_s^2}\right\}. \quad (5)$$

Despite the frequency dependence of the individual fitness function (see Case and Taper 2000, their eqs. 2 and 3), use of the selection gradient is justified because the symmetry of the competition function and phenotypic distribution ensure that selection has no net intraspecific frequency dependence (Lande 1976; Case and Taper 2000). However, competition does generate interspecific frequency dependence in phenotypic evolution.

Next, we model the effects of phenotype-independent hybridization. In this phase, the fitness of an individual of phenotype z, $W_i^{**}(z, x, t)$, is the probability that it chooses as a mate a member of its own species, from all those individuals available at its location:

$$W_i^{**}(z) = \frac{n_i^*}{n_i^* + \beta n_j^*}. \quad (6)$$

This probability is independent of phenotype, so it is also equal to the mean reproductive fitness:

$$\bar{W}_i^{**} = \frac{n_i^*}{n_i^* + \beta n_j^*}. \quad (7)$$

One can interpret β as the consideration given to a member of the opposite species relative to a conspecific (when $\beta = 0$, there is no hybridization). This mean fitness function can be used to find the population size after the second phase; the mean phenotypes are not affected.

$$n_i^{**} = \bar{W}_i^{**}n_i^* \quad \text{and} \quad (8)$$
$$\bar{z}_i^{**} = \bar{z}_i^*. \quad (9)$$

The third phase is dispersal, described by equation (1) acting on the altered values n_i^{**} and $\bar{z}_i^{**}$ in equations (8) and (9). The changes within one generation are thus completed.

Parameter values

Because this model, and the subsequent ones, can only be solved numerically, it is impossible for us to explore the entire parameter space, and we therefore cannot rule out the possibility of equilibrium results in addition to those we will describe. We did, however, investigate a wide range of parameter combinations. In a systematic search, we considered all possible combinations of reasonably high and low values

E. E. GOLDBERG AND R. LANDE

uniform environment, $\theta(x) = 0$ environmental gradient, $\theta(x) = 0.1x$
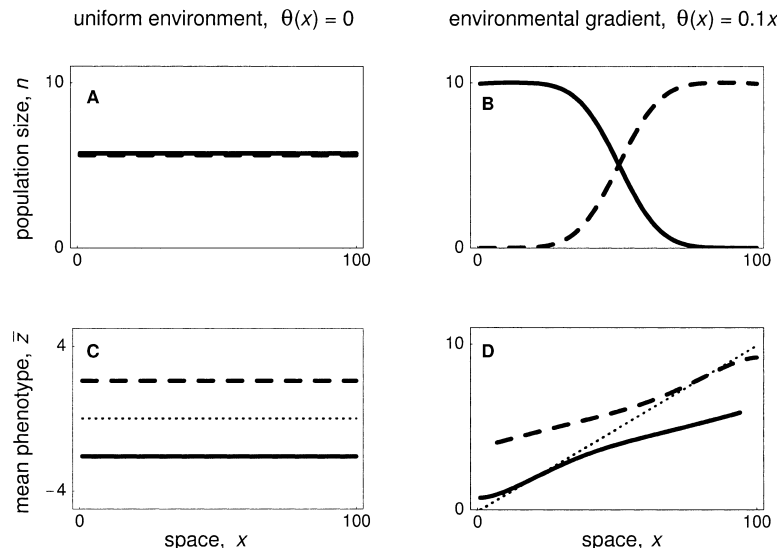
FIG. 2. Model 1, no hybridization. Ecological character displacement may occur with or without a stable border between the species, but a stable border requires an environmental gradient. The left panels show the population sizes (A) and mean phenotypes (C) for each species (solid and dashed lines, truncated at $n_i = 0.001$) when the optimum phenotype (dotted line) is constant over space; the right panels (B, D) show the same when the optimum phenotype varies linearly over space. In (A), the population sizes are exactly equal but the dashed line is displayed slightly lower to make it clear that both species are present. The parameter values used are $r = 0.1$, $K = 10$, $h^2 = 0.5$, $\sigma_z^2 = 1$, $\sigma_s^2 = 300$, $\sigma_u^2 = 10$ (A, C) or $\sigma_u^2 = 25$ (B, D), $\delta = 0.1$, $\beta = 0$. Character displacement occurs in each case, but identifying it requires regions of allopatry, which do not occur without an environmental gradient.

of most of the parameters, subject to the assumptions of the model: $r = 0.2$ and 0.01 (Charnov 1993; growth rate must be small); $\delta = 0.2$ and 0.01, $\theta(x) = 0$ and $0.1x$ (clines cannot vary too rapidly over space); $\sigma_s^2 = 300$ and 100 (Turelli 1984; stabilizing selection must be weak); $\sigma_u^2 = 50$ and 10; $\beta = 0$, 0.01, and 0.1 (Coyne and Orr 1989; small amounts of hybridization). We fixed the values $K = 10$, $h^2 = 0.5$, and $\sigma_z = 1$.

For each of these parameter combinations, we considered two initial conditions: small populations in complete allopatry near the edges of space, and small populations in a limited range of nearly complete sympatry in the center of the available space. In each case, the initial population sizes of the two species were slightly unequal, and the mean phenotypes of each species were displaced slightly, in opposite directions, from the optimum. In the vast majority of cases, the same equilibrium was reached from both initial conditions, though in a few cases, a stable border was obtained under the allopatric initial condition but one species was eliminated under the sympatric initial condition.

In addition to this systematic investigation, we considered many combinations of intermediate parameter values, and representative results are shown in Figures 2–6.

Results

The behavior of this model without hybridization ($\beta = 0$) is described in detail by Case and Taper (2000), so we mention only a few salient points. We then describe the effects of a small amount of hybridization.

No hybridization.—First, in the absence of an environmental gradient ($\theta[x] = $ constant) or when the gradient is sufficiently shallow, a stable border between the species does not form. With no environmental gradient, stable coexistence is, however, possible, with each species maintaining constant population size over space: it may either take the form $n_1 + n_2 = K\sqrt{\sigma_u^2 + \sigma_z^2}(2r\sigma_s^2 - \sigma_z^2)/(2r\sigma_s^2\sigma_u)$ and $\bar{z}_1 = \bar{z}_2 = \theta$ (no character displacement, neutrally stable), or $n_1 = n_2 = \nu$ and $\bar{z}_1 - \theta = \theta - \bar{z}_2 = \zeta$ (symmetric character displacement, stable for particular values of ν and ζ; Fig. 2A, C). If these species elsewhere occurred separately from one another in similar environments, this second situation would be identified as the classic pattern of character displacement; in continuous space, with no disjunct regions of allopatry, character displacement would not be recognized without additional information.

Second, when there is a sufficiently steep environmental gradient, a stable border forms between the species (Fig. 2B). Each species approaches the optimum phenotype in regions of allopatry, but the phenotypes are displaced from the optimum in the region of sympatry (Fig. 2D). Because of the underlying gradient in optimum phenotype, phenotypic differences are greater in allopatry than in sympatry. If the clines were to reverse slope in sympatry (e.g., in Fig. 2D, if the cline shown by the dotted line turned up and the cline shown by the solid line turned down in the region of sympatry, as is seen in Fig. 4C, D), then differences in sympatry could exceed differences in allopatry. That is not observed in this
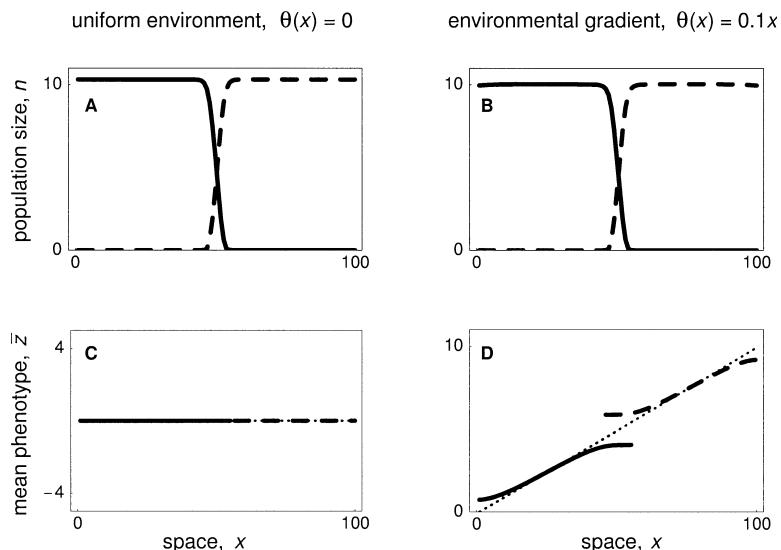
FIG. 3. Model 1, with hybridization. A small amount of hybridization, independent of phenotype, allows a stable border to form in the absence of an environmental gradient (A), but in so doing removes character displacement (C). With an environmental gradient, hybridization narrows the region of sympatry (cf. B with Fig. 2B). The panel layout and parameter values used are the same as in Figure 2, with the exception of $\beta = 0.01$.

model because under strong diversifying selection, the border collapses and the species coexist everywhere, creating a situation analogous to Figures 2A and 2C but with an environmental gradient.

Under this model, an environmental gradient is required to produce both the regions of sympatry and of allopatry for each species that are necessary to identify character displacement in a two-species system, but such a gradient obscures the classic pattern.

