

Evolutionary Branching in Complex Landscapes

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ABSTRACT: Divergent adaptation to different environments can promote speciation, and it is thus important to consider spatial structure in models of speciation. Earlier theoretical work, however, has been limited to particularly simple types of spatial structure (linear environmental gradients and spatially discrete metapopulations), leaving unaddressed the effects of more realistic patterns of landscape heterogeneity, such as nonlinear gradients and spatially continuous patchiness. To elucidate the consequences of such complex landscapes, we adapt an established spatially explicit individual-based model of evolutionary branching. We show that branching is most probable at intermediate levels of various types of heterogeneity and that different types of heterogeneity have, to some extent, additive effects in promoting branching. In contrast to such additivity, we find a novel refugium effect in which refugia in hostile environments provide opportunities for colonization, thus increasing the probability of branching in patchy landscapes. Effects of patchiness depend on the scale of patches relative to dispersal. Providing a needed connection to empirical research on biodiversity and conservation policy, we introduce empirically accessible spatial environmental metrics that quantitatively predict a landscape's branching propensity.

Keywords: spatial environmental heterogeneity, local adaptation, individual-based model, negative frequency-dependent selection, ecological speciation, evolutionary refugia.

Introduction

We have only partial answers to questions such as why there are so many species in the world and why some clades are so much more speciose than others (Hutchinson 1959; Schluter 2000; Coyne and Orr 2004; Butlin et al. 2012). A central question in speciation theory concerns the cause of speciation: in particular, which factors (environmental, ecological, phenotypic, and genetic) promote speciation, and which factors hinder it? According to the ecological speciation model (Schluter 2001), ecology drives speciation: the process of speciation begins with adaptation

to different environments by different populations or subpopulations. From this perspective, evolutionary branching in an ecological trait is the first step toward speciation; reproductive isolation follows, either as a byproduct of ecological divergence or as a result of reinforcement (Schluter 2001).

Empirical support for the ecological speciation model has come from studies in which the adaptive traits that exhibit divergence between different populations also contribute to reproductive barriers (Rundle and Nosil 2005; Hendry 2009; Schluter 2009). Recent theoretical work has also demonstrated that local adaptation in a heterogeneous environment, driven by local competition for resources, can lead to speciation in both sexual and asexual populations (e.g., Doebeli and Dieckmann 2003; Gavrillets and Vose 2005; Birand et al. 2012).

Complex Landscapes

Theoretical models of divergence as a result of local adaptation to different environments necessarily consider some type of spatial heterogeneity. Two types of spatial models have dominated: metapopulation models, in which populations inhabit two or more discrete patches that differ in some way (e.g., Doebeli and Ruxton 1997; Meszena et al. 1997; Geritz et al. 1998; Kisdi and Geritz 1999; Day 2000; Gavrillets et al. 2000a; Geritz and Kisdi 2000; Parvinen and Egas 2004; Gavrillets and Vose 2005; Thibert-Plante and Hendry 2009; Birand et al. 2012), and spatially continuous models of linear environmental gradients (e.g., Kirkpatrick and Barton 1997; Doebeli and Dieckmann 2003; Mizera and Meszena 2003; Leimar et al. 2008; Heinz et al. 2009; Ispolatov and Doebeli 2009; Payne et al. 2011; Irwin 2012), although a few models have tried to bridge the gap between these approaches (Sutter and Kawecki 2009; Debarre and Gandon 2010).

Real environments are more complex than these simple cases. Patchy environments are not always discrete, as metapopulation models assume; rather, spatial environmental heterogeneity is often continuous (Manning et al.

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2004; Fischer and Lindenmayer 2006). On the other hand, this continuous environmental heterogeneity is often not linear, as linear gradient models assume; rather, spatial environmental heterogeneity may be pronounced in some areas and minimal in others. The effects of more realistically complex spatial heterogeneity on adaptive divergence and speciation have not been explored in theoretical models. Given the intimate feedbacks between spatial heterogeneity, dispersal, and local adaptation, we expect such heterogeneity to be important.

Here we model the dynamics of evolutionary branching caused by local competition and dispersal in complex heterogeneous landscapes. These landscapes combine continuously varying patchiness and a nonlinear ecological gradient, thus reconciling and extending the continuous linear gradient and discrete metapopulation approaches of previous models. Environmental heterogeneity in our model has two components (fig. 1; “Landscape Generation,” available online). The first component is an environmental gradient, described by both a linear coefficient, here called the gradient slope, and a quadratic coefficient, here called the gradient curvature. The second component is spatially continuous patchiness, described by its amplitude and its

spatial scale (autocorrelation length [ACL]). Together, these components produce a wide variety of landscapes with patterns of heterogeneity reminiscent of real environments. In the following four sections, we present four hypotheses regarding the likelihood that evolutionary branching will occur in such complexly heterogeneous landscapes.

Intermediate Heterogeneity Maximizes Branching Propensity

Although negative frequency-dependent selection due to competition can cause divergence even in the absence of environmental heterogeneity (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000), some degree of spatial environmental heterogeneity must exist for local adaptation to produce divergence as a result of external environmental effects (Doebeli and Dieckmann 2003). In this way, heterogeneity promotes branching by providing divergent selection among environments. However, if heterogeneity is too pronounced, maladapted colonizer populations will be unable to persist long enough to adapt, and so organisms will be restricted to those areas to which

