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Patterns of Species Ranges, Speciation, and Extinction

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ABSTRACT: The exact nature of the relationship among species range sizes, speciation, and extinction events is not well understood. The factors that promote larger ranges, such as broad niche widths and high dispersal abilities, could increase the likelihood of encountering new habitats but also prevent local adaptation due to high gene flow. Similarly, low dispersal abilities or narrower niche widths could cause populations to be isolated, but such populations may lack advantageous mutations due to low population sizes. Here we present a large-scale, spatially explicit, individual-based model addressing the relationships between species ranges, speciation, and extinction. We followed the evolutionary dynamics of hundreds of thousands of diploid individuals for 200,000 generations. Individuals adapted to multiple resources and formed ecological species in a multidimensional trait space. These species varied in niche widths, and we observed the coexistence of generalists and specialists on a few resources. Our model shows that species ranges correlate with dispersal abilities but do not change with the strength of fitness trade-offs; however, high dispersal abilities and low resource utilization costs, which favored broad niche widths, have a strong negative effect on speciation rates. An unexpected result of our model is the strong effect of underlying resource distributions on speciation: in highly fragmented landscapes, speciation rates are reduced.

Keywords: adaptive radiation, rare species, lognormal, coexistence, fragmentation, trade-off.

Introduction

The complex interactions among species ranges, speciation, and extinction have been the focus of macroecological and macroevolutionary studies for decades (Mayr 1963; Rosenzweig 1995; Gaston 2003). The relationship between species ranges and speciation has been particularly puzzling with two contradictory expectations (Gaston 2003). One view that goes back to Darwin (1859) holds that large range sizes should increase speciation rates.

Larger ranges increase the opportunity to encounter not only new habitats but also barriers that would isolate populations and promote speciation (Rosenzweig 1995; Gaston 2003). Moreover, larger ranges could mean larger population sizes that allow for accumulation of advantageous mutations for selection to act on. There is some evidence to support this view: Owens et al. (1999) found that diversification rates among bird families were positively correlated with generalist feeding habits and good dispersal capabilities as well as large and fragmented geographical ranges (also see Phillimore et al. 2007). Similarly, Cardillo et al. (2003) found a positive correlation between species ranges and diversification rate in Australian mammals.

On the contrary, the same factors that promote larger ranges, such as high dispersal abilities and broad niche widths, should render species insensitive to barriers, which should damp speciation (Mayr 1963; Stanley 1986). Moreover, species with low dispersal abilities or narrower niche widths tend to have more fragmented populations. Isolated populations experience reduced gene flow that could render them more prone to speciation (Gavrilets et al. 2000). Indeed, replicated adaptive radiations tend to occur in taxa that are poor dispersers (Losos 2010). Likewise, Jablonski and Roy (2003) also showed that for Cretaceous and present-day molluscan taxa, the factors that promote large geographical ranges also reduce speciation rates. In an extensive review, Palumbi (1992) showed that in marine systems, species with low dispersal abilities tend to have high speciation rates. Narrow niche widths were also associated with increasing diversity in copepod communities in Kenya (De Troch et al. 2001). For African primates, Eely and Foley (1999) found that in areas of high species richness, species occupied smaller ranges and are relatively specialized in terms of the number of habitats occupied and the number of food types used.

Thus, the exact nature of the relationship between geographical ranges and speciation remains unknown (Gaston

1996, 1998, 2003; Chown 2003). Part of the problem that causes contradictory expectations about species ranges and speciation lies in the assumption that high dispersal abilities and broad niche widths translate into large ranges (Lester et al. 2007). However, high dispersal abilities and broad niche widths may not always promote large ranges (Gaston 1996, 2003). Lester et al. (2007) show that in most cases dispersal abilities do not correlate with range sizes. Likewise, it has also been demonstrated that niche widths do not correlate with range sizes (e.g., Gregory and Gaston 2000; Lehman 2004; Hobbs et al. 2010).

The relationship between species ranges and extinction is also not very intuitive. The global patterns of species range size distributions are strongly right skewed, with a lot of small-range species and a few species with very large ranges (Gaston 1998, 2003). The majority of the distributions are significantly left skewed when log transformed, which implies that there are disproportionately more species with restricted ranges, and there is deficiency in wide ranging species (Gaston 1998). This is puzzling at first, since if range sizes are powerful predictors of extinction probabilities (Kiessling and Aberhan 2007; Jablonski 2008), then the overabundance of species with small ranges would seem to contradict the prediction that they should become extinct.

We have built an individual-based model to shed some light on the joint dynamics of speciation, extinction, and species ranges. Individual-based models have been powerful tools in identifying and understanding emergent behaviors of systems based on individual traits/behaviors (DeAngelis and Mooij 2005). With increasing computing power, complicated evolutionary scenarios are becoming more accessible to modeling, and general conclusions about sympatric speciation and adaptive radiations are beginning to emerge through accumulation of many individual-based models (e.g., Dieckmann and Doebeli 1999; Kawata 2002; Doebeli and Dieckmann 2003; Gavrilets and Vose 2005, 2007, 2009; Gavrilets et al. 2007; Duenez-Guzman et al. 2009; Sadedin et al. 2009; Thibert-Plante and Hendry 2009). Thus, individual-based models are useful tools in identifying key parameters influencing the dynamics of systems and developing our intuition, provided that large parameter spaces are explored (Gavrilets 2004; Waxman and Gavrilets 2005).

Here, we model evolutionary dynamics of hundreds of thousands of sexual and diploid individuals that occupy large landscapes for more than 200,000 generations with realistic mutation rates. Our model is built on a family of individual-based models that have been studied extensively. Gavrilets and Vose (2005, 2009) modeled speciation by adaptation to multidimensional niches and successfully captured the general patterns of adaptive radiations (Schluter 2000; Gavrilets and Losos 2009). Later, the same framework was tailored to specific taxa to make theoretical predictions about the plausibility of speciation in cichlids (Gavrilets et al. 2007), palms (Gavrilets and Vose 2007), snails (Sadedin et al. 2009), and butterflies (Duenez-Guzman et al. 2009). Here, we borrow from previous frameworks by Gavrilets and Vose (2005, 2009) and also by Kawata (2002), with a few differences in the assumptions about resource distributions, dispersal abilities, and the fitness functions. In our model, the patches in the landscape are defined by a single resource they contain rather than by multidimensional niches. The patches have realistic distributions on the landscape through fractal algorithms (Saupe 1988) instead of being randomly distributed. As in Kawata (2002), each individual has a roaming range composed of a few patches where it can collect resources. The individuals' resource utilization efficiencies depend on how well individuals' ecological traits match the resources, as well as on the trade-offs between ecological traits. The trade-off between ecological traits allows for generalists to emerge rather than solely specialists, as observed by Gavrilets and Vose (2005, 2009). Finally, the individuals have varying dispersal ranges. These last two additions to the model are the focus of this study, since we are interested in the effects of dispersal abilities and niche widths on species ranges and on patterns of speciation and extinction.

We show that species ranges are a result of complex interactions between speciation and extinction. Species ranges respond to increasing dispersal abilities, but they do not increase with decreasing trade-offs associated with resource utilization, which favored broad niche widths. We also show that high dispersal abilities and decreasing fitness trade-offs negatively affect speciation rates. Furthermore, fragmented resource distributions on the landscape have a strong negative influence on speciation rates. Fragmented resource distributions created through fractal algorithms are increasingly being used in ecological and evolutionary models to address questions such as effects of habitat fragmentation on species distributions (With et al. 1997), dispersal patterns (King and With 2002), and extinction thresholds (With and King 1999). To our knowledge, this model is the first application of a fractal algorithm demonstrating effects of resource distributions and habitat fragmentation on speciation.

Our main objective behind this study is to model the complex interactions among species ranges, speciation, and extinction; however, there were also a few interesting a posteriori observations from the model that we discuss, namely, coexistence of generalists and specialists and lack of reinforcement among species. Coexistence of specialists and generalists has been documented in several cases in nature (McPeek 1996; Morris 1996; Kido 1997; Hanski et al. 2001; Kassen 2002; Ryan et al. 2007; Traba et al. 2010).

In theoretical models, coexistence has generally been limited to two specialists and/or one generalists (Kisdi 2002; Egas et al. 2004; Abrams 2006, but also see Huisman and Weissing 1999 for coexistence of multiple competitors on fewer resources). In contrast, we show that a high diversity of species, as many as 15, can coexist on four resources. Lastly, we show that divergence in mating traits among populations adapted to different resources may not be as common as previously thought due to the "porous genome" effect, which might explain why complete reproductive isolation among ecological species is rare (Schluter 2001, 2009; Hendry et al. 2007; Hendry 2009).

The Model

In this section, we outline our model. The simulations were written using the programming language C, and the code is available from the authors on request.
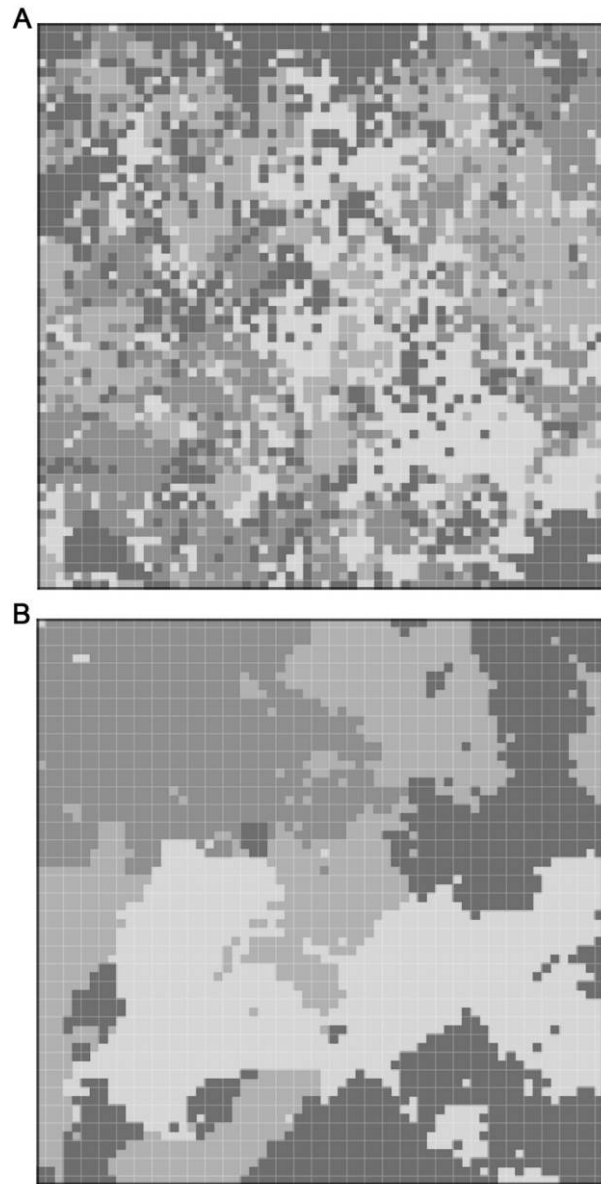
Landscape and Resources

In our model, the landscape is composed of an array of patches, each of which can support a population of a certain size. Individuals, however, are not restricted to single patches. Depending on their preferences, they can use resources from other patches within their roaming ranges and compete with other individuals within those patches. Patches differ in the type of resource they contain. There are k different resources distributed across the landscape.