With hybridization.—With no environmental gradient, the addition of phenotype-independent hybridization to this model destabilizes coexistence of the species in the absence of character displacement: $n_1 + n_2 = K\sqrt{\sigma_u^2 + \sigma_z^2}[2r\sigma_s^2 - \sigma_z^2 - 2\sigma_s^2\ln(1 + \beta)]/(2r\sigma_s^2\sigma_u)$ and $\bar{z}_1 = \bar{z}_2 = \theta$. Because hybridization makes the rarer species less fit and thus even more rare, small asymmetries in the initial population sizes or locations become amplified, allowing the formation of a stable border between the species (Fig. 3A). Because coexistence without character displacement is only neutrally stable for $\beta = 0$, any value of $\beta > 0$ (along with values for the other parameters that would otherwise yield no character displacement) will lead to a stable border; a tiny amount of hybridization can thus have a tremendous qualitative effect on the species' distributions. With a stable border, measurable character displacement does not occur, even under parameter values with which it would occur for $\beta = 0$ (Fig. 3C). The presence of the border allows each species to achieve the optimum phenotype in allopatry; gene flow then overcomes divergent selection in sympatry.

Still in the absence of an environmental gradient, hybrid-

ization does not necessarily destabilize complete coexistence with character displacement. It does, however, substantially reduce the parameter space in which stable coexistence occurs. For example, the parameter values $r = 0.2$, $\sigma_z^2 = 1$, $\sigma_u^2 = 25$ yield stable coexistence with character displacement for $\beta = 0$ (no hybridization) when $\sigma_s^2 > 262.5$. When $\beta = 0.001$ (a very small amount of hybridization), coexistence is stable only when $\sigma_s^2 > 564.1$ (much weaker stabilizing selection).

In the presence of an environmental gradient, hybridization narrows the region of sympatry (cf. Fig. 3B and Fig. 2B). Substantial character displacement is possible (Fig. 3D), where it was not possible in the absence of a gradient (Fig. 3C), because gene flow from the better-adapted regions of allopatry exaggerates divergence rather than opposing it.

Hybridization may also allow some reversal of the clines' slopes in sympatry by maintaining a border between the species under strong divergent selection. When this effect exists, it is usually quite small (not visible in Fig. 3D), but it shows that hybridization may have an impact on the nature of character displacement. The following three models consider situations in which the probability of hybridization depends on phenotype and its influence becomes much stronger.

Our conclusions under model 1 are that the classic pattern of character displacement, that is, greater phenotypic difference in sympatry than in allopatry, is unlikely to emerge in continuous space under competition alone, with or without an environmental gradient, but that a small amount of hybridization may have a substantial effect on the shape and stability of species' borders and character displacement.
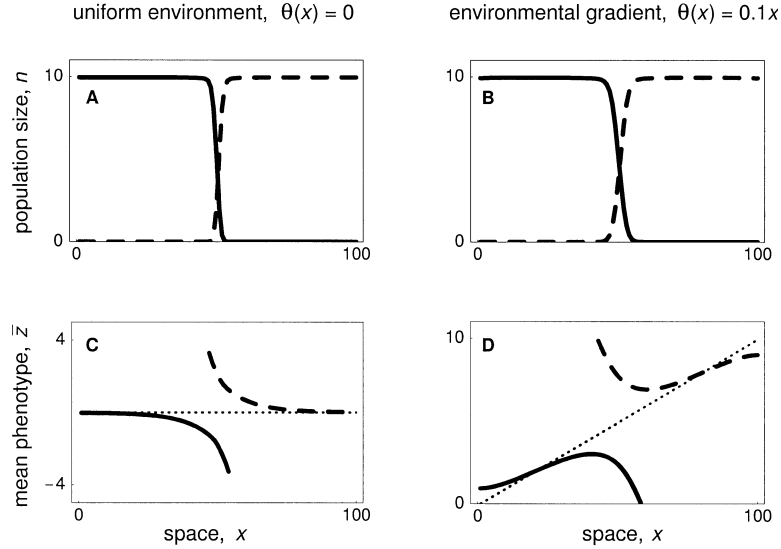
FIG. 4. Model 2: Reproductive character displacement and a stable border arise with or without an environmental gradient. Without a gradient (A, C), the species differ more in sympatry than in allopatry. With a gradient (B, D), this pattern is obscured. The panel layout is the same as in Figures 2 and 3. Parameter values are $r = 0.2$, $K = 10$, $h^2 = 0.5$, $\sigma_z^2 = 1$, $\sigma_s^2 = 500$, $\delta = 0.1$, $\sigma_f^2 = 1$. Assortative mating is quite strong here, because σ_f^2 is no greater than the phenotypic variance, σ_z^2; for weaker assortative mating, hybridization is more common and the region of sympatry decreases, increasing the relative effects of gene flow and thus reducing the opportunity for character displacement.

Model 2: Reproductive Character Displacement

In this model, assortative mating occurs based on a phenotypic character. The probability of mating between individuals is higher when their phenotypes are more similar, regardless of whether they are conspecific. All hybrid offspring are inviable, and there is no reproductive compensation for inviable embryos, thus creating potentially strong selection for phenotypic divergence between the species. There is, however, stabilizing natural selection on this character that prevents unlimited divergence. There is also density dependence imposed by competition, but the strength of intra- and interspecific competition is independent of phenotype. Ours is not a model of the evolution of mate preferences, so we do not consider a male trait and a female preference (cf. Lande 1982; Lemmon et al. 2004). Instead, we simply consider assortative mating based on phenotypic similarity. Examples of such a phenotype include flower morphology (e.g., Whalen 1978; Levin 1985; Armbruster et al. 1994), reproductive timing (Marshall and Cooley 2000), and body size (e.g., Fisher 1918, 1930; Nagel and Schluter 1998; Shine et al. 2001).

Formulation

During the first phase in a generation, competition and stabilizing selection alter the population sizes, mean phenotypes, and phenotypic variances. The mean fitness function can be obtained from that in the first model by broadening the resource utilization curves ($\sigma_u^2 \to \infty$, in eqs. 2 and 4) to eliminate phenotypic effects on competition:

$$\bar{W}_i^* = \exp\left[r\left(1 - \frac{n_1 + n_2}{K}\right) - \frac{\sigma_z^2 + (\theta - \bar{z}_i)^2}{2\sigma_s^2}\right]. \quad (10)$$

The altered population sizes, mean phenotypes, and phenotypic variances (Lande and Arnold 1983) are

$$n_i^* = \bar{W}_i^* n_i, \quad (11)$$

$$\bar{z}_i^* = \bar{z}_i + \sigma_z^2 \frac{\partial \ln \bar{W}_i^*}{\partial \bar{z}_i} = \bar{z}_i + \frac{\sigma_z^2(\theta - \bar{z}_i)}{\sigma_s^2}, \quad \text{and} \quad (12)$$

$$\sigma_{z,i}^{*2} = \sigma_z^2\left(1 + \sigma_z^2 \frac{\partial^2 \ln \bar{W}_i^*}{\partial \bar{z}_i^2}\right) = \sigma_z^2\left(1 - \frac{\sigma_z^2}{\sigma_s^2}\right). \quad (13)$$

The second phase is mate choice and phenotype-dependent hybridization. The consideration that an individual of phenotype z gives to another individual of phenotype z' when selecting a mate in the same locality is defined by the assortative mating function $f(z - z') = \exp[-(z - z')^2/(2\sigma_f^2)]$, so that individuals are more likely to mate with more similar individuals. Smaller values of σ_f^2 indicate that individuals take only very similar mates, and interspecific hybridization will be reduced if the species differ in mean phenotype. When considering only a single species with a normal phenotype distribution with variance σ_z^2, the phenotypic correlation between mates under this mating system is $\sigma_z^2/(\sigma_z^2 + \sigma_f^2)$.

The individual Wrightian fitness of a member of species i is the probability that it mates with a conspecific:

$$W_i^{**}(z) = \frac{\displaystyle\int_{-\infty}^{\infty} n_i^* p_i^*(z') f(z - z') \, dz'}{\displaystyle\int_{-\infty}^{\infty} [n_i^* p_i^*(z') + n_j^* p_j^*(z')] f(z - z') \, dz'}$$

$$= \frac{n_i^*}{n_i^* + \exp\left[\dfrac{(z - \bar{z}_i^*)^2 - (z - \bar{z}_j^*)^2}{2(\sigma_f^2 + \sigma_{z,i}^{*2})}\right] n_j^*}, \quad (14)$$

where the phenotypic distribution of species i is now $p_i^*(z)$ (normally distributed with mean $\bar{z}_i^*$ and variance $\sigma_{z,i}^{*2}$). Equation (14) is analogous to equation (6), but β has been replaced with a factor depending on phenotype.

The mean Wrightian fitness of species i is

$$\bar{W}_i^{**} = \int_{-\infty}^{\infty} p_i^*(z) W_i^{**}(z) \, dz, \quad (15)$$

which cannot be evaluated analytically.

The values of population size and mean phenotype after hybridization are

$$n_i^{**} = \bar{W}_i^{**} n_i^* \quad \text{and} \quad (16)$$

$$\bar{z}_i^{**} = \bar{z}_i^* + h^2 \left[\frac{1}{\bar{W}_i^{**}} \int_{-\infty}^{\infty} p_i^*(z) W_i^{**}(z) z \, dz - \bar{z}_i^*\right]. \quad (17)$$

The third phase is dispersal. Its effects are described by equation (1), acting on the altered values n_i^{**} and $\bar{z}_i^{**}$ from equations (16) and (17). The changes within one generation are thus completed.

Parameter values considered were the same as for model 1, except for the omission of σ_u^2 and β, and the addition of $\sigma_f^2 = 0.1$ and 10.