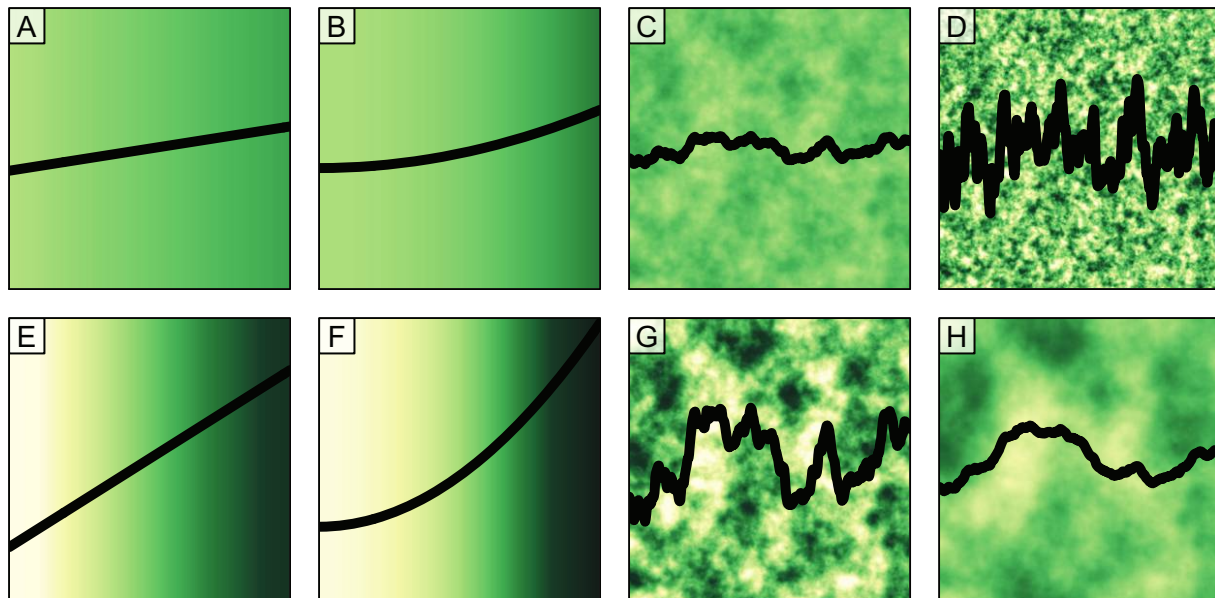


Figure 1: Examples of generated landscapes. We illustrate the effect of the four landscape-generating parameters on the pattern of spatial heterogeneity. *A–D*, Small values of parameters scaled slope (s), scaled curvature (c), scaled amplitude (a), and scaled generating autocorrelation length (l_g), respectively. *E–H*, Larger values of the same parameters, so that each column shows the effect of a low versus high value of one parameter. Colors indicate locally optimal ecological trait values, ranging from white (low) to dark green (high). Black lines show locally optimal ecological trait values across one horizontal transect of each landscape. For purposes of comparison, all panels are generated with the same random-number generator seed so that they are based on the same stochastic spatial structure. For each column, the other landscape-generating parameters are held to zero (except that, to show the effect of the scaled amplitude, a particular autocorrelation length must be specified).

they are already well adapted. An intermediate level of heterogeneity is therefore expected to produce maximal divergence among locally adapted populations and thus to maximally promote evolutionary branching. Doebeli and Dieckmann (2003) demonstrated this phenomenon in a model involving spatial heterogeneity due to a linear environmental gradient; furthermore, their study suggested that the stringency of this optimum depends on dispersal distance, with short-range dispersal allowing branching to occur over a broader range of gradient slopes (fig. 3*b* in Doebeli and Dieckmann 2003). We hypothesize that this finding will generalize to other types of heterogeneity; specifically, evolutionary branching will be maximized also at an intermediate nonlinear gradient curvature and at an intermediate amplitude of spatially continuous patchiness, with the stringency of these optima increasing with increasing dispersal distance.

Additivity of Heterogeneity Types

If different types of heterogeneity have similar effects on evolutionary branching, each with its own intermediate optimum that maximizes branching, then such different types might be expected to have additive effects. For example, if the amount of heterogeneity due to gradient slope is already optimal, such that adding more heterogeneity by increasing the slope decreases the likelihood of branching, then it seems reasonable to think that adding other types of heterogeneity, such as gradient curvature, would also decrease branching. Furthermore, this decrease in branching might be compensated for by reducing the gradient slope as curvature is increased. We thus hypothesize that the maximal branching propensity should be achievable through an essentially additive mixture of different types of heterogeneity (gradient slope, gradient curvature, and patchiness). An increase in one type would be compensated by a decrease in another type, to the extent that such additivity applies.

Refugium Effect

As explained above, different types of heterogeneity may be additive in their effects on branching; however, we expect one major exception to this general principle of additivity. This exception arises because the lethality of a given high level of environmental heterogeneity (and its concomitant negative effect on evolutionary branching) might be lower if some of that heterogeneity is unevenly distributed in the form of spatially continuous patchiness. In particular, such patchiness might provide refugia in areas of an environmental gradient that would otherwise be too lethal to colonize. These refugia might promote evolutionary branching through several complementary

mechanisms. First, a refugium might provide an ecologically distinct patch of sufficient size to allow diversification in situ, despite the harshness of the underlying steep gradient. Second, a refugium might act as a spatial stepping stone, providing a clement habitat patch that could act as a proximate source for repeated colonization attempts into the surrounding inhospitable environment (Havel et al. 2005; Thomas et al. 2012; Travis et al. 2012). Third, a refugium might act as an adaptive stepping stone, providing an environment intermediate between the clement home range and a destination too inhospitable to colonize directly; the refugium would thus allow partial adaptation to occur prior to additional range expansion (Havel et al. 2005; Lombaert et al. 2010; Heinicke et al. 2011; Westley et al. 2013).

For all these reasons, we hypothesize that spatially continuous patchiness should promote evolutionary branching particularly strongly when combined with an environmental gradient so steep as to ordinarily hinder branching. In other words, a positive interaction between patchy heterogeneity and steep gradients should exist, mitigating or even opposing the additivity that would otherwise be expected between these different types of heterogeneity.

Autocorrelation Length and Dispersal

The effects of patchiness previously discussed (both the refugium effect and, more generally, the promotion of branching due to patchiness) should depend on the size of patches relative to the typical dispersal distance. In particular, a population that disperses over a large area containing many patches would adapt to conditions over the whole area, whereas populations with shorter dispersal distance might divergently adapt to local conditions within particular patches (Hovestadt et al. 2001; Bolker 2003, 2010; Snyder and Chesson 2003; Bonte et al. 2010; Hanski and Mononen 2011; Richardson 2012). If dispersal distance is so small relative to patch size that populations effectively never disperse outside their local patch, however, then colonization of the larger landscape would be prevented, and the heterogeneity of the landscape would no longer promote divergence. We thus hypothesize that the ratio of the ACL of environmental heterogeneity to the typical dispersal distance should affect the likelihood of evolutionary branching. As this ratio increases, the scale of patchiness relative to dispersal should increasingly promote evolutionary branching by allowing local adaptation to individual patches, up to some optimum ratio at which branching is maximized. Beyond that optimum, branching should be hindered due to a decrease in the colonization of new patches.

Empirical Landscapes and Evolutionary Branching

Together, these four hypotheses suggest that metrics of heterogeneity could be taken from a real landscape and used to quantitatively predict its propensity for branching. To test the feasibility of this idea, we define simple, empirically accessible metrics (“realized-landscape metrics”) that describe the salient features of our modeled landscapes. Focusing on ecological divergence, which is the first step of ecological speciation, by considering evolutionary branching in asexual populations, we use these metrics to quantitatively predict the branching propensity of our landscapes. This method, which could be easily applied to real landscapes using satellite data and known biodiversity patterns, for example, provides the beginnings of a bridge between theoretical and empirical work on biodiversity and speciation. We end by discussing the implications of these findings for conservation and management.