We created fractal resource distributions across the landscape using the midpoint displacement algorithm by Saupe (1988; also see appendix). With fractal algorithms, it is possible to realistically replicate the habitat structures observed in nature (Hargrove et al. 2002). We varied the spatial contagion of habitat (H; $d = 3 - H$, where H is the Hurst exponent of the fractional Brownian motion and d is the fractal dimension of the surface) to create complex landscape patterns with high and low levels of fragmentation (figs. 1, S1, available online). In highly fragmented landscapes (with low values of H), patches with the same resource form smaller-sized clusters, and most of the patches become "edge habitats," which have a neighboring patch with a different resource. Less fragmented landscapes (with high values of H) provide larger-sized clusters that do not have patches with different resources as neighboring patches. Unlike Gavrilets and Vose (2005), resource distributions do not change over time.

Individuals

Individuals are diploid and have discrete sexes. Each individual has k ecological traits, and k resource preference traits. The resource utilization efficiency of an individual

Figure 1: Sample landscapes created with different fractal dimensions H. Four different resources are shown in different shades of gray. *A*, Having $H = 0.1$ results in highly fragmented landscape (from simulation shown in fig. 2*A*); *B*, $H = 0.9$ results in lower levels of fragmentation (from simulation shown in fig. 2*D*).

(see "Resource Preference and Utilization" below) is determined by its ecological traits x_i (where $i = 1, 2, \ldots, k$). The preference trait y_i controls resource preference, which determines the time spent in each patch within the individual's roaming range (see "Resource Preference and Utilization"), as well as the dispersal probability to a patch within the dispersal range (see "Dispersal of

Offspring"). In addition to the ecological and resource preference traits, each individual has three mating compatibility characters *m*, *f*, and *c*. We assume that *m* is a male display trait expressed only in males, *f* and *c* are female preference traits expressed only in females. The trait *f* is the value of the male trait she prefers the most, and trait *c* determines the degree of her choosiness (see "Mating").

Each trait is additive and is controlled by *L* different unlinked diallelic loci with equal effects. All traits are scaled to be between 0 and 1. Mutations occur at equal rates across all loci and the probabilities of backward and forward mutations are equal. In addition to the above traits, there are *M* unlinked neutral microsatellite loci subject to higher rates of stepwise mutation to observe the levels of genetic divergence within and between species that one would detect using microsatellite markers.

Life Cycle

The life cycle consists of the following events: (1) resource utilization within the roaming range, (2) mating, (3) density-dependent fertility selection and offspring production, and (4) dispersal of offspring. Generations are discrete and nonoverlapping.

Resource Preference and Utilization. Individuals utilize resources from multiple patches within their roaming ranges. The time spent by the individual *I* in a patch within the $n \times n$ roaming range is proportional to the individual's preference ρ for the resource present in that patch. Thus, individual *I* spends $T(I, p)$ of its time in a patch *p*:

$$T(I, p) = \frac{\rho_p}{\sum_{j=1}^{n \times n} \rho_j}, \tag{1}$$

where ρ is the individual's preference for the resource present in that patch. The preference for the resource in a patch is given by a linear function of the preference trait y_i (Gavrilets and Vose 2005):

$$\rho = \tau + (1 - 2\tau)y_i, \tag{2}$$

where *i* is the resource present in that patch and $\tau = 0.001$. Equations (1) and (2) imply that the individual spends more time in patches that it has high preference for.

We assume that the ecological traits x_i that are used to utilize resources within these patches are under directional selection and that the unused ecological traits x_j ($j \neq i$) are costly to the individuals. Thus, individuals' resource utilization efficiencies depend on how well their ecological traits match the resource present in a patch and on the trade-offs between different ecological traits (see "Density-

Dependent Fertility Selection"). The individual's resource utilization efficiency is given by a Gaussian function, where trait values that are close to, but not necessarily at, the optimum value of 1 result in high gains due to efficiency. On the contrary, the trade-off is modeled such that even small trait values of unused ecological traits have relatively high costs. The efficiency e_p of an individual in patch *p* with resource *i* is given by

$$e_p = \exp\left[-\alpha(x_i - 1)^2\right] \prod_{j \neq i} \exp\left(-\beta x_j^{1/2}\right), \tag{3}$$

where α measures the strength of directional selection and β is the trade-off coefficient that affects the cost associated with unused traits (e.g., if $\beta = 0$, then there is no cost for having traits that are not used). Term x_i is the ecological trait that utilizes the resource *i* that is present in patch *p*, and x_j represents $k - 1$ other ecological traits that are not used within that patch. The first term in equation (3) determines the gain from using the resource *i* that is present in patch *p*. The second term governs the trade-off. Note that since there is only one resource per patch, $k - 1$ other ecological traits are not used within patch *p* and the individual suffers a cost for having unused traits. If the cost is high, a specialist (or individuals with a narrow niche width; for species definitions, see appendix) will have an advantage over generalists (individuals with broader niche width). In the simulations, different values of β were chosen such that specialists would have advantages over generalists or vice versa (see fig. S2, available online).

A common approach for modeling fitness trade-offs in evolutionary ecology is to focus on a single trait continuously changing within a certain interval, assuming that extreme values of the trait result in a very efficient use of one resource and a very inefficient use of the other resource. Then the generalists are individuals with intermediate trait values. Two disadvantages of this approach are that it does not allow for individuals who are good in utilizing both resources and it does not generalize to more than two resources. Our model is free from these limitations. In our approach the generalists are individuals who have extreme values for two or more traits that allow them to use two or more resources.

Each individual has a roaming range of $n \times n$ patches where it utilizes resources; thus, the efficiency values e_p are summed across each individual's roaming range:

$$E = \sum_{p=1}^{n \times n} e_p T(I, p), \tag{4}$$

where *E* is the total resource utilization efficiency of the individual, $T(I, p)$ is the time spent by the individual *I* in patch *p* (eq. [1]).

Mating. The relative probability of mating $\psi(m, f, c)$ be-

tween a female with mating traits f and c and a male with mating trait m is calculated as (Dieckmann and Doebeli 1999; Gavrilets et al. 2007; Gavrilets and Vose 2009):

$$\psi(f, c, m) =$$

$$\begin{cases} \exp\left[-(2c-1)^2 \dfrac{(f-m)^2}{2\sigma_a^2}\right] & \text{if } c > 0.5 \\ 1 & \text{if } c = 0.5, \\ \exp\left\{-(2c-1)^2 \dfrac{[f-(1-m)]^2}{2\sigma_a^2}\right\} & \text{if } c < 0.5 \end{cases} \quad (5)$$

where parameter σ_a scales the strength of female mating preference.

Under this parameterization, females with $c = 0.5$ mate randomly, and increasing deviation of c from that implies that preferences get stronger. Females with $c > 0.5$ prefer males with display traits m that are close to their preference traits f (positive assortative mating), and finally, females with $c < 0.5$ prefer males with display traits that are close to $1 - f$ (negative assortative mating).

Females are exposed to males within their patch (which is likely to be the most preferred patch; see "Dispersal of Offspring"). If there are no males in a female's patch, then the female searches for males in other patches within her roaming range. The probability of picking a patch is proportional to her preference for that patch ρ (eq. [2]). All females mate, unless their ranges do not overlap with that of a male, which means that there are no costs of choosiness. Any cost greatly reduces the opportunity for rapid speciation (e.g., Bolnick 2004; Gavrilets 2004); however, it does not really change the patterns in our model due to our definition of species (see appendix). Each mating results in a number of offspring drawn from a Poisson distribution with parameter ν (see next section). The sex of each offspring is determined randomly.

Density-Dependent Fertility Selection. The fertility ν of an individual I is given by the discrete time Beverton-Holt model (Gavrilets and Vose 2009):

$$\nu(I) = \frac{b}{1 + [(b/2) - 1][N_c(I)/K]}, \quad (6)$$

where b is the average number of offspring of the most fit female, $N_c(I)$ is the effective number of competitors experienced by the individual I in the patch, and K is analogous to carrying capacity of a genotype determined by its resource utilization efficiency E (eq. [4]):

$$K = K_0 E, \quad (7)$$

where K_0 is the maximum carrying capacity.

The effective number of competitors experienced by an individual I is calculated through the encounter rate of individuals within its roaming range, which is responsible for the spatial overlap:

$$N_c(I) = \sum_{p=1}^{n \times n} \sum_{I'} T(I, p)T(I', p), \quad (8)$$

where $T(I, p)$ is the proportion of time spent by the individual in that patch (eq. [1]).