Results

Analysis of the nonspatial version of this model shows that coexistence is unstable, with or without character displacement. The spatial model will thus have a stable border between the species (Fig. 4A, B), and character displacement in the region of sympatry (when there is one) occurs readily (Fig. 4C, D), with or without an environmental gradient. When the environmental gradient is nonexistent or shallow, the classic pattern of greater difference in sympatry emerges (Fig. 4C). When the environmental gradient is sufficiently steep, this pattern may be obscured or reversed (Fig. 4D).

In this model, the slopes of the clines show a marked change in sign in the region of sympatry (Fig. 4C, D). This reversal of slope contrasts with model 1, in which the slopes of the clines were reduced but not reversed in sympatry (Figs. 2D and 3D). The qualitative difference in model results illustrates that phenotype-dependent hybridization creates much stronger diversifying selection, especially on the rarer species, than does phenotype-dependent competition.

We conclude that the classic pattern of character displacement is likely to emerge for a reproductive character, although it is less likely to be seen on an environmental gradient.

Model 3: Ecological and Reproductive Character Displacement, One Trait

The first two models show that the classic pattern of character displacement is unlikely to arise for a purely ecological character in continuous space but that it is likely to arise for a reproductive character unless the environmental gradient is steep.

If, however, an ecological character were also to function in assortative mating, it might then exhibit the classic pattern. Perhaps the best example of such a character would be body size, which has been implicated in both resource acquisition (Schoener 1970; Diamond et al. 1989 and references therein; Nagel and Schluter 1998) and assortative mating (Fisher 1918, 1930; Nagel and Schluter 1998; Shine et al. 2001) and is often used in character displacement studies (see Theory and Practice below).

Formulation

Frequency-dependent competition and stabilizing selection act first,

$$n_i^* = \bar{W}_i^* n_i, \quad (18)$$

$$\bar{z}_i^* = \bar{z}_i + \sigma_z^2 \frac{\partial \ln \bar{W}_i^*}{\partial \bar{z}_i}, \quad \text{and} \quad (19)$$

$$\sigma_{z,i}^{*2} = \sigma_z^2 \left(1 + \sigma_z^2 \frac{\partial^2 \ln \bar{W}_i^*}{\partial \bar{z}_i^2}\right), \quad (20)$$

where $\bar{W}_i^*$ is defined as in model 1 by equations (2) and (4). Then, frequency-dependent mating and hybridization occur as in model 2:

$$n_i^{**} = \bar{W}_i^{**} n_i^* \quad \text{and} \quad (21)$$

$$\bar{z}_i^{**} = \bar{z}_i^* + h^2 \left[\frac{1}{\bar{W}_i^{**}} \int_{-\infty}^{\infty} p_i^*(z) W_i^{**}(z) z \, dz - \bar{z}_i^*\right]. \quad (22)$$

where $\bar{W}_i^{**}$ is defined as in model 2 by equations (14) and (15). Finally, dispersal (eq. 1 acting on n_i^{**} and $\bar{z}_i^{**}$ in eqs. 21 and 22) completes the changes in one generation.

Results

The clines in this model of a trait that serves both ecological and reproductive functions (Fig. 5C, D) generally are intermediate between the results of the previous models in which the trait serves only a single function (Figs. 2C, D and 4C, D). However, some qualitative differences do arise. For an ecological character in model 1, with no environmental gradient we found that it was unlikely to have both regions of allopatry and also substantial character displacement in the ecological trait (Figs. 2A, C and 3A, C), but in this model it is common (Fig. 5A, C). Therefore, a character affecting resource acquisition is much more likely to show the classic pattern of character displacement if it also plays a role in assortative mating.

Furthermore, allopatry is not inevitable in this model, as it was in model 2. As resource specialization increases (smaller values of σ_u^2), the region of sympatry grows; the border between the species eventually collapses when divergent se-

uniform environment, $\theta(x) = 0$ environmental gradient, $\theta(x) = 0.1x$
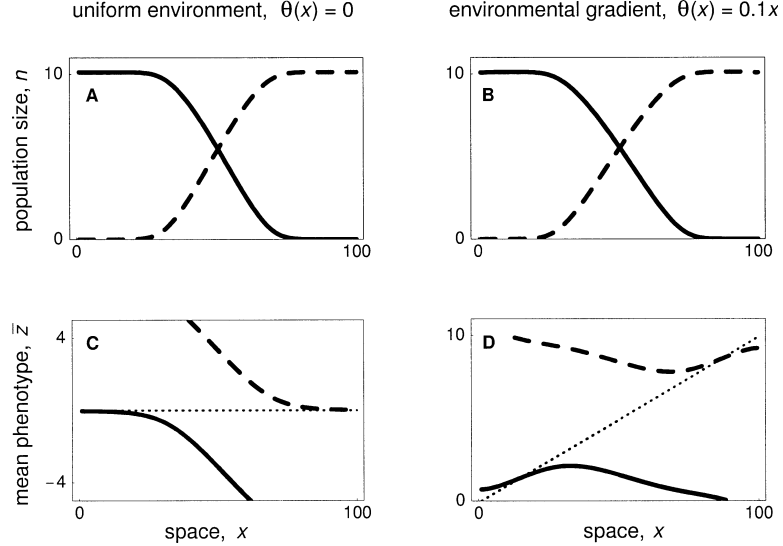

FIG. 5. Model 3: Character displacement occurs in a trait that affects both resource competition and assortative mating. The shapes of the clines are qualitatively intermediate between those in Figures 2 and 4. Hybridization allows a stable border to form even in the absence of an environmental gradient (as in model 2), but when competition depends strongly on phenotype, the border between the species collapses (as in model 1). The panel layout is the same as in Figures 2–4. Parameter values are $r = 0.2$, $K = 10$, $h^2 = 0.5$, $\sigma_z^2 = 1$, $\sigma_s^2 = 300$, $\sigma_u^2 = 25$, $\delta = 0.1$, $\sigma_f^2 = 0.7$.

lection is sufficiently strong for the two species to coexist everywhere (results not shown).

Model 4: Ecological and Reproductive Character Displacement, Two Traits

The situations to which model 3 might apply are somewhat restricted, because it requires that a single character affect both resource acquisition and mating. In this model, we consider two traits, y, determining competition, and z, determining hybridization. Each is subject to stabilizing selection, though the strength of selection and the environmental gradient in the optimum phenotype may differ between the traits. The two traits are assumed to be genetically independent, controlled by different sets of loci in linkage equilibrium, but their evolution is coupled through the population sizes of the two species.

Formulation

The mean fitness function for the first phase in this model contains frequency-dependent competition based on trait y and stabilizing selection on both traits y and z. It can be written as in equations (2) and (4) with an additional factor for stabilizing selection on the reproductive trait:

$$\bar{W}_i^* = \exp\left[r - \frac{r}{K}\sqrt{\frac{\sigma_u^2}{\sigma_u^2 + \sigma_y^2}} \left\{ n_i + n_j \exp\left[\frac{-(\bar{y}_i - \bar{y}_j)^2}{4(\sigma_u^2 + \sigma_y^2)} \right] \right\} \right]$$
$$\times \exp\left[-\frac{\sigma_y^2 + (\theta_y - \bar{y}_i)^2}{2\sigma_{s,y}^2} \right] \exp\left[-\frac{\sigma_z^2 + (\theta_z - \bar{z}_i)^2}{2\sigma_{s,z}^2} \right]. \tag{23}$$

Here, for traits y and z, σ_y^2 and σ_z^2 are the phenotypic variances, $\sigma_{s,y}^2$ and $\sigma_{s,z}^2$ determine the strengths of stabilizing selection, and θ_y and θ_z are the optimal phenotypes. We denote the heritabilities of the characters as h_y^2 and h_z^2. Using this mean fitness function, the first phase of changes in population size, mean phenotypes, and phenotypic variance for the reproductive character are:

$$n_i^* = \bar{W}_i^* n_i, \tag{24}$$

$$\bar{y}_i^* = \bar{y}_i + h_y^2 \sigma_y^2 \frac{\partial(\ln \bar{W}_i^*)}{\partial \bar{y}_i}, \tag{25}$$

$$\bar{z}_i^* = \bar{z}_i + \sigma_z^2 \frac{\partial \ln \bar{W}_i^*}{\partial \bar{z}_i} = \bar{z}_i + \sigma_z^2 \frac{\theta_z - \bar{z}_i}{\sigma_{s,z}^2}, \quad \text{and} \tag{26}$$

$$\sigma_{z,i}^{*2} = \sigma_z^2 \left(1 + \sigma_z^2 \frac{\partial^2 \ln \bar{W}_i^*}{\partial \bar{z}_i^2} \right) = \sigma_z^2 \left(1 - \frac{\sigma_z^2}{\sigma_{s,z}^2} \right). \tag{27}$$

Mating and hybridization then affect population size and the reproductive character. $\bar{W}_i^{**}$ is defined as in model 2 by equations (14) and (15), and the new population sizes and mean phenotypes are

$$n_i^{**} = \bar{W}_i^{**} n_i^*, \tag{28}$$

$$\bar{y}_i^{**} = \bar{y}_i^*, \tag{29}$$

$$\bar{z}_i^{**} = \bar{z}_i^* + h_z^2 \left[\frac{1}{\bar{W}_i^{**}} \int_{-\infty}^{\infty} p_i^*(z) W_i^{**}(z) z \, dz - \bar{z}_i^* \right]. \tag{30}$$