Methods*Model Summary*

To test our hypothesis, we constructed a spatially explicit, stochastic, continuous-time individual-based model, summarized here (for the full model description, see “Model Description,” available online). All parameters of the model are given in table 1.

Our model is derived from the asexual model of Doebeli and Dieckmann (2003), who explored the propensity for evolutionary branching in two-dimensional landscapes in which the optimum phenotype varied across space following a linear environmental gradient. With our model, we explore additional types of spatial environmental heterogeneity through the addition of a nonlinear environmental gradient and continuously varying environmental patchiness (see “Complex Landscapes”). The heterogeneity of the landscape is governed by four model parameters: s , the linear slope of the environmental gradient; c , the nonlinear curvature of the gradient; l_g , the autocorrelation length (ACL) of the continuously varying patchiness; and a , the amplitude of that patchiness (fig. 1; “Landscape Generation”). Generated landscapes are ultimately described through a tabulated function $u_0(x, y)$ specifying the optimum phenotype at each location. Landscapes are always periodic in the y -direction, whereas, in the x -direction, we model four possible boundary conditions: stopping, reflecting, and absorbing, with their usual meanings, and reprising, which entails redrawing invalid locations until a valid location is obtained. The topology of the landscapes is thus cylindrical.

The environmental landscape is inhabited by a population of individuals, with their abundance regulated by a

maximum carrying capacity density K_0 . Individuals are each characterized by a quantitative ecological trait u and a spatial location (x, y) . Their fitness depends on their degree of local adaptation as determined by the difference between u and the locally optimum phenotype $u_0(x, y)$. Additionally, the fitness of each individual is decreased through competition from the other individuals. The strength of competition depends on both the spatial and the phenotypic distances between the focal individual and its competitors. The death rate of each individual is governed by its fitness, whereas the birthrate is constant for all individuals.

Individuals reproduce asexually, with each offspring inheriting its ecological trait nearly faithfully from its parent. Dispersal in the model is natal; offspring are displaced from their parents’ location by a random distance.

The full model description (“Model Description”) discusses these and other aspects of the model in detail. A video of the model is provided as video 1, available online (Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.43cj7>).

Model Realizations

A total of 1,500,000 realizations of the model were generated. One set of 300,000 realizations was generated for each of the four boundary conditions, and an additional set of 300,000 realizations was generated with reprising boundary conditions to serve as an independent test data set. Each realization was supplied with random values for the five governing parameters s , c , l_g , a , and v , with the value for each parameter drawn from a uniform distribution spanning the range of values for that parameter (table 1).

For each realization, a landscape was generated (“Landscape Generation”) and analyzed to determine its standard deviation σ , skewness γ_1 , kurtosis γ_2 , and autocorrelation length l_r , together called the “realized-landscape metrics” (“Landscape Analysis,” available online). The initial state was then constructed, and its evolution was traced for 5,000 generations. A histogram of the ecological trait values in the population was recorded every 10 generations (“Model Description, Observables,” available online). Branching of the population was identified from these histograms as a stable divergence from the initially unimodal phenotypic distribution into a bimodal or multimodal distribution. Finally, a full census of the population was recorded at the end of the realization. A typical model realization is shown in figure 2.

Table 1: Model parameters and landscape metrics with symbols, value/range/formula, and units

Variable	Symbol	Value	Units
Initial number of individuals	N_{init}	100	–
Maximum carrying capacity density; scales the number of individuals in the system	K_0	500	$1/L^2$
Standard deviation of carrying capacity density; scales the reduction in carrying capacity density due to the difference in an individual’s ecological character from the locally optimal ecological character $u_0(x, y)$	σ_K	.3	E
Standard deviation of the spatial competition function; scales the reduction in the strength of competition as the spatial distance between individuals increases	σ_s	.19	L
Scaled standard deviation of the phenotypic competition function	c_p	5	–
Standard deviation of the phenotypic competition function; scales the reduction in the strength of competition as the phenotypic distance between individuals increases	σ_c	$c_p \sigma_K$	E
Probability of a mutation occurring	μ_m	.005	–
Standard deviation of the mutation effect size	σ_m	.05	E
Per capita birthrate; scales time in the model	b	1	T^{-1}
Scaled environmental gradient slope	s	.0–2.0	–
Scaled environmental gradient curvature	c	.0–1.0	–
Scaled environmental patchiness autocorrelation length	l_g	.05–3.0	–
Scaled environmental patchiness amplitude	a	.0–3.0	–
Scaled standard deviation of natal dispersal distance	v	.01–3.0	–
Environmental gradient slope	S	$s\sigma_K/\sigma_s$	E/L
Environmental gradient curvature	C	$c\sigma_K/\sigma_s^2$	E/L^2
Environmental patchiness autocorrelation length	L_g	$l_g\sigma_s$	L
Environmental patchiness amplitude	A	$a\sigma_K$	E
Standard deviation of natal dispersal distance; scales the spatial distance offspring land from their parent	V	$v\sigma_s$	L
Realized-landscape heterogeneity scaled standard deviation	σ	$\sqrt{\mu_2}/\sigma_K$	–
Realized-landscape heterogeneity skewness	γ_1	μ_3/σ^3	–
Realized-landscape heterogeneity excess kurtosis	γ_2	$\mu_4/\sigma^4 - 3$	–
Realized-landscape heterogeneity scaled autocorrelation length	l_r	See text ^a	–

Note: Units are expressed using the symbols L (length), E (ecological phenotype), T (time), and – (dimensionless). The symbols μ_2 , μ_3 , and μ_4 represent the second, third, and fourth moments, respectively, of the distribution of values in the realized landscape.^a

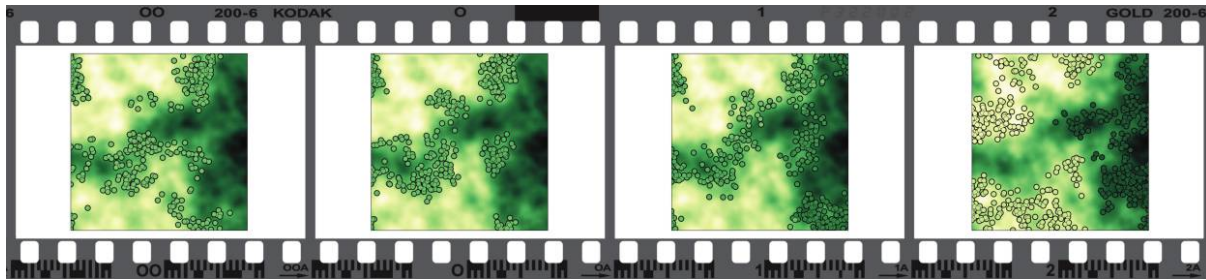
^a See “Landscape Analysis,” available online.

