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.

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
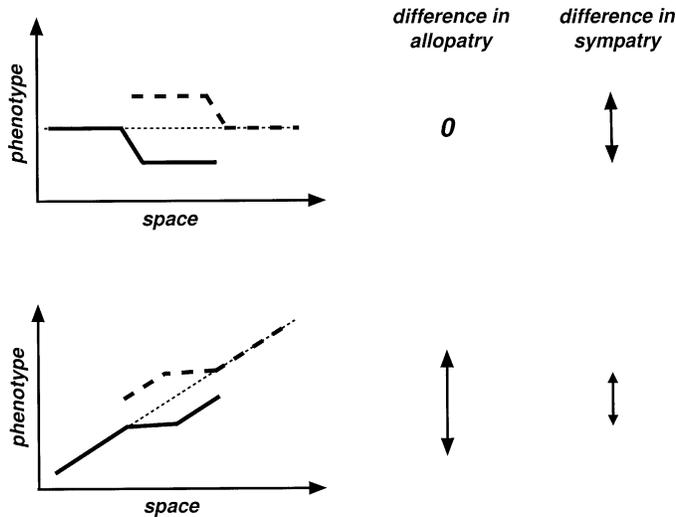
FIG. 1. Differences in sympatry and allopatry. When the optimum phenotype is constant over space, character displacement gives rise to the classic pattern of greater divergence in sympatry than in allopatry (top). When the optimum phenotype increases monotonically over space, phenotypes may differ more 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-

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 σ_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):

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

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

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

where we have approximated the mean Wrightian fitness as

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

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:

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

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:

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

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

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

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.

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

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
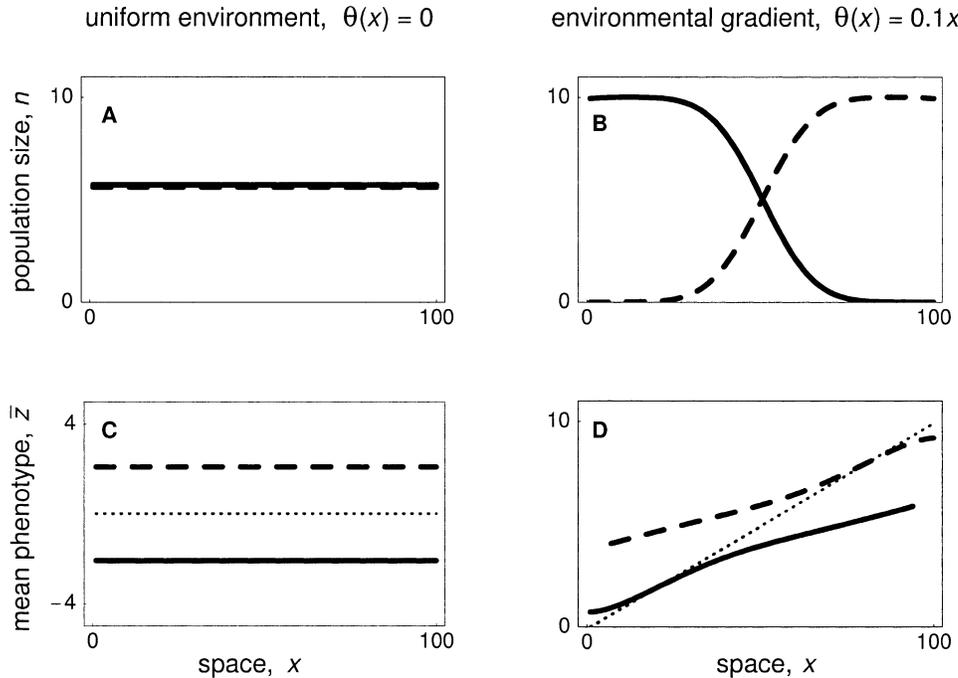
FIG. 2. Model 1, no hybridization. Ecological character displacement may occur with or without a stable border between the species, but a stable border requires an environmental gradient. The left panels show the population sizes (A) and mean phenotypes (C) for each species (solid and dashed lines, truncated 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 $\sigma_z^2 = 1$.