The Beverton-Holt model is the equivalent of continuous time logistic growth (Yodzis 1989), where populations experience density-dependent regulation due to low carrying capacity of the environments or high population sizes experienced by the individuals. In our model, the fertility of a female is density dependent and is reduced if she is not well adapted to the resources and not very efficient in utilizing them (eq. [7]) or if the number of competitors N_c in her roaming range is large. The number of competitors that is experienced by an individual typically is calculated through trait and/or spatial overlap between the focal individual and the other individuals (e.g., Doebeli and Dieckmann 2003). We assume that the number of competitors an individual experiences depends on the time it spends in patches. Time spent $T(I, p)$ is responsible for the encounter rate, or spatial overlap between the individual I and other individuals in patch p. If the individual spends most of its time in a single patch that it prefers the most, it is going to compete with the individuals in that patch more than the ones in a patch where it spends little time (eq. [8]).

Dispersal of Offspring. The offspring can disperse to other neighboring patches within their dispersal ranges D. The probability of dispersal to a patch depends on the preference of the offspring to that patch (eq. [2]). The number of patches available for emigration is reduced according to the number of neighboring patches at the landscape boundaries.

Initial Conditions and Parameters

Each simulation is started with 20 individuals that we introduced to the top left corner patch and that are not adapted to, or have preference for, any of the resources present in the landscape ($x_i = y_i = 0$, $\forall i = 1, 2, \ldots, k$). Individuals are identical homozygotes with the mating traits at $c = f = m = 0.5$ (first two are expressed in females and the latter only in males). Note that initially females are not choosy, and mate randomly. Individuals' sexes are determined randomly.

The following parameters were varied in the simulations: (1) spatial contagion (or simply fractal index) for resource distribution ($H = 0.1, 0.9$) across the landscape,

(2) dispersal range ($D = 3 \times 3, 9 \times 9, 15 \times 15$), and (3) the cost associated with having ecological traits that are not used in the individual's current patch ($\beta = 0.2, 0.4, 0.6$).

Parameters that did not change during the simulations are average number of offspring of the most fit females $b = 4$, maximum carrying capacity $K_0 = 30$, roaming range size $= 5 \times 5$ patches, strength of female mating preference $\sigma_a = 0.05$, strength of directional selection $\alpha = 3$, landscape size $= 64 \times 64$, number of resources/traits $k = 4$, number of loci for all the traits $L = 8$ with mutation probability $\mu_L = 10^{-5}$, and number of microsatellite loci $M = 8$ with mutation probability $\mu_M = 10^{-3}$. Most of these parameters are based on previous theoretical studies and their effect on speciation are well understood (Gavrilets and Vose 2005, 2007, 2009; Gavrilets et al. 2007; Duenez-Guzman et al. 2009; Sadedin et al. 2009). We carried out additional simulations with some of the new fixed parameters ($\tau = 0.01$ and $K = 20$), and they had no significant effects on time to speciation, durations of specialist-generalist coexistence, and range size distributions (Kolmogorov-Smirnov test at 0.05 level).

Theoretical Results

For each of the eighteen ($2 \times 3 \times 3$) parameter combinations given above, we ran 20 simulations for 200,000 generations. Populations survived in all runs for the entire duration of the simulation. Before we present the general results based on the 360 simulations, we present sets of results from four separate runs to provide insight into the workings of the model in figures 2, 3 (also see figs. S3, S4, S5, available online). Figure 2 shows four simulations at generation 200,000 where different species are shown with colored circles that are overlaid on the landscape composed of patches with different resources. Different values of fragmentation H, dispersal range D, and trade-off coefficient β lead to very different communities: some have high diversity (fig. 2A), some have only a single species (fig. 2B), and in some, specialists and generalists coexist (fig. 2D). We provide a more detailed description of our species definition in the appendix. Briefly, specialists utilize only one resource and they have ecological trait values that are close to the optimum trait value of 1 (see eq. [3]). Generalists utilize more than one resource efficiently and are categorized according to the number of resources they utilize. Since there are four resources, there can be 16 species total: an ancestral species that is not adapted to any resource, four specialists, six two-resource generalists, four three-resource generalists, and one four-resource generalist. The number of resources a species utilizes defines the species niche width.

The ecological species as we define them here are also distinguishable genetic clusters (see the same populations in four dimensional ecological trait space in fig. 3). These distinct clusters, or species, emerge very quickly, and remain stable for hundreds of thousands of generations (fig. S3; also see fig. S6, available online, for the distribution of waiting times to speciation across all simulations). Reproductive isolation between the ecological species is further strengthened by the evolution of resource preferences, since mating occurs in patches that the individuals prefer the most. Resource preferences evolve quickly, and there is a strong correlation between the ecological traits x and the preference traits y (fig. S4). Some ecological species also diverge in their mating traits (appendix; fig. S5); however, mating traits were often shared across ecological species (fig. S5A, S5C). Similarly, there was little or no differentiation in neutral loci: F_{st} values across ecological species were generally low. These last two observations relate to lack of reinforcement and porous genome effect that we discuss in "Discussion."