Statistical Analysis

For analysis of the results of these realizations, binomial (logistic) generalized additive models (GAMs; Wood 2006) were fitted. The independent variables in these GAMs were the scaled parameters s , c , l_g , a , and v . The dependent variable was taken to be whether the realization branched, encoded as 0 (not branched) or 1 (branched). This choice was motivated by the clear unimodality of branching times; realizations typically either branched early or did not branch at all (“Distribution of Branching Times,” available online). Nested models that included interactions of the independent variables were constructed (table A1; fig. A1; tables A1–A3 and figs. A1–A15 are available on-

line). In the full model, the hypothesis of an intermediate optimum for each type of heterogeneity, with an interaction of that optimum with dispersal, was represented by $s * v$, $c * v$, and $a * v$ terms. The hypotheses of additivity between heterogeneity types and of deviation from additivity due to the refugium effect was represented by the three-way interaction $s * c * a$ and its component interactions $s * c$, $s * a$, and $c * a$. Finally, the hypothesis regarding the importance of the ratio of the dispersal distance to the ACL was represented by $l_g * v$.

Similarly, logistic GAMs were also fitted using the realized-landscape metrics σ , γ_1 , γ_2 , l_r , and v , with the same dependent variable (not branched vs. branched). Nested



Video 1: Video of the model realization depicted in figure 2 (video 1, available online). In this video, frames show the population census at every tenth generation, superimposed on the generated landscape, which includes both a spatial gradient and spatially continuous patchiness. Background colors indicate locally optimal ecological trait values, whereas circle colors indicate the trait values of individuals, both ranging from white (low) to dark green (high). Available from the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.43cj7/1> (34.9 MB).

models that included interactions of the independent variables were constructed (table A2; fig. A2). In the full model, the hypothesis that an intermediate optimum for the overall realized-landscape heterogeneity would exist and would be affected by dispersal distance was represented by $\sigma * \nu$, and the hypothesis regarding the importance of the ratio of the dispersal distance to the realized-landscape ACL was represented by $l_r * \nu$.

The Bayesian Information Criterion (BIC; Schwarz 1978) was used to select the best model from each of these two sets of nested models. Several other metrics were also calculated for each model: the Nagelkerke R^2 , a standard substitute for R^2 in the context of logistic regression (Nagelkerke 1991); C , the area under the receiver operating characteristic curve (Metz 1978); D , the discrimination coefficient (Tjur 2009); and the proportion of realizations in which the outcome (branched or unbranched) was correctly predicted by the model.

To fit the GAM models, we used the `gam()` function in the `mgcv` package of R (ver. 1.7–20; Wood 2006). Tensor product smooths, `te()`, were used for both variables and interactions to ensure proper nesting (S. Wood, personal communication). Restricted maximum likelihood was used for fitting because it is the best method with a binary dependent variable (S. Wood, personal communication). Apart from these choices, default values were used for all fitting parameters.

Visualizations of two-dimensional slices through the five-dimensional GAM spaces were generated using a modified version of the `vis.gam()` function of `mgcv`. These slices show the predicted probability of branching for given combinations of all five independent variables of the GAM (given that three variables are held constant across a slice while varying the other two). Because only these slices are shown, caution must be used in interpreting the patterns observed. However, results presented are qualitatively ro-

bust to variation of the parameters fixed for each slice except where otherwise noted.

To confirm that our hypotheses encompassed all important interactions among the parameters varied, we conducted ex post facto data exploration using logistic generalized linear models (GLMs). GLMs were used instead of GAMs for this purpose because fitting GAMs that included every possible interaction, up to the full five-way interaction of all parameters, was computationally infeasible. This exploration indicated that other interactions were of very small effect size, and the prediction rate and Nagelkerke R^2 for these GLMs was never as high as for the best GAMs; results from these GLMs are thus not presented here.

Results

A data set containing the parameter values, realized-landscape metrics, and outcomes for all realizations is published in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.43cj7>; Haller et al. 2013), with R code to fit the GAMs presented. End-of-realization censuses and per-generation results comprise approximately 500 GB, and the generated landscapes comprise several thousand GB; because these sizes greatly exceed Dryad's 10 GB data set limit, online provision of these data was not possible.

Reprising boundaries constitute a middle ground between the extremes of stopping boundaries, which mostly promote branching by generating disruptive selection, and absorbing boundaries, which generally inhibit branching by generating stabilizing selection (R. Mazzucco, M. Doebeli, and U. Dieckmann, unpublished manuscript). For this reason, reprising boundaries were used for all main results, to minimize the influence of the boundary con-