The generation finishes with dispersal (eq. 1, with the equation for $\Delta \bar{y}_i$ analogous to that for $\Delta \bar{z}_i$, acting on the values of n_i^{**}, $\bar{y}_i^{**}$, and $\bar{z}_i^{**}$ in eqs. 28–30).
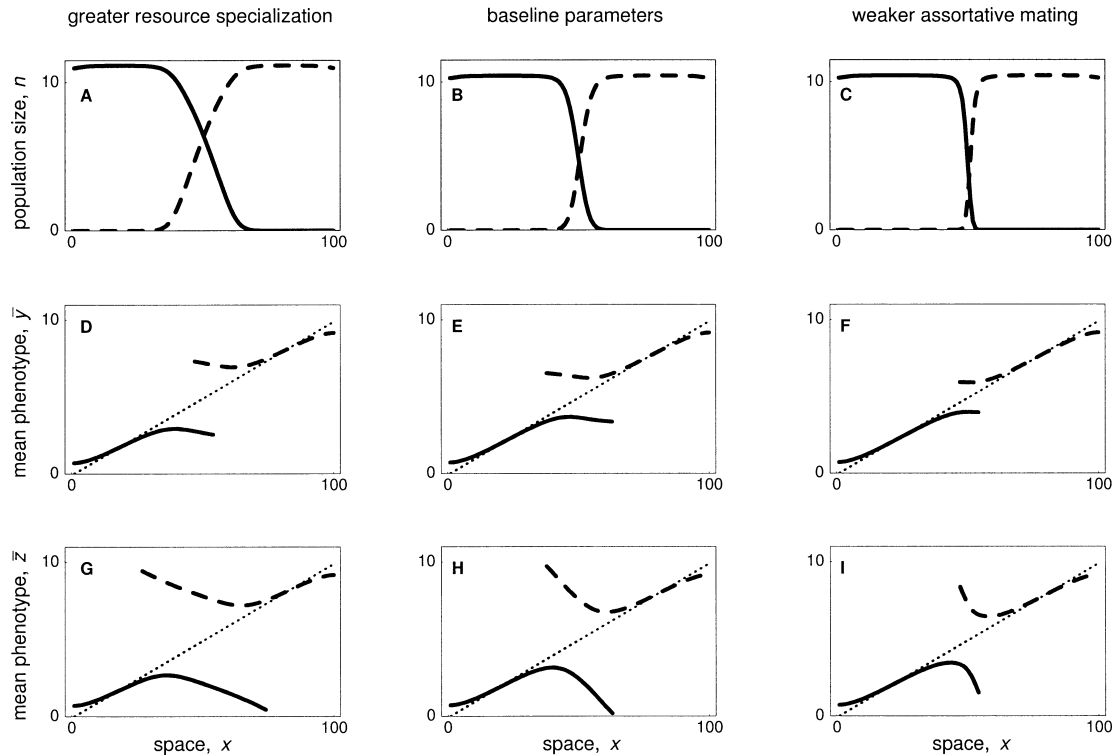
FIG. 6. Model 4: Changing the action of one trait (either ecological or reproductive) has an indirect effect on the evolution of the other trait. The top row shows the population sizes, the middle row shows the mean ecological phenotypes, and the bottom row shows the mean reproductive phenotypes. The thick solid and dashed lines show the results for each of the two species, and the thin dotted lines show the optimum phenotype. Each column shows the results for one set of parameter values: all three columns: $r = 0.1$, $K = 10$, $h_y^2 = h_z^2 = 0.5$, $\sigma_y^2 = \sigma_z^2 = 1$, $\sigma_{s,y}^2 = 300$, $\delta = 0.1$, $\theta(x) = 0.1x$; left column: $\sigma_u^2 = 3$, $\sigma_f^2 = 0.1$; center column: $\sigma_u^2 = 6$, $\sigma_f^2 = 0.1$; right column: $\sigma_u^2 = 6$, $\sigma_f^2 = 1$. Comparing the left and center columns shows that increasing resource specialization increases the region of sympatry and makes displacement of the reproductive character less steep. Comparing the right and center columns shows that weaker assortative mating decreases the region of sympatry and the amount of ecological character displacement and steepens displacement of the reproductive character. For these parameter values with $\theta_y(x) = \theta_z(x) = 0$, stable borders arise but ecological character displacement does not occur, and reproductive character displacement occurs only in the cases of strong assortative mating ($\sigma_f^2 = 0.1$).

Results

Example results (Fig. 6) for the case of an environmental gradient demonstrate that the evolution of each phenotypic trait affects the evolution of the other trait, even though the traits are genetically independent; these effects are transmitted through the population sizes. Increasing resource specialization (decreasing σ_u) widens the region of sympatry (Fig. 6A, B). The broader border between the species leads to shallower divergence of the reproductive character (Fig. 6G, H) due to the smaller differences in population size of the two species at each location. Decreasing the strength of assortative mating (increasing σ_f) narrows the region of sympatry (Fig. 6B, C) because more hybridization occurs. The narrower border between the species leads to reduced ecological character displacement in the decreased area of sympatry. These effects are not large but are strongest for resource specialists with strong assortative mating.

DISCUSSION

Analyzing the mechanisms of character displacement will help to clarify its possible outcomes so that it can be recognized even when it does not lead to the classic pattern of greater phenotypic differences between species in sympatry than in allopatry. Observation of this classic pattern does not guarantee that character displacement is occurring, but it is commonly used to indicate that a system is worthy of further investigation. However, in the presence of an environmental gradient in the optimum phenotype, character displacement may occur but go unnoticed by this method. We analyzed spatial models of the coevolution of species based on quantitative ecological and reproductive traits to investigate more general processes of character displacement and to suggest more general methods for detecting it. We will first discuss the results and limitations of our models and then present a brief literature survey intended to highlight methods by which

E. E. GOLDBERG AND R. LANDE

theory can improve the power of empirical searches for character displacement.

Model Results and Limitations

For a character that affects only resource competition in continuous space between two species that do not interbreed (model 1, $\beta = 0$), character displacement will not exhibit the classic pattern of greater difference in sympatry than allopatry. In the absence of a gradient in the optimum phenotype, a stable border between the species will not form (Fig. 2A), and so character displacement, if it occurs (Fig. 2C), will not be identified because there are no regions of allopatry for comparison. An environmental gradient may allow a stable border to form (Fig. 2B), but in such cases, phenotypic differences in allopatry exceed those in sympatry (Fig. 2D).

With even a small amount of hybridization between the species, when hybrids are inviable, (model 1, $\beta > 0$ and model 4), the outcome may change dramatically. A stable border between the species is more likely to form, but ecological character displacement will be reduced (in the case of an environmental gradient) or absent (in the case of no gradient; Figs. 3, 6A–F), whether or not displacement can evolve in a reproductive character to reduce the probability of hybridization.

We therefore conclude that a character affecting only resource acquisition is unlikely to exhibit greater difference in sympatry than allopatry in continuous space. If, however, the character also plays some role in mate choice (model 3), the classic pattern of character displacement is likely to emerge (Fig. 5C), though it may still be obscured by an environmental gradient (Fig. 5D).

Displacement of a reproductive character, for which phenotypic similarity increases the probability of interspecific hybridization and the production of inviable offspring (assortative mating, models 2 and 4), occurs more readily than ecological character displacement. Near the edges of the zone of sympatry, where one species is much less common than the other, individuals of the rare species are disfavored by hybridization but have a competitive advantage, so divergence is more likely to evolve in a reproductive character. In the absence of an environmental gradient, the classic pattern of character displacement is likely to emerge for a reproductive character (Fig. 4C); with a gradient, the classic pattern is somewhat obscured (Fig. 4D). If the reproductive character also affects competition (model 3), ecologically driven divergence of the character may collapse the border between the species, making character displacement harder to detect.

From our models, we therefore conclude that ecological character displacement may be much more common than is appreciated by simply looking for greater phenotypic differences in sympatry than allopatry, and especially so for systems with continuous spatial structure. Reproductive character displacement is more likely than ecological character displacement to be observed in continuous space, but it, too, may go undetected when there is an underlying environmental gradient. Ecological or reproductive character displacement on an environmental gradient could be identified using more detailed spatial information. The slopes of the clines

in mean phenotype differ with the relative abundances of the two species, so measurements of phenotype up to and through a region of sympatry could reveal the presence of character displacement. We return to the issue of observational methods of detecting character displacement in Theory and Practice below.

Our models of character displacement could be generalized in several respects, for example, by including additional characters, additional species, and two spatial dimensions. We restrict our models to the case where all hybrids are completely inviable. If hybrid offspring were instead viable but infertile, the phenotypic evolution of the two species would be somewhat affected, perhaps causing further divergence, because the hybrids would be competing for resources and possibly for mating opportunities. Including viable but infertile F_1 or F_2 and backcross hybrids would be feasible, but allowing fertile hybrids and consequent gene flow between species would require more complicated population genetic models.

We have only analyzed results for a simple linear environmental gradient. More elaborate gradients could easily be considered and might complicate the patterns that we describe. If there were, for example, a shallower environmental gradient in the region of sympatry, a reduced slope in the clines in that region could reflect adaptation to the shallower gradient rather than character displacement. Such a situation may be unlikely, however, because the border between the species is attracted to regions with a steeper environmental gradient (Case and Taper 2000; E. E. Goldberg and R. Lande, unpubl. results). If the two species were experiencing stabilizing selection toward different optima, the strength of their interaction would be reduced, potentially broadening their region of sympatry and reducing the amount of character displacement. In an examination of two shifted (e.g., $\theta_1[x] = \theta_2[x] + 1$) linear environmental gradients for models 1 and 2, we found no qualitative differences in the shapes of the borders or clines (unpubl. results).