### Coexistence of Generalists and Specialists

An interesting result observed in our model is the coexistence of generalists and specialists: in some simulations 15 species with varying niche widths coexisted on four resources (tables 1, 2; also see figs. 2A, 3A). Coexistence of generalists and specialists is a puzzling phenomenon (Wilson and Yoshimura 1994; Egas et al. 2004; Abrams 2006) because if a specialist has higher fitness due to utilizing one resource, it should exclude the generalist. Or alternatively, if a generalist has an advantage utilizing multiple resources despite the associated costs, it should exclude the specialist. In our model, the spatial structure and the way individuals' fitnesses depend on their resource preferences create complex fitness landscapes that allow for coexisting specialists and generalists. The effects of fragmentation H, trade-off coefficient β, and dispersal ranges D on coexistence of generalists and specialists are similar to their effect on speciation rates (see below): high habitat fragmentation, high dispersal, and broad niche widths reduce the duration of coexistence (table 1); note that the terms "specialists" and "generalists" are used in quotes in the title since we included the cases when the two species differ only in one dimension. For example, in figures 2D and 3D, even though the maroon-colored specialist ($x \approx 0, 0, 1, 0$) and the blue colored two-resource generalist ($x \approx 1, 0, 0, 1$) are true specialists and generalists, they differ in three dimensions and in not really coexisting on a "shared" resource. However, there are multiple species that differ only in a single dimension in figures 2A and 3A. For example, the red-colored specialist $x \approx (1, 0, 0, 0)$ and the light-blue-colored two-resource generalist $x \approx (1, 0, 0, 1)$ coexist on one resource.
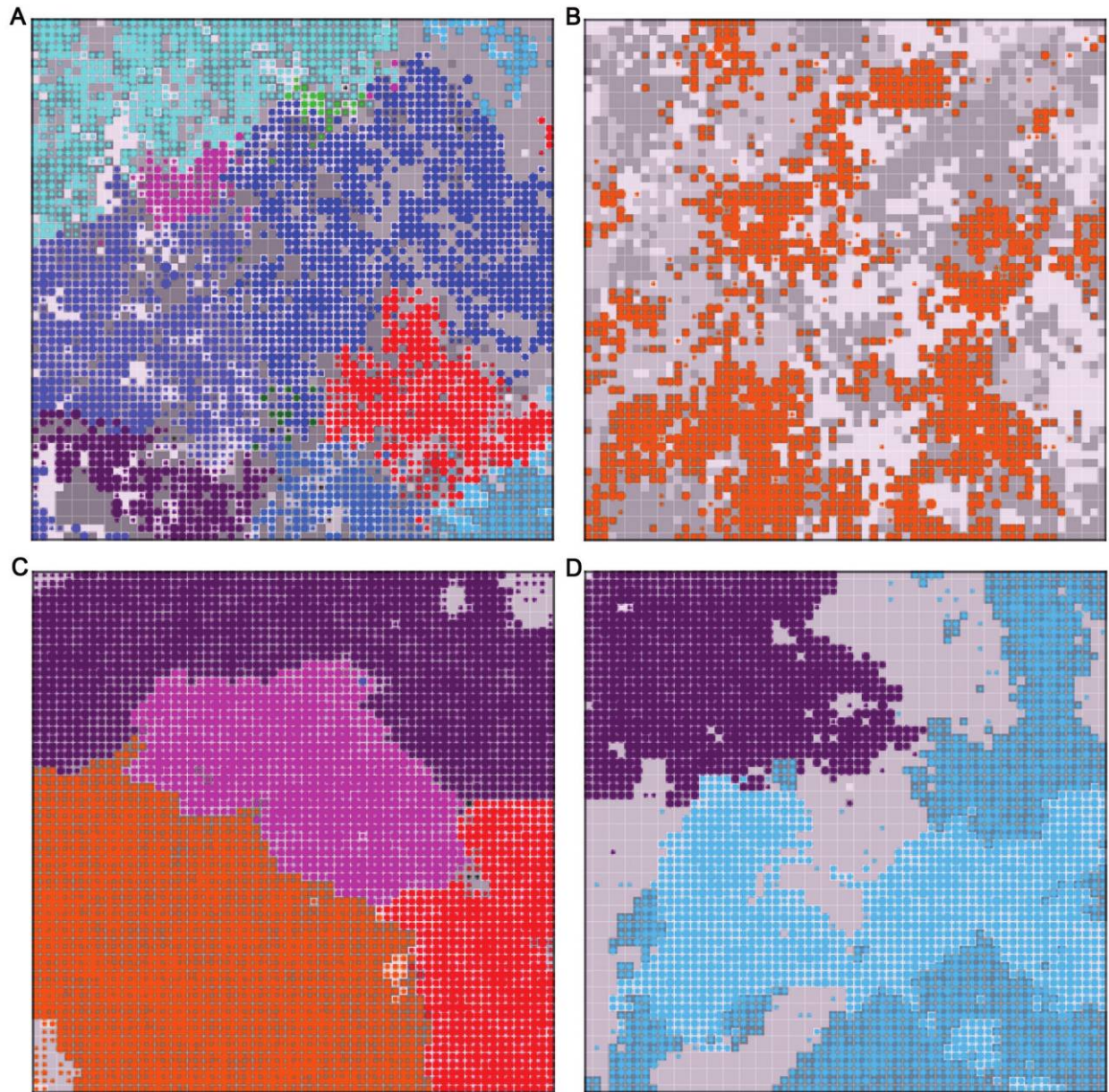
Figure 2: Examples of simulations after 200,000 generations with different values of fragmentation H, dispersal range D, and trade-off coefficent β. The landscape has 64×64 patches. Patches with different resources are shown as squares in different shades of gray in the background. Populations are represented as colored circles, the size of which is proportional to the population size (the maximum radius corresponds to a population at its carrying capacity). The color of each circle represents the most abundant species in the patch. Since there are four resources, there can be four specialists (shades of red), six two-resource generalists (shades of blue), four three-resource generalists (shades of green), and one four-resource generalist (white). The fractal index $H = 0.1$ for the simulations on the first row (A, B); $H = 0.9$ for the simulations on the second row (C, D). The dispersal range is low (3×3) in the left column (A, C) and high (9×9) in the right column (B, D). A, There are three specialists, five two-resource generalists, and two three-resource generalists coexisting ($H = 0.1$, $D = 3 \times 3$, $\beta = 0.4$). B, Single specialist ($H = 0.1$, $D = 9 \times 9$, $\beta = 0.6$). C, Four specialists coexisting ($H = 0.9$, $D = 3 \times 3$, $\beta = 0.4$). D, A specialist with a two-resource generalist coexisting ($H = 0.9$, $D = 9 \times 9$, $\beta = 0.4$).
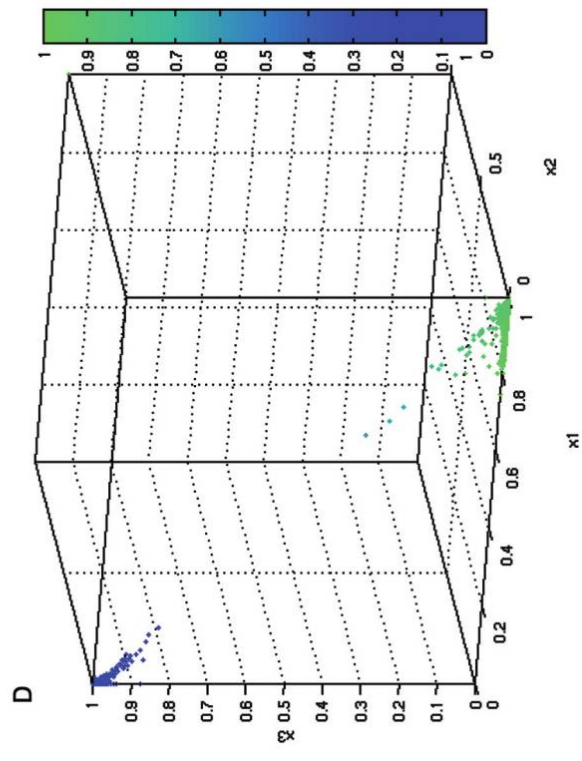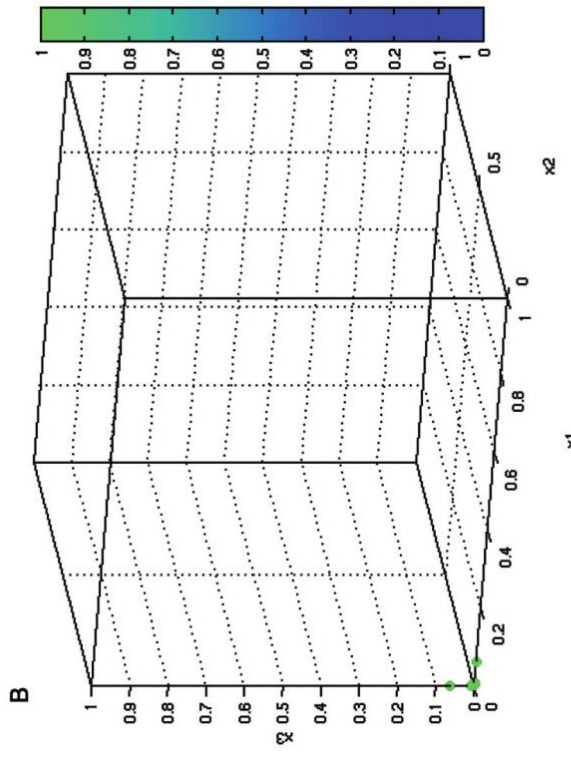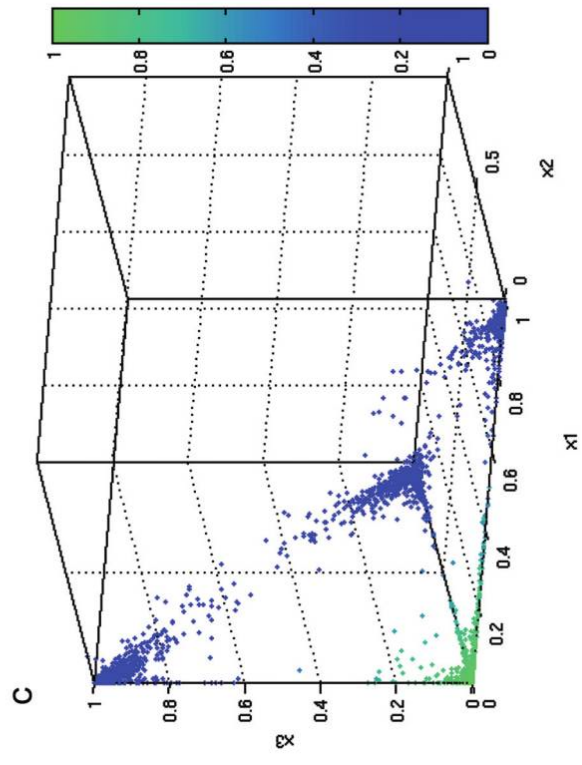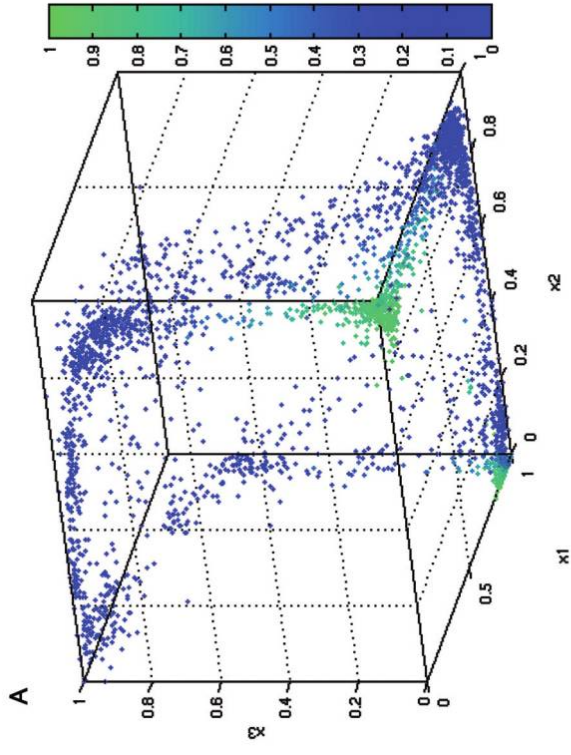
Range Sizes and Distributions

Range sizes respond to increases in dispersal ranges D; however, trade-off coefficients β did not influence the species ranges significantly (fig. 4; range size is calculated as the number of patches that are occupied by a species; maximum range size is the entire landscape composed of patches). Moreover, there were no significant differences between the range sizes of specialists and generalists. The species range size distribution across all simulations (fig. 5) follows a typical pattern observed in many taxa, where there are a lot of species with small ranges and a few species with large ranges (Gaston 1996, 1998, 2003). The resulting log–range size distribution from these simulations is also significantly left skewed (skewness: −1.06, SE of skewness: 0.06).

Extinctions

When we look at the species that became extinct during the simulations, we see that range sizes are the best predictor of extinction probabilities (fig. 6). There is a strong negative correlation ($R^2 = 0.79$) between species range sizes and proportion of species that became extinct. Even though a strong right skew of the species range size distributions was still observed at generation 200,000 (fig. 5), more than a half of the species with range sizes of fewer than 100 patches became extinct before the simulations ended (fig. 6). However, the median duration of the species with very small ranges (<200 patches) is 100,000 generations with very high variation, which suggests that species with small ranges are not necessarily transient species (fig. S8). Interestingly, the proportion of species that became extinct did not differ significantly with different niche widths or with landscape fragmentation levels, which means that specialists are as likely to become extinct as generalists, and the background extinction rate in an already fragmented landscape is not different from that of an unfragmented landscape.

Speciation Rates

The effect of dispersal ranges on rates of speciation is very pronounced: dispersal clearly reduces speciation rates. The number of species that are present at generation 200,000 declines as dispersal ranges of individuals increase (figs. 7,

8; also see figs. S9, S10 for the total number of species that emerge during the simulations). Typically, when dispersal range is small, there are more species present in the landscape, and species coexist for longer durations (table 2). On the contrary, large dispersal ranges result in fewer species: mostly a single generalist or a specialist will spread across the entire landscape with little or no opportunity for species coexistence (compare the simulations with different dispersal ranges D in fig. 2).

The effect of the trade-off coefficient β on speciation rates is more subtle, yet still clear (fig. 9): irrespective of the dispersal ranges and habitat fragmentation, high costs (due to high values of the trade-off coefficient β), which favor narrow niche widths, result in higher speciation rates (also cf. different columns in figs. 7, 8, S9, S10).

Habitat Fragmentation

We were able to create significantly different landscapes by using different values of H (figs. 1, S1). Intriguingly, landscape patchiness or fragmentation also had a significantly negative effect on speciation rates and on species coexistence (figs. 7, 8, S9, S10; table 2). When the landscapes are less fragmented ($H = 0.9$ in figs. 8, S10), even simulations with high dispersal ranges (which reduce speciation rates) showed higher diversity compared to more fragmented landscapes ($H = 0.1$ in figs. 7, S9). Indeed, when resources were distributed randomly, which resulted in highly fragmented landscapes (figs. S1, S11), there was always only one species regardless of the dispersal range D and trade-off coefficient β (of the 90 simulations initiated with all the parameter combinations of β and D, only one simulation resulted in two species).