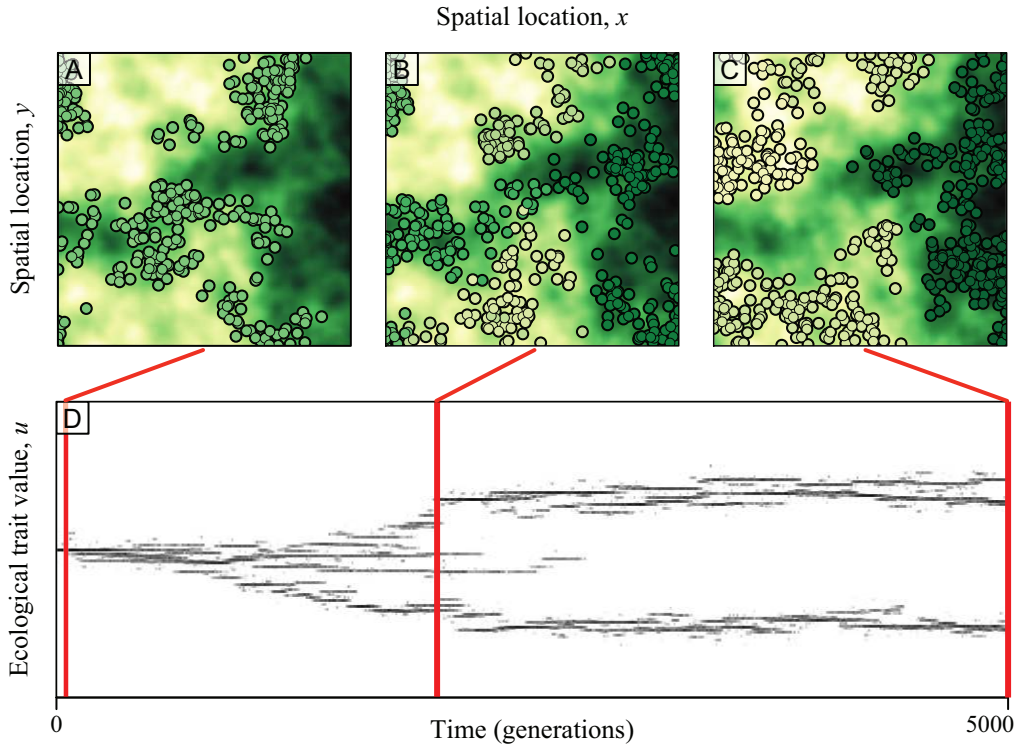


Figure 2: One realization of the model. A–C, Census of all individuals in the model after 50 (A), 2,000 (B), and 5,000 (C) generations (circles), superimposed on the generated landscape, which includes both a spatial gradient and spatially continuous patchiness. Background colors indicate locally optimal ecological trait values, whereas circle colors indicate the actual trait values of individuals, both ranging from white (low) to dark green (high). D, Plot of ecological trait values (Y-axis) through time. For each time, the plot shows the distribution of the ecological trait values of the individuals extant at that time in the model. Red lines indicate time points for A–C. Evolutionary branching can be observed at several points, and three branches exist at the end of execution, two of which are phenotypically similar; note also that one lineage became extinct after approximately 2,600 generations.

dition on the results. Results for the other boundary conditions are qualitatively similar and are presented in “Effects of Boundary Conditions,” available online (table A3; figs. A7–A10).

Generalized Additive Models

Of the 300,000 main realizations using reprising boundary conditions, 64,858 (21.6%) exhibited evolutionary branching. We fit two nested sets of models to the results of these realizations, using, in addition to the dispersal parameter ν , either the landscape-generating parameters (s, c, l_g, a ; table A1; fig. A1) or the realized-landscape metrics ($\sigma, \gamma_1, \gamma_2, l_r$; table A2; fig. A2), as described in “Statistical Analysis.”

The best GAM model using the landscape-generating parameters (henceforth “GAM_g”) was the full model including all interactions predicted by our hypotheses,

$$\begin{aligned} \text{branched} &\sim s + c + l_g + a + \nu + s * \nu \\ &+ c * \nu + a * \nu + l_g * \nu + s * c \\ &+ s * a + c * a + s * c * a. \end{aligned}$$

GAM_g, with 13 terms and 167.0 effective degrees of freedom, provided a fit with a Nagelkerke R^2 of 0.642 and correctly predicted the outcome of 89.5% of realizations, as compared with the null model prediction rate of 78.4% (table A1). GAM_g also correctly predicted 89.6% of the outcomes of the 300,000 realizations in the separate test data set, indicating that overfitting did not occur.

The best GAM using the realized-landscape metrics (henceforth GAM_r) was also the full model including all predicted interactions,

$$\text{branched} \sim \sigma + \gamma_1 + \gamma_2 + l_r + \nu + \sigma * \nu + l_r * \nu.$$

GAM_r, with only 7 terms and 49.3 effective degrees of freedom, provided a fit with a Nagelkerke R^2 of 0.681 and correctly predicted the outcome of 90.6% of realizations,

as compared with the null model prediction rate of 78.4% (table A2). GAM_r also correctly predicted 90.7% of the test data set outcomes, again indicating that overfitting did not occur.

Although GAM_g and GAM_r were chosen on the basis of their BIC scores, the other model metrics assessed (Nagelkerke R^2 , C , D , and prediction accuracy; see “Statistical Analysis”) were also optimized by this choice (tables A1, A2; figs. A1, A2). For additional discussion, see “Comparison of Nested GAM Models,” available online.

Intermediate Heterogeneity Maximizes Branching Propensity

For all types of heterogeneity explored, branching propensity was maximized at some particular level of heterogeneity, showing a hump-shaped relationship. In particular, an intermediate slope was found to maximally promote branching (optimum $s \approx 0.75$; fig. 3A), and likewise for an intermediate curvature (optimum $c \approx 0.25$; fig. 3B). An intermediate patchiness amplitude similarly appeared to maximally promote branching (optimum $a \approx 2.75$; fig. 3C), but this effect depended on the boundary conditions, being most apparent with absorbing boundaries (fig. A7C) and least apparent for stopping boundaries (fig. A7O). For reflecting and reprising boundaries, the optimum value appeared to be close to the edge of the parameter space explored (fig. A7G, A7K). Branching was also maximally promoted at an intermediate level of overall landscape heterogeneity, as measured by the standard deviation of the realized landscape, σ (optimum $\sigma \approx 2.0$

for $v \leq 0.5$; fig. 3D). The probability of branching always decreased with increasing dispersal distance, but dispersal distance had little effect on the optimal values of s , c , and a (fig. 3A–3C). The optimum σ decreased with increasing dispersal distance, reaching zero for $v \geq 0.5$ (fig. 3D), although this effect varied somewhat among boundary conditions (fig. A7).

Additivity and the Refugium Effect

The different types of heterogeneity also interacted in their effects on branching, making the complete picture somewhat more complex. Slope and curvature showed simple additivity (fig. 4A). This was not the case, however, for the combination of slope and patchiness amplitude (fig. 4B); here, as amplitude increased, the sensitivity to slope decreased, indicating less than full additivity between slope and amplitude. This effect was even more pronounced for curvature and amplitude (fig. 4C); here, for $c \geq 0.4$, the probability of branching actually increased with increasing amplitude, up to a point, indicating a net positive interaction between large curvature and amplitude.