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
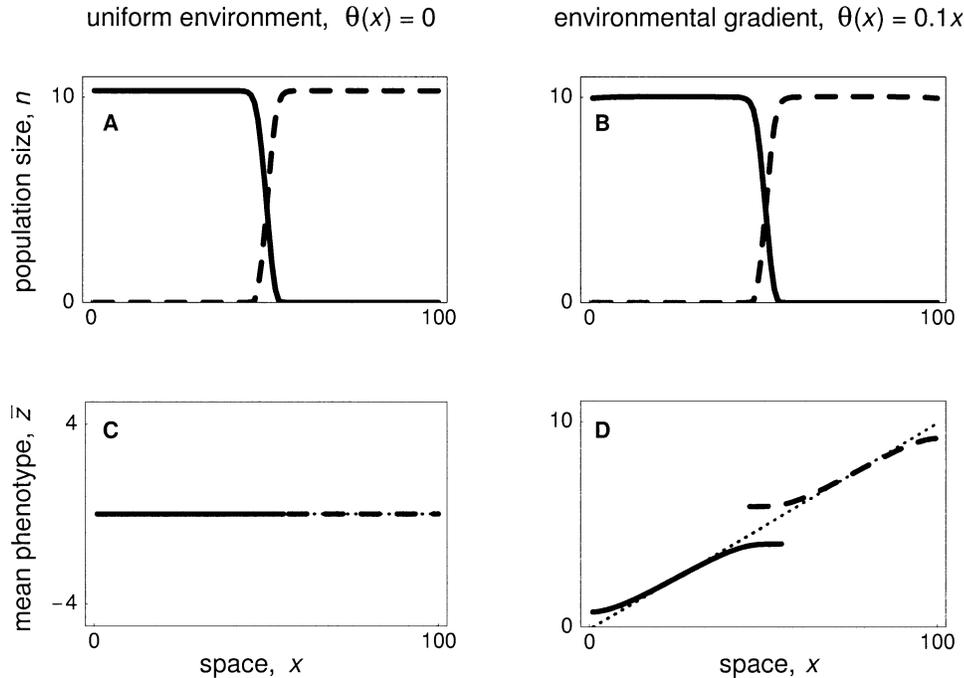
FIG. 3. Model 1, with hybridization. A small amount of hybridization, independent of phenotype, allows a stable border to form in the absence of an environmental gradient (A), but in so doing removes character displacement (C). With an environmental gradient, hybridization narrows the region of sympatry (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.
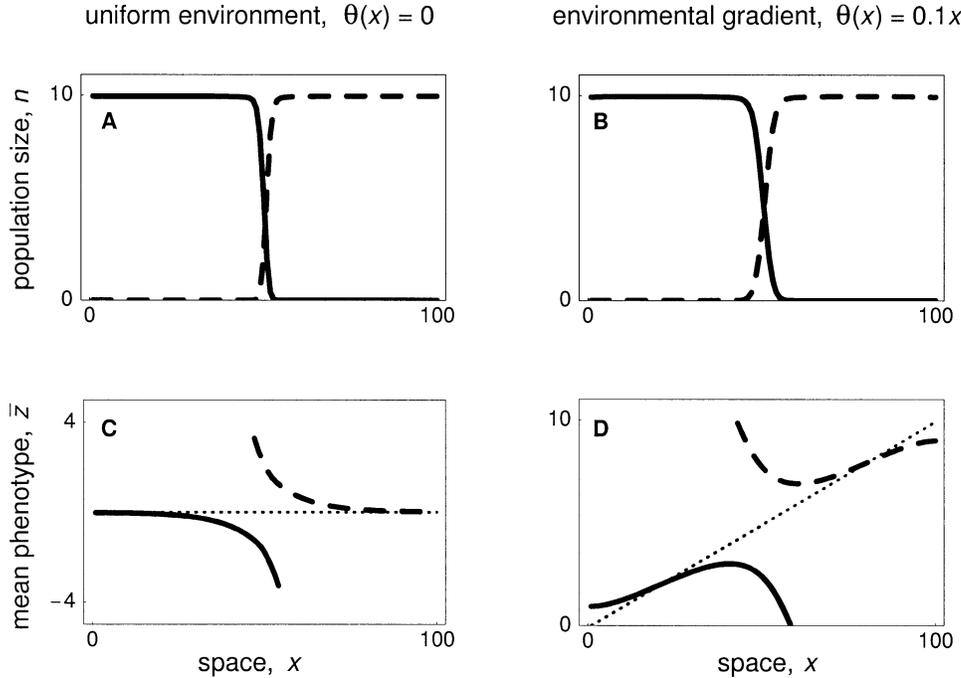
FIG. 4. Model 2: Reproductive character displacement and a stable border arise with or without an environmental gradient. Without a gradient (A, C), the species differ more in sympatry than in allopatry. With a gradient (B, D), this pattern is obscured. The panel layout is the same as in Figures 2 and 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:

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

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

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, $\theta(x) = 0.1x$
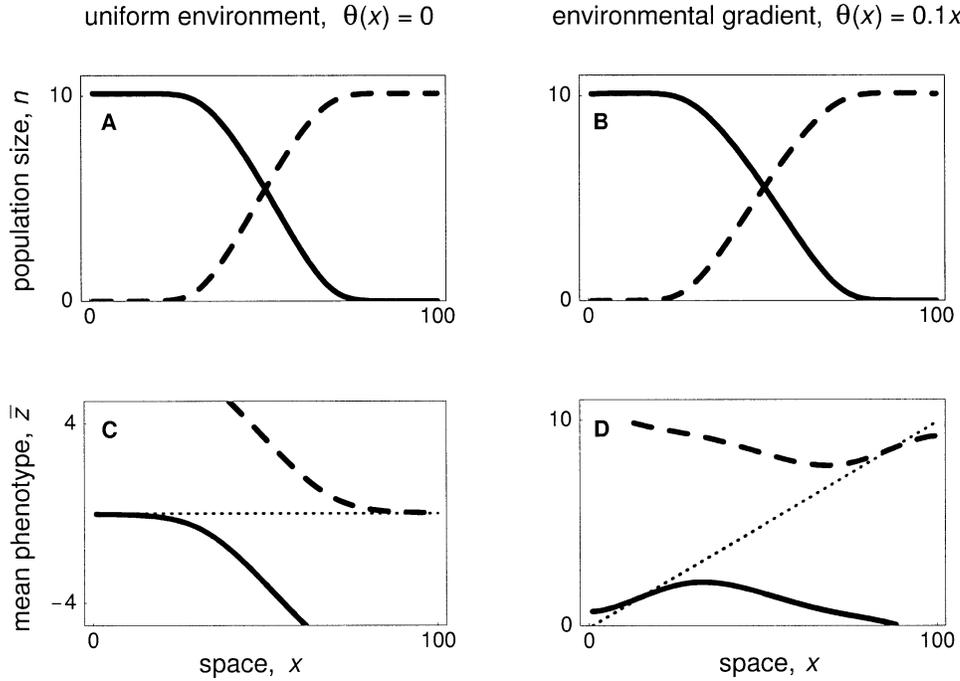
FIG. 5. Model 3: Character displacement occurs in a trait that affects both resource competition and assortative mating. The shapes of the clines are qualitatively intermediate between those in Figures 2 and 4. Hybridization allows a stable border to form even in the absence of an environmental gradient (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:

$$\bar{W}_i^* = \exp\left[r - \frac{r}{K}\sqrt{\frac{\sigma_u^2}{\sigma_u^2 + \sigma_y^2}}\left\{n_i + n_j\exp\left[\frac{-(\bar{y}_i - \bar{y}_j)^2}{4(\sigma_u^2 + \sigma_y^2)}\right]\right\}\right]$$

$$\times \exp\left[-\frac{\sigma_y^2 + (\theta_y - \bar{y}_i)^2}{2\sigma_{s,y}^2}\right]\exp\left[-\frac{\sigma_z^2 + (\theta_z - \bar{z}_i)^2}{2\sigma_{s,z}^2}\right].$$

$$(23)$$

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:

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

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

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

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

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

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

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

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

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).
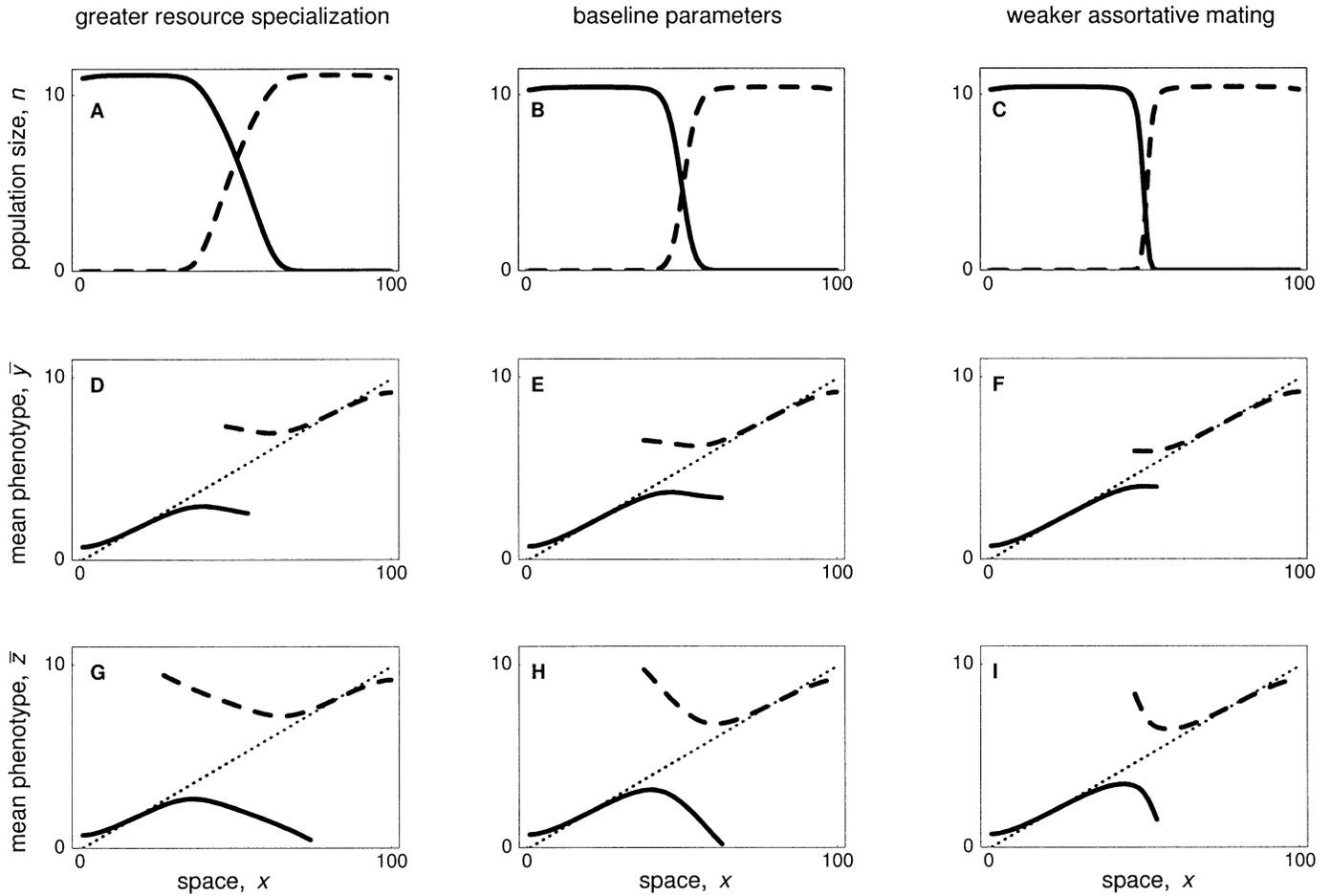
FIG. 6. Model 4: Changing the action of one trait (either ecological or reproductive) has an indirect effect on the evolution of the other trait. The top row shows the population sizes, the middle row shows the mean ecological phenotypes, and the bottom row shows the mean reproductive phenotypes. The 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

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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