Effects of the Three Parameters on Species Ranges, Speciation, and Extinction Rates

Overall, high costs of having unused ecological traits (i.e., high values of the trade-off coefficient β) increased the speciation rates, multiple species coexistence durations, and coexistence durations of generalists and specialists but did not influence species range sizes or extinctions significantly. High dispersal range D resulted in larger ranges and reduced the speciation rates and coexistence dura-

Figure 3: The average trait values of the same populations as in figure 2 in four-dimensional trait space (where the fourth dimension is the color) after 200,000 generations. Each circle represents the average trait value of the population in a patch rather than the individuals due to high population sizes. At the corners of these trait cubes, ecological trait values are $x_i \approx 1$ or 0, and the resource utilization efficiencies are maximized. *A*, Seven visible clusters correspond to two specialists and five two-resource generalists. Note that due to low population sizes (and because the circles represent average values) it is hard to notice three species that differ in the fourth dimension (color) only. *B*, A single cluster corresponds to a specialist. *C*, Four clusters correspond to four specialists. *D*, Two clusters correspond to a specialist and a two-resource generalist.

Table 1: Average number of generations during which "specialists" and "generalists" coexist on the same resource (SD in parentheses; both × 1,000 generations)

Fragmentation *H*, dispersal range *D*	$\beta = .20$	$\beta = .40$	$\beta = .60$
.1:			
3 × 3	69.00 (45.88)	109.70 (48.58)	104.50 (29.93)
9 × 9	.30 (.47)	7.75 (19.80)	28.35 (62.80)
15 × 15	.00 (.00)	.05 (.22)	.05 (.22)
.9:			
3 × 3	120.90 (59.17)	100.45 (30.75)	108.05 (20.67)
9 × 9	34.05 (51.86)	105.20 (67.11)	112.55 (43.23)
15 × 15	6.00 (19.95)	53.40 (60.60)	86.00 (82.47)

tions. Finally, low values of fractal index *H*, which leads to highly fragmented landscapes, reduced the speciation rates and the coexistence durations but did not influence extinction rates significantly.

Discussion

Here, we have built a spatially explicit individual-based model investigating the relationship among species ranges, speciation, and extinction. In our model, we followed the evolutionary dynamics of hundreds of thousands of diploid individuals, each with 11 unlinked ecological (x), resource preference (y), and mating (m, f, c) traits, for 200,000 generations across a large landscape. Individuals adapted to resources present in the landscape and formed distinct genetic clusters in multidimensional trait spaces. We identified several important factors that strongly influence the species range dynamics and speciation and extinction rates, and we observed coexistence of multiple species with varying niche widths on a few resources.

Range Sizes

We showed that habitat availability, niche width, and dispersal ability interact in complex ways. Dispersal ability is commonly cited as the main determinant of species range; however, the assumed positive relationship among range sizes and dispersal abilities is often not present (for an extensive review of empirical data, see Lester et al. 2007). We showed that large dispersal ranges could cause larger species ranges.

We did not find significant relationship between niche widths, or specialization, and range sizes. Several studies across a wide range of taxa refute the niche breadth hypothesis (that species with broad niche widths have wide ranges) and show that there is no correlation between the niche widths and range sizes of birds of the United Kingdom (Gregory and Gaston 2000), coral reef fishes (Hobbs et al. 2010), and eight primate species in Guyana (Lehman 2004). Indeed, range sizes are results of complex interactions between speciation and extinction (Gaston 1996, 2003) and are also strongly influenced by the presence of other species (Case and Taper 2000; Holt and Barfield 2009; Price and Kirkpatrick 2009; Jankowski et al. 2010).

Range Size Distributions

In our model, the resulting species range size distribution is strongly right skewed, which means that there are many species with small ranges and a few species with large

Table 2: Average number of generations during which multiple species coexist (SD in parentheses; both × 1,000 generations)

Fragmentation *H*, dispersal range *D*	$\beta = .20$	$\beta = .40$	$\beta = .60$
.1:			
3 × 3	193.00 (26.83)	199.00 (.00)	199.00 (.00)
9 × 9	1.60 (1.90)	49.55 (78.61)	86.85 (97.06)
15 × 15	.40 (.50)	.55 (.51)	.45(1.00)
.9:			
3 × 3	199.00 (.00)	199.00 (.00)	199.00 (.00)
9 × 9	166.20 (56.58)	199.00 (.00)	198.95 (.22)
15 × 15	28.15 (56.64)	145.00 (81.83)	198.75 (.91)

ranges. Empirical studies across many taxa also show similar skewed range-size distributions (Gaston 1998). As in our model, the few studies that tested for departures from lognormal distribution (see the references in Gaston 1998) reported distributions that were significantly left skewed rather than lognormal (for global range size distributions of birds, see Orme et al. 2006). Understanding the mechanisms underlying these distributions remains one of the fundamental questions in ecology and evolution (Gaston 2003). Similar to species abundance distributions, the "null" expectation for a range size distribution would be that they follow a lognormal distribution, mostly due to the central limit theorem and large number of independent multiplicative events (Šizling et al. 2009). However, Williamson and Gaston (2005) show that logit transformation is the best fit for range size distributions of British and Swedish breeding birds and argue that lognormal distribution may not be an appropriate null model for range size distributions.

Extinctions

One challenge that skewed range size distributions present is explaining overabundance of species with small ranges despite the fact that they are the ones most prone to extinction. It is well established that extinctions are nonrandom (Jablonski 1989; McKinney 1997; Purvis et al. 2000). For Cretaceous mollusks, species with large ranges were resistant to background extinctions (Jablonski 1989); moreover, genus-level geographic ranges enhanced survival during the end-Cretaceous mass extinction (Jablonski 2008). Similarly, benthic macro-organisms from the Triassic and Jurassic periods suggest that range sizes were critical in determining extinction probabilities (Kiessling and Aberhan 2007). Extinctions are influenced by a variety of factors; organismal traits such as body sizes, reproductive rates, generation times, and local abundance are often significantly correlated with extinction rates in some taxa (Purvis et al. 2000). Since wide-ranging species often occupy nonrandom regions of the trait spaces (e.g., widely ranging species often have large body sizes), these traits give mixed signals across different taxa. Jablonski (2008) considers these correlations as hitchhiking effects and argues that range size is the most significant predictor of extinction probabilities. We also found that extinctions are biased toward species with small ranges or range restricted species.

Species with small ranges do experience high rates of extinction but also high rates of speciation (Stanley 1986). Despite the extinction bias toward range-restricted species, we still observed significantly skewed range size distributions with a large number of range-restricted species still present at the end of simulations. Since constructed
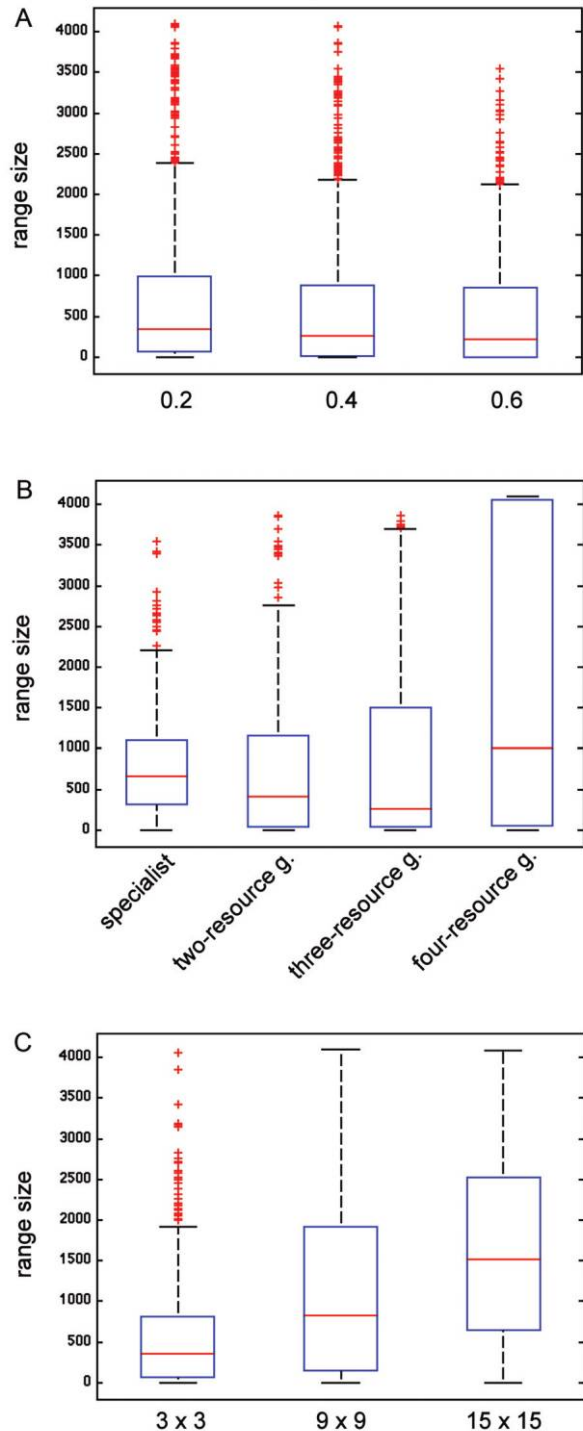
Figure 4: Boxplots of range sizes of species with different values of trade-off coefficient β (*A*), niche widths (*B*), and dispersal ranges D (Kruskal-Wallis, $\chi^2 = 192.62$, $P < .0001$; *C*). For each box, the central mark is the median, the edges of the box are twenty-fifth and seventy-fifth percentiles, the whiskers extend to the most extreme data points not considered outliers, and outliers are plotted individually.
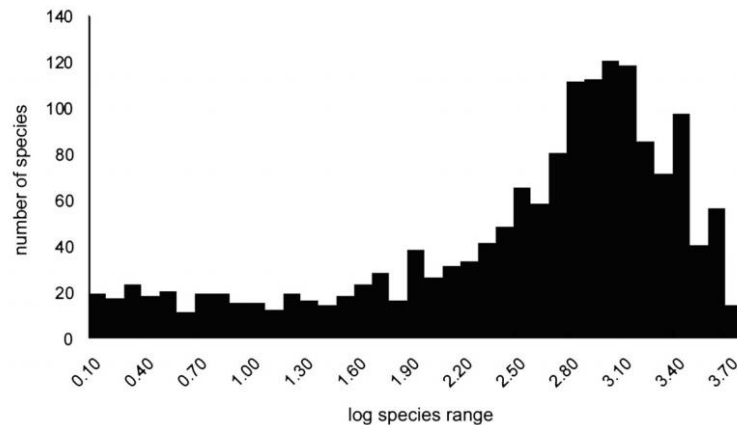
Figure 5: The distribution of log$_{10}$-transformed range sizes of the species present at generation 200,000. The log species range distribution is significantly left skewed (skewness: -1.06, standard error of skewness: 0.06).