Autocorrelation Length and Dispersal

Landscapes with a larger realized autocorrelation length l_r produced a higher probability of branching (fig. 5). An interaction between the effects of l_r and dispersal distance v was also observed: the branching probability decreased more strongly with increasing v when l_r was larger (fig. 5). The generating autocorrelation length l_g had little effect

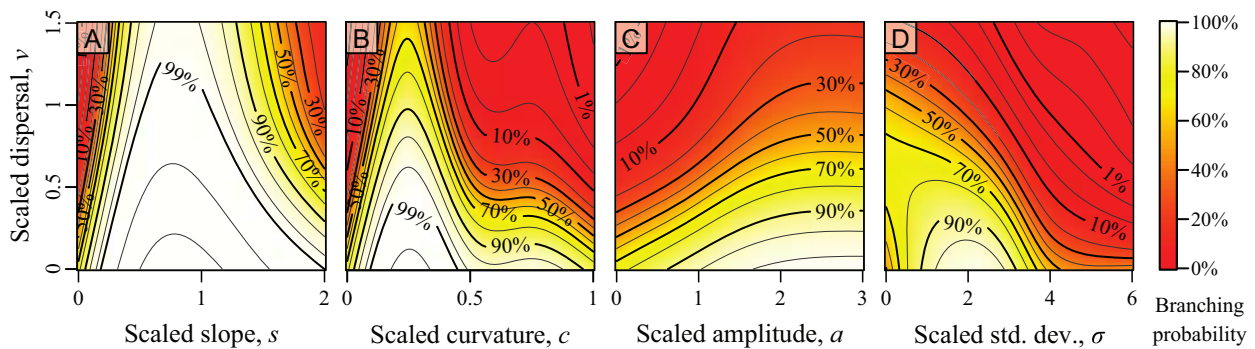


Figure 3: Predicted branching probabilities from generalized additive models (GAMs), showing effects of dispersal distance and different heterogeneity types. We show that an intermediate level of heterogeneity typically maximizes the branching probability. Panels show contour plots of the branching probability as a function of the scaled dispersal distance v and scaled slope s (A); scaled curvature c (B); scaled amplitude a (C); and scaled landscape standard deviation σ (D). Red (white) indicates predicted low (high) branching probability (see color scale at right). The probability of branching is maximized at an intermediate value of s , c , and perhaps a , regardless of the dispersal distance; an intermediate value of σ also maximizes branching for $v \leq 0.5$. Results shown are for reprising boundaries; results for other boundary conditions are qualitatively similar (see “Effects of Boundary Conditions” and fig. A7, available online). Other parameters: A–C, $s = 0$, $c = 0$, $a = 0$, and $l_g = 0.15$; D, $\gamma_1 = 0$, $\gamma_2 = 0$, and $l_r = 0.15$. Contour lines below 10% and above 90% are placed to best show the contours of the data in each panel.

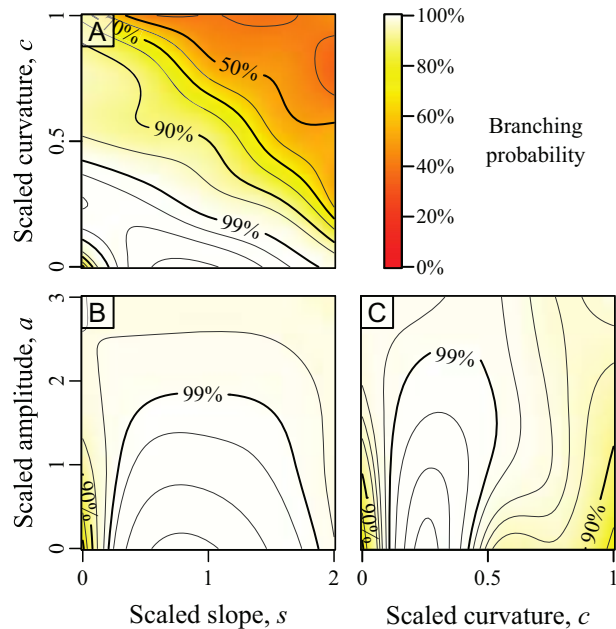


Figure 4: Predicted branching probabilities from GAM_g (the best generalized additive model using the landscape-generating parameters), showing interactions between heterogeneity types. We show additive effects (and deviations therefrom due to the refugium effect) between scaled slope s , scaled curvature c , and scaled amplitude a . Panels show the branching probability as a function of s and c , demonstrating additivity between the two (A); s and a , demonstrating nonadditive effects between the two, and a weak mitigation of the negative effect of steep slope on branching when combined with large amplitude (B); and c and a , demonstrating nonadditive effects between the two, and a strong mitigation of the negative effect of high curvature on branching when combined with large amplitude (C). Red (white) indicates predicted low (high) branching probability (see color scale at right). Results shown are for reprising boundaries; results for other boundary conditions are qualitatively similar (see “Effects of Boundary Conditions” and fig. A8, available online). Other parameters: $s = 0$, $c = 0$, $a = 0$, $l_g = 0.15$, and $\nu = 0.075$. Contour lines above 90% are placed to best show the contours of the data in each panel.

(see “Landscape-Generating Parameters versus Realized-Landscape Metrics,” available online).

Other Results

We had no specific hypotheses regarding the role that the realized-landscape skewness, γ_1 , and kurtosis, γ_2 , would play. For this reason, although substantial and significant effects were observed for both (table A2; fig. A10), they are presented in “Effects of Skewness and Kurtosis,” available online.

Analysis using the alternative cluster-based assessment of branching (“Model Description, Observables”) produced results very similar to those presented here, which

suggests that our findings are robust to variations in the method used to assess branching (“Alternative Assessment of Branching,” available online).

Branching times for realizations that branched were typically less than 1,000 generations, following an approximately lognormal distribution, and showed little correlation with the predicted probabilities of branching given by the GAM models (fig. A11; “Distribution of Branching Times”). Branching was thus generally binary: it happened early or not at all, for most realizations. Nevertheless, some effects of parameters on branching time were observed (figs. A12, A13; “Correlations with Branching Times,” available online).

Although branches occasionally became extinct, merging of branches, or “reverse speciation” (Seehausen 2006), was not observed. Furthermore, the phenotype of unbranched lineages often drifted over time, whereas branched lineages appeared to be stabilized by competition and typically exhibited evolutionary stasis after arriving at equilibrium. These and other qualitative observations are presented further in figures A14 and A15 (“Patterns of Evolutionary Branching,” available online).

Discussion

Here we have shown that complex spatial heterogeneity affects evolutionary branching in several ways previously unexplored by theoretical models. An intermediate optimum level of environmental heterogeneity exists that maximally promotes branching, and such an intermediate optimum also appears to exist for particular types of heterogeneity, such as linear gradients, nonlinear gradients, and spatially continuous patchiness. The effects of these different types of heterogeneity are additive to some extent, but linear gradients of an optimal slope are more effective in promoting branching than are the other types of heterogeneity investigated. A refugium effect also causes a departure from additivity of different types of heterogeneity because patchiness can break up an otherwise hostile environment, leading to a higher branching propensity for landscapes than would otherwise be expected given the overall level of heterogeneity present. The scale of patchiness relative to the dispersal distance of organisms is also important: large patch size relative to dispersal distance isolates populations in distinct areas, promoting local adaptation.