Our models also make simplifying assumptions about the genetics and population dynamics of the species. The two species have the same generation time, though this assumption is not unreasonable because character displacement and hybridization are more common in closely related species (Schluter 2001). Moreover, the two species are completely symmetric in their behavior and their ecological and reproductive capacities. Asymmetries between the species could lead to a proliferation of possibilities but may be important to consider because many empirical examples of character displacement are asymmetric (Schluter 2000b). For model 1 without hybridization, Case and Taper (2000) found that differences in growth rates, heritabilities, and dispersal rates could lead to the exclusion of one species or to the formation of a stable border that is not centered in the available space. In an investigation of asymmetries in model 1 with hybridization and model 2, we confirmed these results (results not shown). We also modeled only local migration (between adjacent locations in discrete space); a broader dispersal function produces qualitatively similar results unless the environmental gradient is very steep in places or there are major habitat discontinuities or strong barriers to migration.

These models are based on quantitative traits with a poly-

TABLE 1. Empirical studies of character displacement. For each study in our literature review (details in the text), we categorized the data analysis as comparing phenotypic values in sympatry and allopatry (S vs. A), looking for overdispersion or minimum size ratios in a single location, or using other methods (including species-for-species matching, phylogenetics, isolation-by-distance, comparing continental with island populations, evidence of positive or disruptive selection, changes in phenotype or hybridization frequency over time, and customized spatial or functional models); some studies used more than one method. We categorized the spatial structure of each study system as continuous (if there did not appear to be hard barriers to dispersal) or discrete (e.g., well-isolated lakes or islands); a few studies included sampling both within and between islands. We also recorded how many studies presented (though map, graph, or table) spatially explicit phenotypic information that went beyond simply identifying allopatric and sympatric populations, and how many of those used that information in the analysis of character displacement. Finally, we recorded the number of studies that reported data on relative species abundances or mentioned abundance in the discussion of character displacement, and of those the number that used such data in the character displacement analysis.

Trait type	No. studies	Analysis			Spatial structure		Spatial phenotype info.		Abundance info.	
		S vs. A	Overdispersion	Other	Continuous	Discrete	Presented	In analysis	Mentioned	In analysis
Ecological	60	32	24	13	37	27	17	3	6	3
Reproductive	43	38	3	7	37	7	23	3	5	1
Both	40	24	12	13	27	17	21	4	7	2
Total	143	94	39	33	101	51	61	10	18	6

genic basis and neglect the influence of gene flow in augmenting genetic variability. This simplification is justified if phenotypic clines and population density gradients are not very steep over typical migration distances and the effective number of genetic loci influencing the characters is not very small (Lande 1982; Barton 1999). The more loci involved in the inheritance of a character, the smaller the increase of variance from gene flow (Wright 1968, ch. 15; Lande 1981). Allowing the phenotypic variance to evolve would considerably complicate the models and might best be addressed by simulation.

Theory and Practice

We conducted a literature survey of empirical character displacement studies to estimate the relative frequencies of various observational and analytical methods and to assess the extent to which theoretical methods and results are applied to natural systems. Our intent is not to review the evidence for character displacement (as was done by Grant 1972; Schluter 2000b; Dayan and Simberloff 2005), but to summarize the methods used by researchers in identifying potential character displacement systems. We focused on observational studies because we hope to broaden the use of such data in identifying systems that may exhibit character displacement. Further work, often including experiments, is of course needed before character displacement can be accepted as an important force in any particular system (Waage 1979; Schluter and McPhail 1992).

A Web of Science search in April 2006 for papers with ''character and (displacement or divergence)'' in the title returned 109 articles presenting or reanalyzing observational data. Although there are certainly other character displacement studies, these search limits provided a manageable and presumably unbiased (except for the likely underrepresentation of studies that searched for and failed to find evidence for character displacement) collection of work on this topic. Some authors presented multiple systems or analyses in a single paper, so we use the word ''study'' to refer to the analysis of a particular trait type (ecological, reproductive, or both [generally body size or a proxy thereof]) in organisms of a particular family and geographic location. We categorized each study according to its data collection and analysis

methods, the spatial structure of its system, the use of spatially explicit phenotype data, and the use of species abundance data. The results are presented in Table 1.

The character displacement models we developed here are for systems in continuous space with two species, where comparison of sympatry and allopatry is necessary. From Table 1, it is clear that the majority of empirical studies also are conducted in continuous space and by comparing conditions in sympatry and allopatry.

Few studies, theoretical or empirical, have examined character displacement in an explicitly spatial context. Two articles in our literature review compare slopes of clines in sympatry and allopatry (Grant 1975; Dayan et al. 1989), and a few others (notably Whalen 1978; Kawano 2003) present data that could be used in such a clinal analysis. Grant's (1975) procedure was to extrapolate phenotypic trends in allopatry to the region of sympatry and then compare the results with the observed phenotypes in sympatry. Our models show quantitatively that this is an excellent method, and they illustrate the manner in which slopes of phenotypic clines in sympatry and allopatry might be expected to differ (Figs. 2D; 3D; 4C, D; 5C, D; 6D–I).

Two other articles (Väisänen and Heliövaara 1989; Gabor et al. 2005) use an isolation-by-distance analysis. Both expect that differences between conspecific individuals will be greater over larger distances; this expectation is supported by our models (clear through inspection of Figs. 2–6, though less so when there is an environmental gradient) but is certainly not unique to character displacement. One (Väisänen and Heliövaara 1989) expects that differences between heterospecific individuals will be less over larger distances; this expectation is not generally supported by our models (see Figs. 2–6 in the region of sympatry), especially along an environmental gradient.

Because nearly every model of character displacement incorporates species abundances, it is surprising that so few empirical studies mention, let alone analyze, abundance data. Five articles in our literature review (Dunham et al. 1979; Frier 1979; Saloniemi 1993; Pfennig and Murphy 2003; Tynkkynen et al. 2004; see also Nosil et al. 2003; Peterson et al. 2005) use quantitative data on observed abundances, with the qualitative expectation that displacement of the trait

in one species should be greater where the relative abundance of the other species is greater. In our models, the log of the abundance ratio ($\log[n_i/n_j]$, where $n_i \geq n_j$) and the difference in phenotypic values ($|\bar{z}_i - \bar{z}_j|$) show a roughly positive, linear relationship, though linearity breaks down near the region of equal abundance ($n_1 \approx n_2$). This relation holds for all four models, with or without an underlying environmental gradient (results not shown), but it is not a conclusive test of character displacement. Other situations in which the species do not interact, such as when the range of each is limited by a region of reduced population growth rate, can yield a qualitatively similar relation between relative abundance and phenotypic difference (unpubl. results).

When analyzing observational data in search of character displacement, our main recommendation is that data from different spatial locations not be pooled. Such pooling is common practice, but it greatly reduces the power of phenotype-abundance and phenotype-space analyses. Even in the case of discrete space, pooling of samples may be less informative than comparison of well-chosen replicate populations. We also suggest that data on relative species abundances be gathered and incorporated into the analysis. Plots of abundance and mean phenotype over space can be extremely helpful in assessing both the continuity of external factors (including environmental conditions) and the symmetry of the species' responses. When clines in mean phenotype appear relatively smooth, quantitative comparison of their slopes in sympatry and allopatry will suggest the extent and perhaps the nature of the species' effects on each other. If no clear patterns are seen in the clines (or if space is disjunct), character displacement may still be supported by a more customized analysis incorporating additional information: methods that combine habitat data with models of species interactions to predict optimum phenotypic values (Case 1979; Schluter et al. 1985; Hansen et al. 2000) or to estimate the contribution of character displacement to phenotypic differences (Dunham et al. 1979) seem particularly powerful.

Our models also indicate that even a small amount of deleterious hybridization between species, manifested as inviable (or infertile) hybrids, can be quite important in forming biogeographic patterns of species abundance and character displacement. Such hybridization between closely related species often occurs in nature (Arnold 1997; McCarthy 2006) and in laboratory studies of the final stages of speciation (Dobzhansky 1951; Coyne and Orr 1989, 2004), but its potential role in biogeography and ecological character displacement has not been appreciated. We suggest that measurements of interspecific hybridization rates and hybrid fitness be incorporated in future studies of both ecological and reproductive character displacement.

Finally, we emphasize the importance of studying character displacement in a spatial context, where it is closely connected to our understanding of range limits, perhaps especially in the case of lower-latitude borders that may often be affected by species interactions (MacArthur 1972). Broadening the search for character displacement by gathering spatially explicit data on both phenotype and abundance, especially from regions with environmental gradients, may reveal this phenomenon to be more common than we now realize.

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Chapter 3, in full, is a reprint of the material as it appears in Goldberg, Emma E, and Russell Lande. 2006. Ecological and reproductive character displacement on an environmental gradient. Evolution 60:1344–1357. The dissertation author was the primary investigator and author of this paper.

Chapter 4

Species' borders and dispersal barriers

Abstract

Range limits of species are determined by combined effects of physical, historical, ecological, and evolutionary forces. We consider a subset of these factors by using spatial models of competition, hybridization, and local adaptation to examine the effects of partial dispersal barriers on the locations of borders between similar species. Prompted by results from population genetic models and biogeographic observations, we investigate the conditions under which species' borders are attracted to regions of reduced dispersal. For borders maintained by competition or hybridization, we find that dispersal barriers can attract borders whose positions would otherwise be either neutrally stable or moving across space. Borders affected strongly by local adaptation and gene flow, however, are repelled from dispersal barriers. These models illustrate how particular biotic and abiotic factors may combine to limit species' ranges, and they help to elucidate mechanisms by which range limits of many species may coincide.