phylogenies may not reliably reflect extinction rates and range restricted species are potentially less preserved in the fossil record because they occur at fewer fossilization sites (Koch 1987; Jablonski 1988; Russell and Lindberg 1988; Eldredge et al. 2005; Valentine et al. 2006), it is possible that the actual turnover rate of range-restricted species through speciations and extinctions is much higher than currently believed. Species with small ranges that were present at the end of simulations had long durations, some with durations similar to those with large ranges, which means that rare species, or species with small ranges, are not simply transient species. An interesting question is to find the underlying causes of this rarity (Kunin and Gaston 1997). Our initial analyses failed to pinpoint a specific cause since common and rare species did not differ in their niche widths or dispersal abilities. We suspect that species interactions could be the major influence in causing rarity (Price and Kirkpatrick 2009; Jankowski et al. 2010). Whatever the cause for rarity is, the consequence of rarity seem obvious: higher probabilities of extinction. With recently accelerated extinction rates (Pimm et al. 1995), prioritizing range-restricted species for conservation seems justified (Grenyer et al. 2006).

Speciation Rates

Dispersal abilities and the strength of trade-offs have clear effects on speciation rates: low dispersal abilities and high trait costs that favor narrower niche widths increase speciation rates, while high dispersal and low costs that favor broad niche widths reduce speciation rates (sensu Mayr 1963). Our results are consistent with the expectations based on earlier models. Gavrilets et al. (2000) modeled parapatric speciation, and found that increasing local pop-

ulation size and/or migration rate significantly reduced the probability of speciation. Kawata (2002) showed that speciation could happen due to adaptation on different-sized resources, provided that the dispersal distance of offspring is not too large. Finally, Heinz et al. (2009) extended the model of Doebeli and Dieckmann (2003) to look at the joint evolution of local adaptation and dispersal and found that speciation happens in conjunction with short dispersal ranges. Our results are also consistent with empirical research on various taxa: low dispersal abilities result in higher speciation rates in marine organisms (Palumbi 1992), copepods (De Troch et al. 2001), Neogene bivalves (Stanley 1986), Cretaceous mollusks (Jablonski and Roy 2003), and primates (Eeley and Foley 1999). In general, low dispersal abilities set the stage for replicated adaptive radiations (Losos 2010).

However, there is some empirical evidence for the opposite pattern as well. Cardillo et al. (2003) found positive correlation between species ranges and diversification rate in Australian mammals. Similarly, Owens et al. (1999) found that diversification rates among bird families were positively correlated with generalist feeding habits and good dispersal capabilities as well as large and fragmented geographical ranges (also see Phillimore et al. 2007). It is possible that speciation rates increase with dispersal abilities in groups where the major mode of speciation is allopatry (for birds: Barraclough and Vogler 2000; for some mammal groups: Fitzpatrick and Turelli 2006). In this study, the lack of any geographical barriers in the landscape could be considered as a caveat; however, despite the common belief during most of the twentieth century that the main mode of speciation was allopatric, empirical and theoretical studies over the past few decades suggest that reproductive isolation could evolve in parapatry and sym-
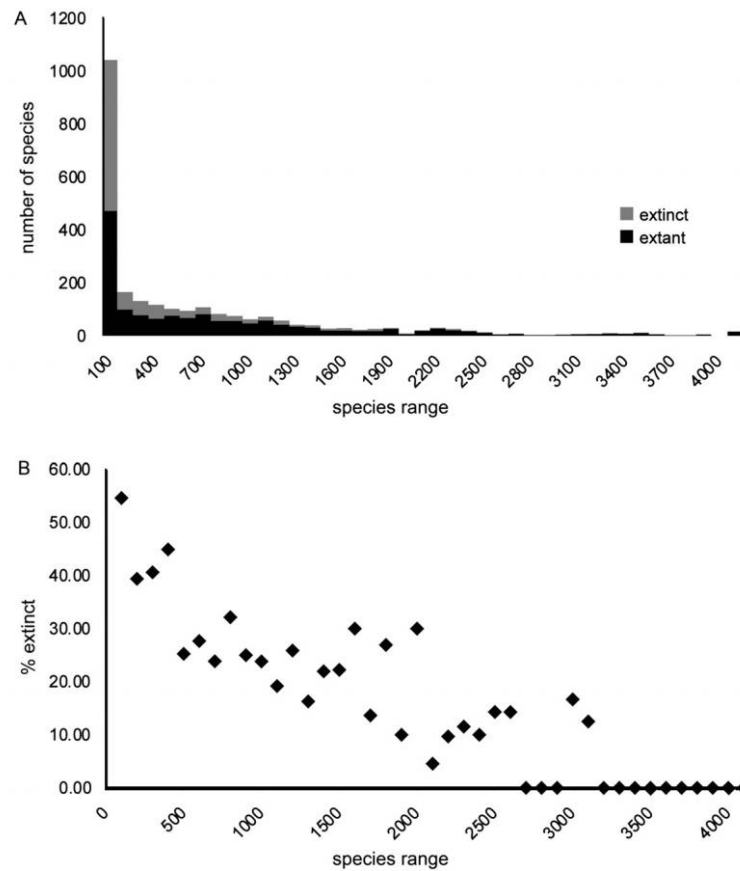
Figure 6: *A*, Species range size distribution of all the species that existed during the simulations. Extant refers to the species that were present at the end of simulation at generation 200,000 (which are log transformed in fig. 5). *B*, Proportion of species that went extinct within each range category.

patry generating diversity (for reviews in the last decade, see Via 2001; Kirkpatrick and Ravigne 2002; Gavrilets 2003; Dieckmann et al. 2004; Fitzpatrick et al. 2008). Overall, that we reproduced some patterns of adaptive radiations (see "A Posteriori Observations") and obtained realistic species range size distributions with minimal assumptions gives us confidence about the generality of our model's result: speciation is hindered by higher dispersal abilities and low resource utilization costs that favor broad niche widths.

Habitat Fragmentation

An unexpected result of our model is the strong influence of underlying resource distributions on patterns of speciation. We created fractal landscapes with two significantly different levels of fragmentation. In less fragmented landscapes, there are fewer clusters of patches that have the same resource because the sizes of these contiguous resource clusters are larger. Moreover, in less fragmented landscapes, the percentage of patches that are on the edges of these clusters (i.e., edge habitats) is much smaller than in more fragmented landscapes, increasing the amount of "core" habitat that is available. These landscape features resulted in significant differences in the number of species that emerged in the simulations. When the habitats are fragmented, the species diversity is reduced compared to landscapes with less fragmentation. Indeed, if the resources are distributed randomly across landscapes, which results in very highly fragmented landscapes, there is almost always only one species in the landscape, irrespective of individuals' dispersal abilities and their niche widths. Large contiguous resource clusters, or "core" habitats, allow species to withstand the deleterious effects of gene flow from populations or species utilizing other resources in the neighboring patches. In highly fragmented landscapes,
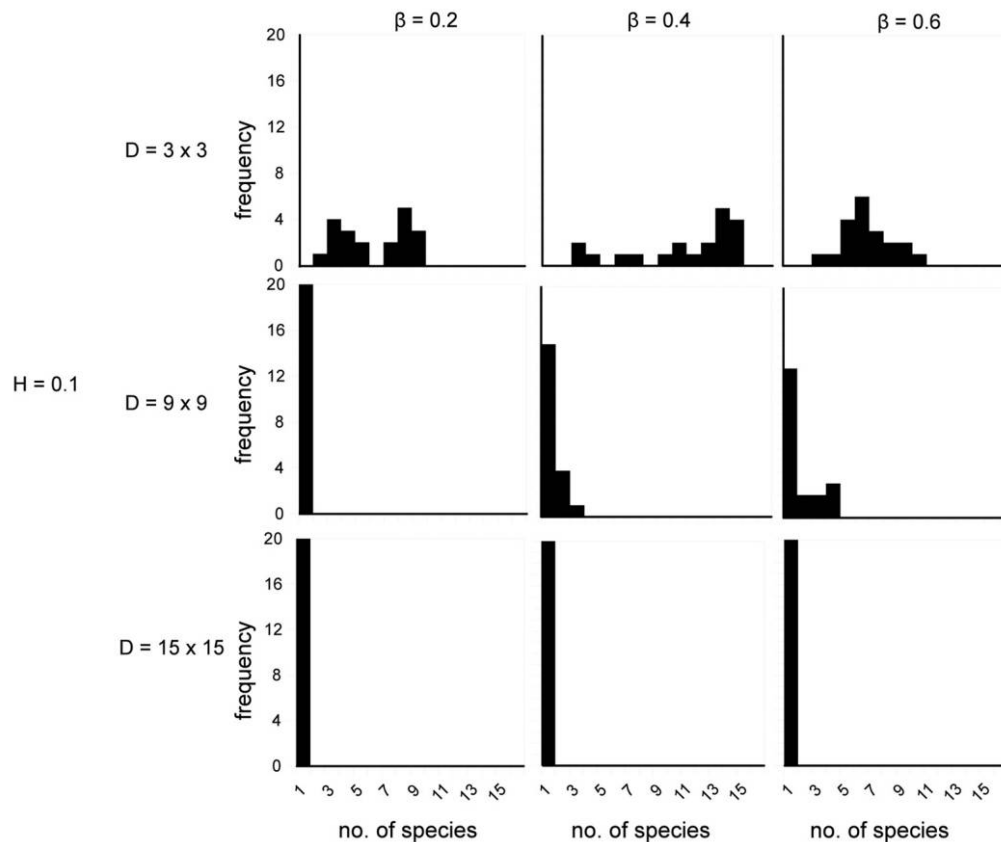
Figure 7: The distribution of the number of species that existed at 200,000 generations with different dispersal ranges (D) and trade-off coefficients (β) when the fractal landscape dimensions are $H = 0.1$. We ran 20 simulations for each parameter combination, and all the simulations lasted for 200,000 generations. Note that as D increases, more simulations end with only one species. Increasing β has a more subtle effect.