Furthermore, our results allow us to quantitatively and accurately predict the branching propensity of heterogeneous landscapes through empirical metrics that might often be easily obtained. This method could be used to predict the branching propensity of real landscapes. The effects of complex spatial environmental heterogeneity might help explain some contentious observations, such

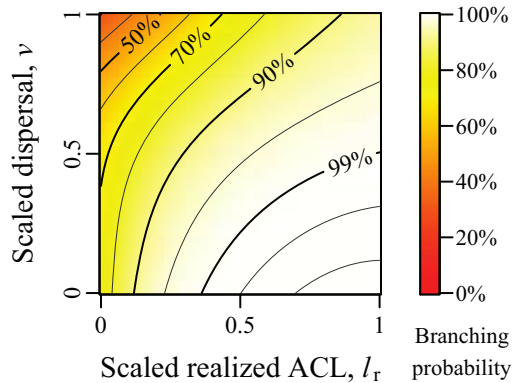


Figure 5: Predicted branching probabilities from GAM₁ (the best generalized additive model using the realized-landscape metrics), showing interaction between dispersal distance and realized-landscape autocorrelation length (ACL). Contours show branching probability as a function of the scaled realized autocorrelation length l_r and the scaled dispersal distance ν , demonstrating the importance of the relative scale of the two. Red (white) indicates predicted low (high) branching probability (see color scale at right). Branching probability decreases with increasing ν but increases with increasing l_r ; ν and l_r also interact, with ν having less effect when l_r is small. Results shown are for reprising boundaries; results for other boundary conditions are qualitatively similar (see “Effects of Boundary Conditions” and fig. A9, available online). Other parameters: $\sigma = 2.0$, $\gamma_1 = 0$, and $\gamma_2 = 0$. Contour lines above 90% are placed to best show the contours of the data.

as the higher biodiversity of the tropics, differences in the speciosity of parapatric sister clades, the causes of adaptive radiation (or the lack thereof) in different environments, and the evolutionary effects of differences in dispersal behavior among species. This connection between our model and real landscapes also has potential implications for conservation.

Intermediate Heterogeneity Maximizes Branching Propensity

Previous research indicates that an intermediate environmental gradient slope maximally promotes evolutionary branching (Doebeli and Dieckmann 2003; Heinz et al. 2009): very shallow slopes provide little opportunity for adaptive divergence, while very steep slopes are likely to be lethal for dispersers and provide little habitable space in which a colony might settle. Our model confirmed this result (fig. 3A), with good agreement to previous findings (fig. 3B in Doebeli and Dieckmann 2003).

Going beyond previous results, we also observed an intermediate optimum for the degree of curvature of an environmental gradient (fig. 3B) and for the overall measured heterogeneity of the landscape (fig. 3D). These findings support our hypothesis that an intermediate optimum

level should exist for other types of heterogeneity (see “Introduction: Intermediate Heterogeneity Maximizes Branching Propensity”). In fact, the argument that steep slopes are lethal for colonizers readily generalizes to other kinds of heterogeneity, because the area of suitable habitat for each species shrinks as heterogeneity increases (Allouche et al. 2012). The existence of an intermediate optimum for the amplitude of spatially continuous patchiness depended on the boundary condition, however, and was not always apparent (fig. A7). This may be because a very high level of patchiness can have both negative effects on speciation, by hindering colonization, and also positive effects on speciation, by providing obstacles that increase the geographic isolation of populations and thus promote divergence (Golestani et al. 2012). Separating these competing effects of heterogeneity would be an interesting direction for future research.

Additivity and the Refugium Effect

If there is an optimum overall level of spatial environmental heterogeneity, as discussed in the previous section, then it might be natural to expect particular types of heterogeneity (gradient slope, gradient curvature, and patchiness amplitude, in our study) to be additive in their effects (see “Additivity of Heterogeneity Types”). This effect was observed for the interaction of slope and curvature (fig. 4A). If both are too low, then the optimum level of heterogeneity is not attained and branching is hindered. Increasing either one to its optimal level maximizes branching due to that type (although curvature is less effective than slope in promoting branching even at its optimum level, presumably because curvature can only optimize a fraction of the whole landscape for branching). Finally, mixtures of both slope and curvature exhibit nearly straight, diagonal isoclines, which indicates a high degree of additivity. This supports our hypothesis that the overall magnitude of heterogeneity determines the branching propensity of the landscape to a first approximation. However, other heterogeneity types showed more complex interactions, as we now discuss.

We also hypothesized that a refugium effect should cause a deviation from this additivity for the combination of patchiness with an extreme gradient due to either slope or curvature. This effect is strongest for curvature, because increasing patchiness amplitude actually increases the branching propensity for all magnitudes of curvature substantially greater than the optimum curvature (fig. 4C). The effect is less pronounced for slope; here, increasing amplitude merely has less strong of an effect than would be expected from pure additivity, and at very steep slopes increasing amplitude has almost no effect at all (fig. 4B). The refugium effect, then, causes a positive, synergistic

interaction between high curvature and patchiness, but merely acts to partially mitigate the expected additivity between high slope and patchiness. This difference might be because, without patchiness, only a small section of a curved gradient is likely to be hospitable; if patchiness can open up the entire landscape to colonization, the refugium effect may thus be quite large.

Because of the refugium effect, the probability of branching (let us here call this p) increased substantially with an increase in patchy heterogeneity in some cases (from <85% to >95% for the largest curvatures explored in our realizations with reprising boundaries; fig. 4C), and even more with absorbing and stopping boundaries (fig. A8). However, the probability that branching will not occur, $1 - p$, shows a proportionately much larger effect, decreasing from >15% to <5%. The odds ratio, $p/(1 - p)$, is a standard metric that unifies these two perspectives; using it, we can see that, in the best case, the refugium effect more than tripled the odds in favor of branching, from approximately 5.5 : 1 to 19 : 1. Such a large change in odds could produce very large effects on the net biodiversification rate in empirical scenarios in which branching is not otherwise very likely to occur.