Introduction

The locations of species range limits are determined by a wide array of physical, historical, and biotic factors. Among these, competition, hybridization, and local adaptation may be quite important in shaping the borders between closely related or ecologically similar species. Here we modify existing theoretical models to illustrate how these processes can interact with spatial structure, in the form of a partial barrier to dispersal, to affect the locations of borders between species. The situations we consider therefore encompass a variety of population dynamic and geographic scenarios. Our focus is on understanding the relative locations of the range limits of various species (e.g. whether many range limits tend to occur in the same location) rather than identifying factors causing range limits of particular species. The approach we use connects results from theoretical population genetics with population dynamic models and biogeographic observations.

A feature of the environment that entirely prevents individual dispersal can obviously limit the range of a species. Environmental features that only partially reduce dispersal may slow rates of range expansion, but they are not expected, by themselves, to impose range limits. Such partial or "porous" (Rapoport 1982) barriers to dispersal may, however, interact with other ecological or evolutionary factors to induce range limits. Partial barriers may be imposed by, for example, sudden changes in currents or topography, a limited passageway like a strait or an isthmus, or a relatively narrow habitat feature such as a river.

Range limits of groups of species are often observed to align with one another (e.g. Horn

and Allen 1978; Pielou 1979; Baker et al. 1998; Roy et al. 1998; Hughes et al. 2003; Swenson and Howard 2005). At the largest spatial scales, this is driven by geologic processes such as glaciation and plate tectonics (Pielou 1979; Cox and Moore 2005) and has led to the designation of faunal and floristic realms (Wallace 1876; Takhtajan 1986; Cox 2001). At smaller spatial scales, co-occurrence of species' range limits to form biotic provinces may be driven more by contemporary physical conditions (Pielou 1979; Halffter 1987; Gaylord and Gaines 2000; Unmack 2001; Morrone 2006). Species interactions, particularly hybridization, can cause borders between species (Key 1981; Hewitt 1988) and have also been suggested as driving range limit alignment [forming "suture zones" in which hybrid zones of many species pairs coincide (Remington 1968; Swenson and Howard 2005)]. Here we consider some of these mechanisms to examine how species interactions may combine with abiotic conditions to cause co-occurrence of range limits.

In addition to such biogeographic observations, this investigation is prompted by an analogy with results from population genetics. Bazykin (1969) and Barton (1979a) showed that selection against heterozygotes can produce a geographic cline in allele frequency, or "tension zone" (Key 1968; Barton and Hewitt 1985) which moves toward a region of reduced individual dispersal. Such a cline is analogous to the border between the ranges of hybridizing species when hybrids have reduced fitness. This suggests that a border between hybridizing species will be attracted to a region of reduced dispersal, and we investigate this situation.

We use models of intra- and interspecific competition and mating to examine the effect of a partial barrier to dispersal on the position of the border between species. We find that borders maintained purely by competition or those maintained primarily by hybridization tend to move toward (be "attracted" to) dispersal barriers.

We also employ the model of Case and Taper (2000) to examine the situation in which two species experience stabilizing selection toward an optimum phenotype that varies over space, due to an underlying environmental gradient. Dispersal decreases the degree of local adaptation for each species, and we show that the border between such species is "repelled" from a dispersal barrier because it diminishes detrimental gene flow. Finally, we discuss the influences of asymmetric species differences and temporal changes in dispersal barriers on biogeographic patterns.

Models

Much work has been done on population genetic models of clines in allele frequencies, and the intuition and logic of this area are relevant to the population dynamic models we use below. We therefore begin by discussing previous cline models.

Spatial models of allele frequencies (e.g. Haldane 1948; Bazykin 1969; Slatkin 1973, 1975, 1978; Nagylaki 1975, 1976, 1978; Barton 1979a,b) typically assume constant population size across space and treat dispersal as diffusive and independent of space. A stable cline can be maintained by selection against heterozygotes (Bazykin 1969; Slatkin 1973; Barton 1979a) or by a balance between migration and spatially-varying selective pressure (Slatkin 1973; Nagylaki 1975, 1976, 1978). For clines maintained by reduced heterozygote fitness (underdominance), regions of lower dispersal or lower population density tend to attract clines that would otherwise have a neutrally stable position, or to stop clines that would otherwise be moving due to unequal fitnesses of the two homozygotes (Bazykin 1969; Barton 1979a). Such regions may accumulate multiple underdominant clines (Bazykin 1969; Slatkin 1975; Barton 1979b), thereby reducing gene flow and contributing to reproductive isolation between incipient species (Bazykin 1969; Barton 1979b; Walsh 1982).

The above models of allele frequencies do not, however, include population dynamics: population size at each location is assumed to be fixed rather than determined by growth rates, dispersal, and species interactions. In the following three models, we investigate the impact of a dispersal barrier on the border between two species, and we therefore require models that explicitly include population dynamics. We use the term "border" to describe a limited region of sympatry in which the abundances of the two species decline to zero in opposite directions. A border may be broad (if the region of sympatry is large) or narrow (if there is little sympatry), and its "position" is the location where the lines depicting abundance of the two species cross.

The results of Bazykin (1969) and Barton (1979a) suggest that, for two species forming hybrids with reduced fitness, the position of the border between the species may be attracted to a barrier to dispersal, and we investigate this possibility in Model 2 below. In Model 1, we examine a similar situation: for two species with greater interspecific than intraspecific competition, individuals of the rarer species will be less successful, causing competitive exclusion and possible formation of a stable spatial border between them. In Model 3, we allow phenotypes to evolve in response to competition and environmental conditions. For each model, we illustrate the effects of a partial barrier to dispersal on the position of the border between the species.

The models below are based on standard diffusive Lotka-Volterra models describing competition between two similar species, but we make time and space discrete rather than continuous to simplify the treatment of hybridization and selection and to facilitate numerical analysis. We therefore assume that each species has non-overlapping generations and that movement of individuals is only to neighboring spatial units or "demes" (Kimura and Weiss 1964). The models are straightforward modifications of previous work, so we only describe them briefly in the text

and summarize them in the Appendix. We consider only one-dimensional space and two species, but the methods are easily extended. Initially, we consider species with symmetric ecological interactions such that, in homogeneous space, a border with a stable shape but neutrally stable spatial position can form between the species. We also discuss results of asymmetric differences between species, which can produce a traveling border in the absence of a barrier to dispersal.

In Bazykin's (1969) model with continuous space, a dispersal barrier is defined by a sharp impediment to dispersal or a region in which the diffusion coefficient (describing the variance of individual dispersal distance per generation) is reduced. In discrete space with nearest-neighbor dispersal, the diffusion coefficient is replaced by the probability that an individual will disperse to a neighboring deme, and so we reduce this probability at or within the dispersal barrier (more details in the Appendix). Model 3 includes a dispersal barrier and an environmental gradient as distinct factors. This separates the concepts of individual movement, which may be impeded by barriers in the form of abrupt changes in habitat type (e.g. a river) or topography (e.g. a cliff) or other extrinsic factors (e.g. cross-winds or currents), from individual fitness, which is affected by the degree of adaptation to a smooth environmental gradient (e.g. continuous changes in temperature or elevation).

We consider two initial conditions in determining the effect of a dispersal barrier on the shape and location of the border between species: beginning with a few individuals of each species at opposite ends of the available space, and beginning with the border formed in the absence of the barrier. For the parameter values used in the figures, the results from these two initial conditions are identical, so we show only the second. However, when the region of sympatry around the border does not extend into the barrier, the barrier does not affect the position of the border. We address implications of this scenario in the Discussion.

Model 1: Strong interspecific competition

First, we consider a model of competition between two species in one-dimensional space. At each location in space, competition within and between species follows Lotka-Volterra dynamics, and individuals can disperse to adjacent locations in space (see the Appendix for details). Competition is spatially homogeneous (all model parameters are constant across space). The possible outcomes are analogous to, but somewhat more complicated than, the three possible non-spatial outcomes (e.g. Roughgarden 1979). First, if both species coexist stably in the non-spatial model, they coexist everywhere in space. Second, if one species always excludes the other in the non-spatial model, it will exclude the other everywhere in space, though there may be a transient border between them in the form of a travelling wave. And third, if in the non-spatial

model the surviving species is determined by the initial abundances, a border with a stable shape will form when initial abundances are not too asymmetric in number or space (Case et al. 2005). This third situation occurs when interspecific competition is stronger than intraspecific competition; such strong interspecific competition is observed in natural systems, though less commonly than the reverse (Connell 1983; Fowler 1986; Goldberg and Barton 1992). In this third situation, when the species are symmetric (have identical parameter values), the border's location will be neutrally stable, with an arbitrary position determined only by the initial conditions. When the species are asymmetric, the border will be a travelling wave. [Related models in which population growth rates or carrying capacities differ between species and across space have shown other more complex conditions under which a stable border between the species may form (Bull and Possingham 1995; García-Ramos et al. 2000; Case et al. 2005).]

A partial barrier to dispersal can attract the borders formed in Model 1, which would otherwise be neutrally stable or a travelling wave. Figure 4.1A shows the border formed by strong interspecific competition, and it also shows that this border moves toward a region in space where individual dispersal is reduced, ultimately centering itself in the dispersal barrier. Figure 4.1B shows a travelling wave border, driven by unequal competitive strengths, that is stopped by a region of reduced dispersal. Although the species on the right is a weaker competitor, it sends more individuals into the region of sympatry than does the species on the left, which is affected by the dispersal barrier, and so the position of the border is stabilized.