populations or species in small resource clusters are subject to increased exposure from populations adapted to different resources and cannot withstand effect of gene flow from neighboring patches. Even though more thorough investigation on this should be done, our results indicate that habitat fragmentation could have significant consequences for biodiversity, not only by increasing extinction rates (Pimm 1998; Earn et al. 2000) but also by reducing speciation rates. We should also note that the spatial scales of ecological interactions and dispersal in our model could be argued to be very similar, which could mean that the difference in speciation rates is not due to habitat fragmentation, but rather it is due to individuals being exposed to highly heterogeneous habitats within their roaming ranges. If this were the case, one would expect more specialization (Futuyma and Moreno 1988) and species diversity (MacArthur 1965), which, however, are not observed in our simulations.

A Posteriori Observations

Adaptive Radiations. Our model borrows from the models by Gavrilets and Vose (2005, 2009); however, there are essential differences in the assumptions about resource distributions, dispersal abilities, and the fitness functions. Yet, our model provides further theoretical support for the generality of several patterns of adaptive radiation outlined by Gavrilets and Losos (2009): (i) early burst of speciation, (ii) the "overshooting" effect, (iii) expected stages of radiation, (iv) nonallopatric speciation, and (v) porous genome effect. (Our model's framework was not suitable to check for the other effects outlined by Gavrilets and Losos [2009]: area effect, selection gradient effect, spatial dimensionality effect, least-action effect, and effect of the number of loci.) Due to high initial ecological opportunity, there are multiple speciation events that take place very quickly (Schluter 2000; Losos 2010; Yoder et al. 2010). The early increase in species diversity is followed by a reduction
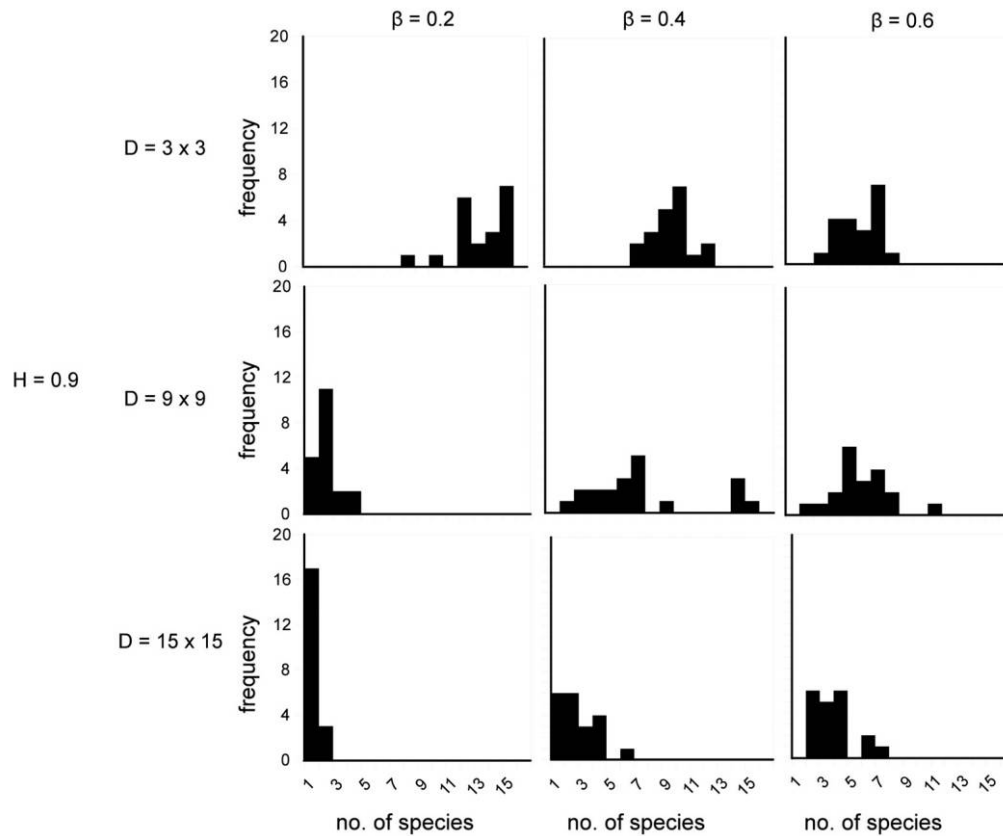
**Figure 8:** Same as in figure 7, but the fractal landscape dimensions is $H = 0.9$.

in speciation rates and by an increase in extinction rates, which is known as the "overshooting" effect in the literature (Gillespie 2004; Gavrilets and Vose 2005; Gavrilets and Losos 2009). The adaptive radiation in our model also followed the expected sequence of events (Gavrilets 2004): individuals quickly adapted to resources forming ecological species, which was followed by evolution of preferences for those resources, and in some cases, by divergence in mating traits. Adaptive divergence was observed despite gene flow and without strict allopatry. The ecological species that emerged in our model formed distinguishable genetic clusters that were stable for hundreds of thousands of generations; however, these species did not show any differentiation in neutral loci: F_{st} values across ecological species were generally low. Since neutral loci are generally not linked to the loci that are under selection (as in our model), they could flow freely across the ecological species. This observation about porous genomes in the previous models (Gavrilets and Vose 2005, 2009) has recently been put to more rigorous theoretical test by Thibert-Plante and Hendry (2010), who showed that ecological speciation may not be easy to detect at neutral loci.

Reinforcement. Ecological species tend to form very quickly (Hendry et al. 2007): populations adapt to different environments, followed by evolution of resource preferences that further strengthens adaptive divergence (Hendry et al. 2007; Hendry 2009; Schluter 2001, 2009). One would typically expect to observe divergence in mating traits via reinforcement (selection on premating isolation mechanisms), strengthening the reproductive isolation between the ecological species. However, evidence from empirical studies show that ecological species shows different levels of reproductive isolation and that complete isolation is rare (Schluter 2001, 2009; Hendry et al. 2007; Hendry 2009). In our model, we observed that multiple mating morphs (or "sexual species") were often shared across ecological species (also see Gavrilets and Vose 2009). Even though there is divergence in mating traits, the fact that these traits are often shared across the ecological species shows that reinforcement is rare or absent in our model. The lack of reinforcement is due to strong resource preferences that influence the mating probabilities and reduce the production of less fit hybrids. Reduced possibility of reinforcement, along with the porous genome effect ex-

plains why we see some mating traits flowing across the boundaries between ecological species. Despite the lack of complete reproductive isolation, ecological species in our model differed in genetically controlled ecological traits adapted to different environments/niches and showed strong discontinuous adaptive variation that remained distinct for hundreds of thousands of generations (figs. 3, S3; appendix).

Coexistence of Generalists and Specialists. We observed co-
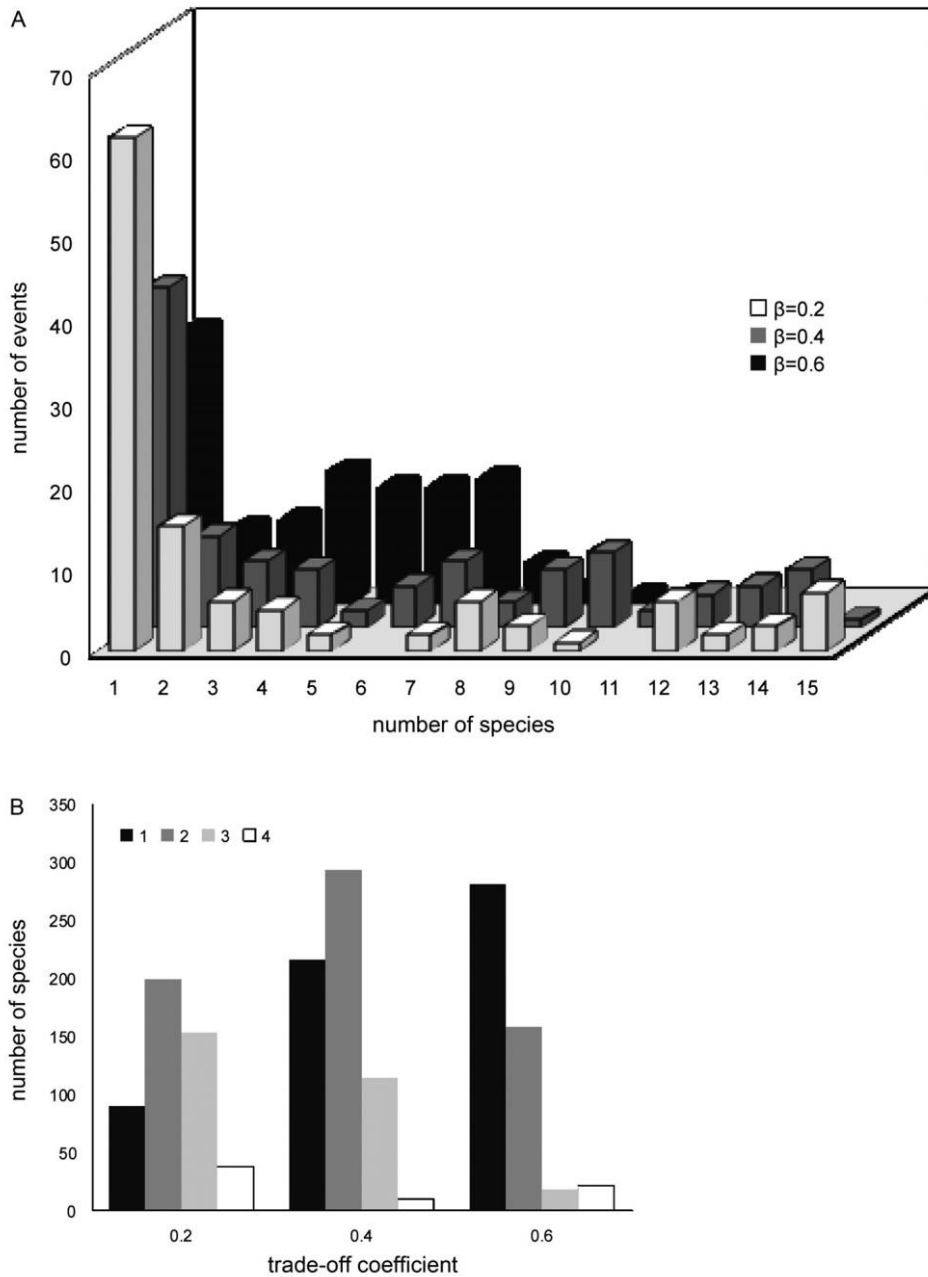
Figure 9: *A*, Distribution of number of species that are present at generation 200,000 with different values of trade-off coefficient β. Note that with increasing β, the number of simulations that yield only one species decreases and the number of simulations with higher species diversity increases. *B*, Distribution of number of species with different niche widths that emerged in simulations with different values of β. Note that with increasing β, the number of species with narrow niche widths increases; that is, higher values of β favor specialists.