Model 2: Competition and hybridization

Model 1 shows that species' borders can be attracted to a region of reduced dispersal, but it only applies when interspecific competition is stronger than intraspecific competition. Adding interspecific hybridization to the previous model, however, allows a stable border to form in homogeneous space even when intraspecific competition is greater, and we show that this also results in borders being attracted to barriers.

We assume that hybrids are inviable, to limit the models to situations with two clear species. This limitation is restrictive but not unreasonable: such hybridization occurs between closely related species in laboratory studies (Dobzhansky 1951; Coyne and Orr 1989) and nature (Arnold 1997), and it may be more common that is realized because hybrid phenotypes are not seen. In addition to situations where embryos are inviable, our formulation is also appropriate whenever individual mating success is reduced by the presence of members of the other species, such as if an abundance of heterospecifics makes mate identification or courtship inefficient.

In the model, the chance of an individual of the first species mating with a conspecific is

greater in demes where the first species is more common than the second, and vice versa (details in the Appendix). Fitnesses of the species are therefore frequency-dependent, and a border with a stable shape and neutrally stable position may exist between the species, even when it would not under competition alone (Ribeiro and Spielman 1986; Case et al. 2005). This is true for any amount of hybridization (Goldberg and Lande 2006); the more hybridization, the smaller the region of sympatry.

Figure 4.2 shows this border, and it also shows that the border is attracted to a partial barrier to dispersal. In this instance, the border is not centered in the barrier, as it was in Figure 4.1A, because the width of the region of sympatry is narrower than that of the barrier. The species on the right retreats because it sends fewer individuals toward the border than does the species on the left; when the region of sympatry is entirely within the barrier, this migration differential is not present and the border stops moving.

Model 3: Competition and local adaptation

Finally, we include genetics in the model, allowing adaptation in a single quantitative character to an underlying environmental gradient (details in Case and Taper 2000, with a summary in the Appendix). This character affects competition, with stronger competition between individuals of more similar phenotypes; because the phenotype distribution of each species at each location is assumed to be Gaussian, the average intraspecific competition is stronger than the average interspecific competition. Because the optimum phenotype varies across space, gene flow inhibits local adaptation and thus reduces the fitness of each species. The combination of competition and gene flow can create a stable border between the species (Case and Taper 2000).

The presence of a barrier to dispersal reduces gene flow, thus allowing better adaptation (Fig. 4.3) and increasing fitness. The species that the barrier affects more (the species on the right in all our figures) benefits more, thus expanding its range (pushing the border to the left in Figure 4.3A). [If the barrier in Figure 4.3 extended just past the center of the border (e.g. if the barrier were from $x = 45$ to $x = 65$), the border would also be pushed to the left.] The dispersal barrier therefore repels the border to some extent. This repulsion stops when the region of sympatry is mostly outside the barrier. These results hold for any combination of parameter values under which a stable border forms in the absence of a barrier (see Case and Taper 2000).

When hybridization is included, as in Model 2, the direction of movement of the border is determined by the balance between the forces of hybridization and local adaptation. With appreciable hybridization and a strong barrier, the border moves toward the barrier; when the environmental gradient is relatively steep, the border moves away from the barrier (results not

shown).

Discussion

Range limits of species are determined by combinations of physical, ecological, evolutionary, and historical factors. Among these, we investigated how dispersal barriers, competition, hybridization, and local adaptation determine the spatial position of species' borders. With strong interspecific competition (Model 1), or with matings between species with inviable hybrids, even when interspecific competition is weak (Model 2), we found that the border between two species often will be attracted to a region of reduced dispersal. In these two situations, a balance between dispersal and the reduced fitness of the rarer species maintains a border with a stable shape between the species. When part of the sympatric area falls in a region of reduced dispersal, the dispersal asymmetry at the edge of the barrier will give an advantage to the species that has larger population size just outside the barrier than inside, thus pushing the border into the barrier (Figs. 4.1A, 4.2). For a barrier that is narrow compared to the region of sympatry, pushing from the two edges of the barrier will center the border within the region of reduced dispersal (Fig. 4.1A). For a wider barrier, the border will be attracted only part way into the barrier, stopping when the sympatric area is mostly inside the barrier (Fig. 4.2). At this point, asymmetric dispersal no longer aids the advancing species because there is essentially no population size difference across the edge of the barrier.

With local adaptation to a smooth environmental gradient, the border between the species will be repelled by a dispersal barrier (Fig. 4.3A). In this case, asymmetric gene flow across the edge of the barrier is more detrimental to the species with greater population size just outside the barrier than inside. This result contrasts with the effect of an ecotone, which attracts species' borders (Case and Taper 2000; Goldberg and Lande 2006). A narrow region across which the environment changes rapidly may therefore either attract a border, if this change affects the optimum phenotype but does not reduce individual dispersal, or repel a border, if this change impedes dispersal but does not affect the optimum phenotype. Some narrow regions of rapid environmental change may affect both the optimum phenotype and dispersal, making it difficult to predict whether they will attract or repel species' borders.

The model results that we describe concerning attraction or repulsion of species' borders from dispersal barriers occur for any size or strength of barrier, though stronger barriers cause more rapid changes in species' borders. However, for a border with a neutrally stable position in the absence of a dispersal barrier, the imposition of a barrier outside the area of sympatry will not attract or repel the border, although it may still trap a travelling border. Species pairs with

wider areas of sympatry at their borders can be affected by barriers in more locations and may therefore be more likely to have borders that coincide with other species pairs.

We show one example of how biotic and abiotic factors may combine to limit species ranges. When one species would likely exclude a weaker competitor in homogeneous space, the presence of a partial dispersal barrier can allow them to coexist stably (Fig. 4.1B). Thus, while neither competition nor the region of reduced dispersal would alone impose a stable range limit, the interaction of these two factors can create a border between the species with a stable shape and location. This effect of a partial dispersal barrier stopping the advance of a species is consistent with previous work showing that patchy spatial structure can interact with an Allee effect to limit the range of a species (Keitt et al. 2001). In our model, however, the negative growth rate at the edge of the advancing species' range results from the greater local abundance of the competitor rather than being an intrinsic feature of the population.

Real physical barriers change over time, due to changing geologic or climatic conditions. A barrier that increases in size would have an increasing effect on nearby borders, and one that disappears would leave any borders it had affected as neutrally stable in their new positions. A barrier that moves slowly across space could carry or push borders with it, thus perhaps collecting borders between many pairs of species. Even if the barrier then vanished, this could leave many range limits co-occurring.

Real species pairs are not likely to interact in a perfectly symmetrical way. We illustrate one possible result for asymmetry in competitive ability (Fig. 4.1B), and here we briefly summarize results of other asymmetries between the species, which are easily incorporated in the models. In the absence of local adaptation (Models 1 and 2), if one of the species has a higher dispersal rate, a higher carrying capacity, or is a stronger competitor, it will have an advantage. Asymmetries in intrinsic growth rates are somewhat more complicated: when the border is maintained by hybridization (Model 2), the species with the higher growth rate has the advantage, but when the border is maintained by strong interspecific competition (Model 1), the species with the higher intrinsic growth rate is at a disadvantage because it declines more rapidly when in the minority. When the asymmetry is large relative to the strength of the barrier, the species with the advantage will expand its range, forcing its competitor to retreat and eventually excluding it from the available space. When the barrier is relatively strong, it can stop the advance. With local adaptation to an environmental gradient (Model 3), the species with the higher carrying capacity, higher intrinsic growth rate, lower dispersal rate, or higher heritability will have the advantage. This species will expand its range through a weak barrier, but the other species will still maintain itself near the edge of available space since it is not disadvantaged there by gene

flow. An advancing border can be repelled by a strong barrier. These outcomes suggest a variety of possible mechanisms by which biotic exchange may be asymmetric (Vermeij 1991).

Application of our results to empirical data on species ranges could help elucidate the importance of partial barriers to dispersal, species interactions, and local adaptation in setting range limits. Model 2 predicts that borders between closely-related, hybridizing species will be more clustered in space than will borders between other species pairs, and that these clusters of borders will coincide with regions of reduced dispersal. When a smooth environmental gradient extends over a much larger scale than the sympatric regions of species' borders, Model 3 predicts that clustering of species' borders will be more pronounced when the slope of this gradient is small (or zero) than when it is large. In Models 1 and 2, broader borders are more likely to overlap dispersal barriers and become centered in them, facilitating the alignment of borders between multiple pairs of species. Additional tests may be possible using data on changes in species' borders over time. For example, borders are predicted to move in concert with slow-moving barriers, and borders are predicted to move faster toward (Models 1 and 2) or away from (Model 3) stronger barriers, stopping when the barrier's edge does not fall in the region of sympatry. The increasing availability of databases on species ranges will aid searches for the above patterns predicted by these models. While the observation of any of these patterns in a particular system would not rule out all alternative hypotheses, it would strongly suggest that the interaction of dispersal barriers with competition (Model 1), hybridization (Model 2), or local adaptation (Model 3) drives range limits, and the relevance of these processes could then be assessed more directly with tests in the field.

Our results illustrate how population dynamic and genetic forces can interact with partial barriers to dispersal, affecting the spatial distribution of borders between similar species. They thus emphasize that our understanding of species' range limits and biogeographic patterns will be more complete when ecological, evolutionary, and physical forces are considered together.

Acknowledgments

Appendix: Model details

In Models 1–3, we use a discretized version of the diffusive Lotka-Volterra competition model. In each time step (generation), population size in each deme is altered first by competition, then (in Model 2 and optionally in Model 3) by hybridization, and then by dispersal.

Let $n_i(x)$ denote the population size of species i at location (or deme) x. Population size is also a function of time, but we outline here only changes within a single time step, and so we omit the time argument to keep the notation simpler. Let R_i be the intrinsic growth rate and K_i be the carrying capacity of species i, which we assume are constants across space and time. The competition coefficient α_{ij} is the effect of species j on species i. The degree of hybridization is determined by the value of β, which is the amount of consideration given to a heterospecific individual, relative to a conspecific individual, when choosing a mate. The actual amount of interspecific matings depends on the abundances of the two species (see Eq. 4.2 below).

The probability that an individual disperses to the adjacent deme to the left is $\delta_-(x)$, and the probability of dispersal to the right is $\delta_+(x)$. In the limit of infinitesimal units of time and space, these dispersal probabilities can be related to the diffusion coefficient and transport velocity (e.g. Nagylaki 1976; Shigesada and Kawasaki 1997, p. 57). We consider only barriers in which dispersal is reduced by a constant fraction c in a block of demes. Therefore, for demes well away from the barrier, $\delta_-(x) = \delta_+(x) \equiv \delta$; within the barrier, $\delta_-(x) = \delta_+(x) = c\delta$; for the deme to the left of the barrier, $\delta_-(x) = \delta$, $\delta_+(x) = c\delta$; and for the deme to the right of the barrier, $\delta_-(x) = c\delta$, $\delta_+(x) = \delta$. The edges of space are reflecting.

For Models 1 and 2, in one time step, the new population size of species i at location x due to competition is

$$n_i^*(x) = n_i(x) \left[1 + R_i \left(1 - \frac{n_i(x) - \alpha_{ij} n_j(x)}{K_i} \right) \right], \tag{4.1}$$

the population size after hybridization is

$$n_i^{**}(x) = \frac{[n_i^*(x)]^2}{n_i^*(x) + \beta n_j^*(x)}, \tag{4.2}$$

and finally, the population size after dispersal is

$$n_i^{***}(x) = [1 - \delta_-(x) + \delta_+(x)]n_i^{**}(x) + \delta_+(x-1)n_i^{**}(x-1) + \delta_-(x+1)n_i^{**}(x+1). \tag{4.3}$$

For the next generation, $n_i^{***}(x)$ becomes $n_i(x)$ in Eq. 4.1.

In Model 3, the evolution of a quantitative trait is affected by stabilizing selection toward an optimum value that varies over space, by competition with con- and heterospecifics (strongest for more similar phenotypes, independent of species identity), and by gene flow. The

derivation of this model is fairly complicated, so we refer the reader to Case and Taper (2000) for the original derivation and to Goldberg and Lande (2006) for the discretized version and incorporation of hybridization. Here, we define the parameter values only qualitatively, to assist with interpretation of Figure 4.3: $\theta(x)$ is the optimum phenotype, r is the intrinsic growth rate (in continuous time), σ_u is the width of the Gaussian resource utilization function, σ_z^2 is the variance of the Gaussian phenotypic distribution of each species at each location, σ_s^2 is the variance of the Gaussian stabilizing selection function, and h^2 is the heritability.
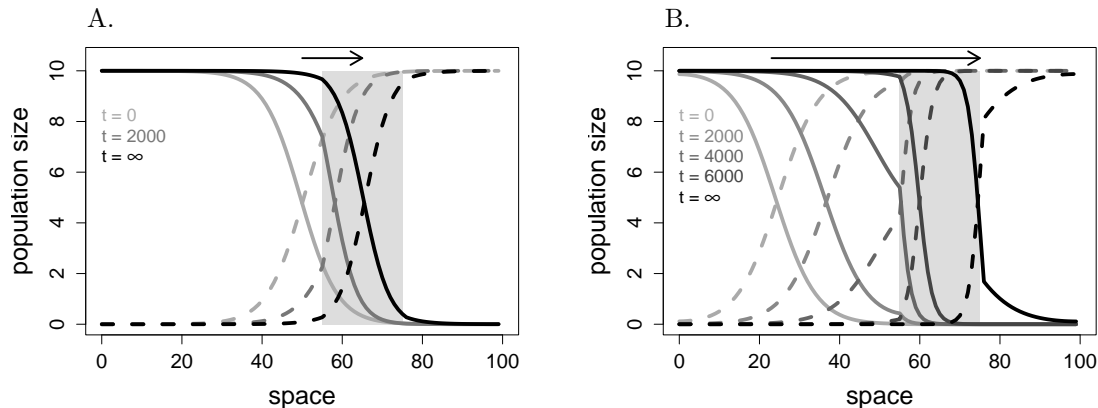
Figure 4.1: Model 1. A border between species, occurring when interspecific competition is stronger than intraspecific competition, is attracted to a partial dispersal barrier. (A) A border with a stable shape but neutrally stable spatial position (without a barrier) is attracted to the center of a region of reduced dispersal. Solid lines indicate the population size of one species, and dashed lines show that of the other species. Light gray lines (border at $x = 50$) give the equilibrium without a dispersal barrier; black lines (border at $x = 65$) show the equilibrium after a dispersal barrier (shaded rectangle) is imposed. The medium gray lines (border at $x = 58$) show an intermediate state with motion (indicated by the arrow) left to right. Parameter values are identical for each species: $R_i = 0.1$, $K_i = 10$, $\alpha_{ij} = 1.1$, $\delta = 0.2$, $c = 0.5$, $\beta = 0$; see Appendix for definitions. (B) A border that is otherwise a travelling wave is attracted to the edge of a region of reduced dispersal. The arrow indicates the direction of movement. Darkening shades of gray show three intermediate times, and black lines indicate the equilibrium position (border at $x = 75$). Parameter values are the same as in (A), except for $\alpha_{12} = 1.05$ and $c = 0.1$.
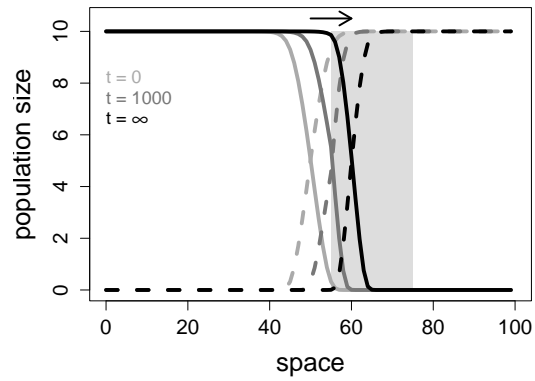
Figure 4.2: Model 2. Hybridization between species (with inviable hybrids) allows a border to form even when interspecific competition is not stronger than intraspecific competition, and this border is attracted to a partial dispersal barrier. The border does not become centered in the barrier, as it did in Fig. 4.1A, because the region of sympatry is narrow compared to the width of the barrier. Figure components are the same as in Fig. 4.1A (the final position of the border is $x = 61$), and parameter values are the same except for $\beta = 0.01$ and $\alpha_{ij} = 0.75$.
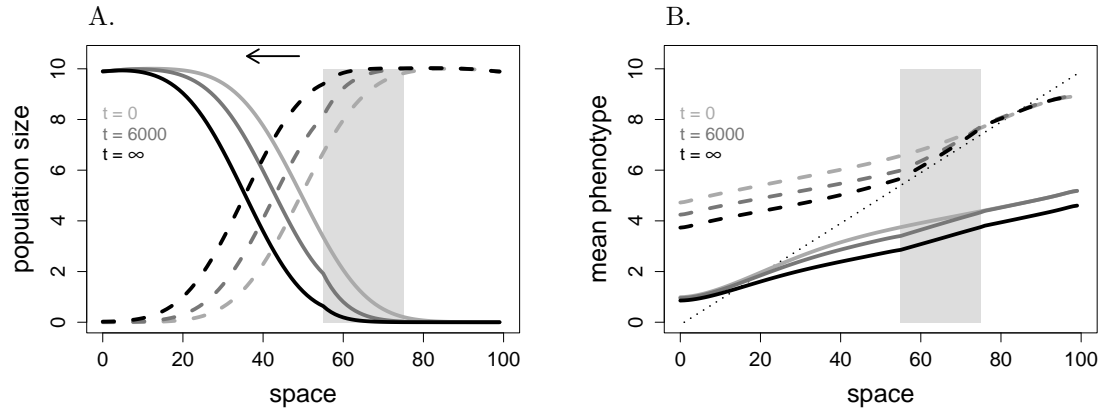
Figure 4.3: Model 3. A partial barrier to dispersal will repel, to some extent, a border maintained by local adaptation. In the species shown by the dashed line, local adaptation improves in the region of reduced dispersal, in which the mean phenotype evolves closer to the optimum (B), and the population size therefore increases in that region, pushing the border to the left (A). Figure components in (A) are the same as in Figs. 4.1A and 4.2; the border's final position is $x = 35$. Mean phenotypes are plotted in (B), and the optimum phenotype is shown by the thin dotted line. Parameter values are $r_i = 0.1$, $K_i = 10$, $\sigma_z^2 = 1$, $\sigma_u^2 = 25$, $\sigma_s^2 = 300$, $h^2 = 0.5$, $\theta(x) = 0.1x$, $\delta = 0.2$, $c = 0.5$, $\beta = 0$; see Appendix for definitions.

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