existence of multiple specialists and generalists, up to 15 species (the maximum possible using four resources, excluding the ancestral species). In nature, specialists and generalists can coexist for various reasons: habitat selection in rodents (Morris 1996; Traba et al. 2010), spatial structure of resources in gobies (Kido 1997), temporal fluctuations in resource abundance in seed predator insects (Ostergard et al. 2009), cycling prey species in predators (Hanski et al. 2001), predator avoidance and resource utilization abilities in *Ischnura* damselfly and *Enallagma* species in ponds (McPeek 1996). Temporal or spatial heterogeneity in resources leads to the evolution and coexistence of generalists and specialists in microorganisms (references in Kassen 2002). Different seed sizes led to parallel ecological speciation of *Nesospiza* finches, a generalist and a specialist, on two small islands in the south Atlantic Ocean (Ryan et al. 2007). Earlier theory suggested that either only two specialists or only a generalist could survive on two resources due to trade-offs in their ability to utilize both resources (e.g., Armstrong and McGehee 1980). Later, Wilson and Yoshimura (1994) showed that coexistence of generalists and specialists was possible when there was stochastic variation in the abundances of the two resources utilized. Subsequent theoretical work focused on the emergence of two specialists and generalists from a single ancestral species rather than simply coexistence (e.g., Kisdi 2002; Egas et al. 2004), and showed that it was possible for a narrow range of parameters. With explicit resource dynamics, Abrams (2006) showed that the systems could evolve to these states under a wider range of parameters, due to fluctuations caused by cycling resource dynamics. Recently, Ravigne et al. (2009) showed that these expectations could change qualitatively if habitat choice is allowed to evolve along with traits for local adaptation; for example, even under weak trade-offs, specialists are favored over generalists which would have been favored if there were no habitat choice. In our model, spatial structure and correlated evolution of ecological and preference traits create complex fitness landscapes that allow for coexistence of multiple specialists and generalists on four resources.

Environmental Stochasticity

A necessary simplification in our model was to exclude environmental stochasticity. Gavrilets and Vose (2005) showed that resource or patch extinctions influence speciation patterns by reducing population sizes and by increasing turnover of patches/resources. Lack of environmental stochasticity in our model is reflected in three observations that may not reconcile with empirical data. First, range sizes of species in our simulations increased rapidly postspeciation, declined rapidly during extinctions,

and fluctuated around a stationary value during the existence of the species. Even though fossil record suggests stasis in geographical range sizes of some taxa (Jablonski 1987), this mode is viewed unrealistic considering the suite of environmental changes through evolutionary times (Gaston 1998, 2008). In a recent study, Liow and Stenseth (2007) analyze the global microfossil database and show that the range sizes of many marine taxa are not static over geological time scales, and that the temporal trajectories of range sizes are hump shaped, and asymmetric: the rise is quicker than the fall. Second, the proportion of species that became extinct did not differ significantly with different niche widths, which means that specialists are equally likely to become extinct as generalist. We should note that some generalists do have restricted ranges, which increases their chances of becoming extinct. It is also possible that the specialists escape the extinction risk through what is known as "extinction filtering" (specialists are better adapted locally and have high local abundances, where as generalists suffer from gene flow across suboptimal environments and have low abundances; Johnson 1998; Williams et al. 2009). However, both neoecological and paleoecological studies indicate that specialized species are more prone to extinction (Colles et al. 2009). Moreover, since the dynamics of specialists are closely tied to the dynamics of those resources and habitats they specialize on, specialists are of particular concern due to increased habitat loss (Brook et al. 2003; Munday 2004; McKinney 1997). Finally, extinction rates in landscapes with different fragmentation levels did not differ significantly. This might seem to conflict with the increasing body of work demonstrating the effect of habitat fragmentation on extinctions (Pimm 1998; Earn et al. 2000). However, since speciation rate is low in fragmented landscapes, once the species adapts to the landscape, it does not necessarily experience higher rates of extinction. Incorporating patch extinctions in our model that alter the landscapes from less fragmented to highly fragmented would result in more extinctions. Thus, as a next step it would be interesting to include environmental stochasticity and explore the effects of extinctions of patches/resources on species ranges, and on patterns of speciation and extinction.

A main objective behind building mathematical models is to identify crucial parameters and develop our intuition about complex biological phenomena. Species ranges are results of complex interactions between speciation and extinction (Gaston 2003). We showed that high dispersal abilities can result in large range sizes, whereas species with wide niche widths do not necessarily have large range sizes. Moreover, we also showed that dispersal abilities and fitness trade-offs have strong influence on speciation rates: high dispersal ability and low resource utilization costs that favor broad niche widths reduce speciation rates.

APPENDIX

Fragmented Landscapes

The basic principle behind the midpoint displacement algorithm is to assign random numbers to four corner patches of the landscape and to assign the average value of those four corners to the central patch with an introduced small random variation. The values of patches that are on the edges of the landscape are assigned as average values of the two corner patches and the central patch with small random variation. Once the central patch and the four patches at the edges of the landscape between the corners (like a diamond shape) are assigned, this creates four new central patches. This recursive procedure is repeated many times until values are assigned to all the patches. The introduced random variation is modified with the spatial contagion of habitat H. Lower values of H generate landscapes with low spatial autocorrelation, and the resulting resource/habitat distribution is highly fragmented; higher values of H lead to resource/habitat distributions that are more clumped (figs. 1, S1).

These values are typically thought of as "elevations" creating fractal mountain ranges; here we converted them to discrete values to assign different resources (e.g., With 1997; King and With 2002). Since there are multiple resources in the landscape, each resource is distributed independently. If more than one resource is assigned to a single patch, contentions are decided based on the abundance of the resources in the landscape while conserving the fractal dimension with a similar algorithm described by Hargrove et al. (2002).

Ecological Speciation

Ecological speciation is defined as the evolution of reproductive isolation between populations adapting to different environments/niches (Schluter 2001, 2009). In our model, we define "ecological" species as follows. We assume that when the individual is fairly well adapted to a single resource, the individual is considered a resource specialists (i.e., when the ecological trait value $x_i \geq 0.8$; note that in eq. [3], the resource utilization efficiency is maximized when $x_i = 1$). Resource specialists, by our definition, utilize other resources very inefficiently (we assume that $x_j < 0.5$, where $j = 1, \ldots, k$ but $j \neq i$). We define resource generalists as individuals who utilize more than one resource relatively efficiently. We assume that a generalist is well adapted to at least one resource, and has other ecological traits that allows it to utilize other resources fairly well (i.e., the individual has at least one ecological trait utilizing resource i that is $x_i \geq 0.8$ and also has other trait values that are $x_j \geq 0.5$ for some $j = 1, \ldots, k$, where $j \neq i$). Generalists are classified depending on the number of resources they utilize efficiently, that is, two-resource generalist, three-resource generalist, and so on. For example, the individual with ecological trait values (0.9, 0.2, 0.1, 0.2) is a specialist, where as the individual with (0.9, 0.6, 0.8, 0.2) is a three-resource generalist. The ecological species, as we define here, differ in genetically controlled ecological traits and remain to be distinguishable genetic clusters (fig. 3) for the hundreds of thousands of generations (fig. S3), and hybrids between two species have reduced fitness in parental species environments.

Since mating occurs in patches that individuals prefer the most (note that the females disperse to the patches they prefer the most as offsprings), reproductive isolation between the ecological species is further strengthened by the evolution of resource preferences. There is a strong correlation between ecological and preference traits (fig. S4). Moreover, ecological species also diverge in their mating traits (fig. S5D); however, mating traits diverge much later than ecological speciation (cf. figs. S6, S7), and typically the same mating traits spread through the entire landscape (fig. S5A, S5C). Hendry (2009) argues that ecological speciation should be treated as a continuum from adaptive variation in panmictic populations to complete and permanent reproductive isolation between adaptively divergent groups. The ecological species in our model fit the definition of stage 3 of Hendry (2009), where they show strong discontinuous adaptive variation with reversible reproductive isolation (stage 4 is the final stage where there is complete and irreversible reproductive isolation). Two other observations from our model agree with the patterns established with empirical and theoretical research and further reinforce the usefulness of our species definition: first, ecological speciation is generally very fast (Hendry et al. 2007); second, large number of speciation events occur very early during adaptive radiations, followed by subsequent decline in speciation rates (Schluter 2000; Gavrilets and Vose 2005, 2009; Gavrilets and Losos 2009).

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