Autocorrelation Length and Dispersal

We also hypothesized that the effects of patchiness (both the refugium effect and the overall promotion of branching by patchy heterogeneity) should depend on the relative scales of dispersal and patchiness (Hovestadt et al. 2001; Bolker 2003, 2010; Snyder and Chesson 2003; Bonte et al. 2010; Hanski and Mononen 2011). Specifically, as the ratio of the autocorrelation length (ACL) of patchiness to the typical dispersal distance increases, local adaptation to individual patches should be increasingly favored (up to a point), promoting evolutionary branching (see “Introduction: Autocorrelation Length and Dispersal”). This hypothesized interaction between ACL and dispersal was observed for the realized ACL, l_r (fig. 5). For small values of l_r , patches are too small for local adaptation to be possible, and so the dispersal distance is relatively unimportant. For larger l_r , however, local adaptation becomes possible as long as dispersal distance is sufficiently short range; the longer the dispersal distance, the less likely branching is. For very large l_r and short-range dispersal, the isoclines flatten out, indicating an insensitivity to l_r ; patches in this case are large enough relative to dispersal that making them even larger has little effect on branching, because populations are already able to fully adapt to their local conditions. These findings demonstrate that, for a patch to provide a good site for local adaptation, it must be much larger than the individual dispersal distance, both because many individuals in a population will not be lo-

cated at the center of the patch, and because the flat bottom of the patch that provides a relatively constant environment is much smaller than the overall patch size; for much of the radius of a patch, the environment is changing, with a gradient from inside-patch to outside-patch conditions.

This interaction between dispersal distance and ACL was not observed for the generating ACL, l_g (fig. A3B); indeed, l_g had almost no effect. This was expected, because the realized ACL is not highly correlated with the generating ACL due to stochasticity and system size constraints (fig. A3A), and because it also depends on the other landscape-generating parameters. For these reasons, l_g contains much less information than l_r and is a poor predictor of evolutionary branching (“Landscape-Generating Parameters versus Realized-Landscape Metrics,” available online).

Empirical Implications

We have suggested that empirical studies might use our realized-landscape metrics to measure the heterogeneity of real landscapes and then test the predictions of our model against the actual biodiversity of clades endemic to that landscape. This exciting opportunity to confront theory with data is, however, not without challenges.

Sampling a landscape at high resolution may be non-trivial for some environmental metrics not provided by existing resources such as satellite images (e.g., soil mineral concentrations; Yost et al. 2012). However, many environmental variables are typically correlated (e.g., temperature, altitude, and rainfall), and in some cases, sophisticated methods exist for predicting unknown environmental variables across a landscape using such correlated proxies (McKenzie and Ryan 1999). Studies might also compare the predictive value of all available metrics, or might compress multiple metrics into a single axis of environmental variation, using principal components analysis (PCA). PCA might be particularly appropriate when local adaptation to a suite of correlated environmental variables is believed to have occurred; however, it should be used with caution, because the axis of greatest environmental variation might not correspond to the axis of variation to which a particular clade adapted.

Furthermore, clades should be chosen that match the biology modeled here (e.g., unbiased natal dispersal, asexual reproduction); additional theoretical exploration will be needed before other radiations can be studied within this framework (see “Future Directions”). We suggest that adaptation of asexual or clonal plants and fungi to serpentine soil outcrops might present an attractive opportunity, because of the many independent instances of speciation due to local adaptation to serpentine soils in heterogeneous landscapes (Brady et al. 2005; Harrison and Rajakaruna 2011). Experimental evolution of microbial

systems in heterogeneous culture media might also be a worthwhile approach (Rainey and Travisano 1998; Bailey and Kassen 2012). There may also be cases in which historical data, perhaps from paleoclimatological reconstructions and dated phylogenies, are sufficiently complete to test our model's predictions for cases such as postglacial radiations (Linder 2008) or adaptation to different islands (Givnish 2010). Finally, natural heterogeneity also commonly varies over time; to test our model's predictions, a landscape would have to be chosen that has been relatively invariant over the time in which speciation occurred (or this model would have to be generalized to spatiotemporal patterns of heterogeneity; see "Future Directions").

Natural heterogeneity might exhibit patterns not modeled here. For example, sudden transitions in habitat type may be superimposed on less extreme heterogeneity (e.g., ocean-to-land transitions); the ACL may vary depending upon the spatial axis or the position in space (e.g., "basin-and-range" topography); or the landscape structure may not be reducible to a single ACL due to hierarchical structure (Kolasa et al. 2012). In such cases, model predictions could still be generated by replacing our generated landscapes by a representation of the actual landscape.

If environmental conditions that promote biodiversification also promote the maintenance of biodiversity (Rosenzweig 2001, 2003), then our results have implications for conservation policy. Specifically, the loss of, or alteration of, patterns of environmental heterogeneity may lead to "reverse speciation" or the loss of locally adapted taxa (Seehausen et al. 1997, 2008; Templeton et al. 2001; Seehausen 2006; Crispo et al. 2011; De León et al. 2011; Vonlanthen et al. 2012). One implication is that even if a large reserve is ideal habitat for a given species, the variation within that species may not be maintained unless environmental heterogeneity is preserved to provide divergent selective pressures. A second implication is that refugia may provide stepping stones, both spatially and adaptively (see "Refugium Effect"), allowing more rapid and effective colonization and adaptation than would otherwise be possible in the face of anthropogenic disturbances such as climate change (Havel et al. 2005; Thomas et al. 2012). Indeed, assisted migration programs might do well to consider introducing species into carefully chosen refugia within a larger hostile environment, rather than into a larger area of compatible habitat, to maximally accelerate adaptation toward anticipated future conditions. The plausibility of this approach is illustrated by the importance of heterogeneity, refugia, and adaptation in the spread of invasive species (Havel et al. 2005; Lombaert et al. 2010; Heinicke et al. 2011; Tingley et al. 2012; Westley et al. 2013). Given this, our results might also help to predict biological invasions (Kolar and Lodge 2001), extending approaches such as environmental niche modeling

(Herborg et al. 2007) by adding consideration of dispersal and evolution.

Future Directions

There are many future directions for this research that we expect to be fruitful. Because our model is asexual with natal dispersal, it applies most strongly to selfing and asexual plants; extending the model to the sexual case would reveal the importance of gene flow due to hybridization (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2003). The need to establish assortative mating in the sexual case can hinder speciation, particularly when mate choice is based on an ecologically neutral marker trait (Felsenstein 1981; Dieckmann and Doebeli 1999; Servedio et al. 2011). However, this negative effect of sexual reproduction on speciation has been shown to be mitigated greatly by effects of spatial distance and environmental heterogeneity (Doebeli and Dieckmann 2003). We expect this to apply also for complex spatial heterogeneity, mediated by the interaction between the relative spatial scales of heterogeneity and dispersal.

Similarly, the addition of different types of dispersal, such as nonnatal dispersal, conditional dispersal, and habitat preference, would allow an exploration of the effects of complex spatial heterogeneity with dispersal behaviors more typical of animal species (Ronce 2007; Edelaar et al. 2008; Clobert et al. 2009; Payne et al. 2011; Webster et al. 2012). Allowing the evolution of dispersal rate (Doebeli and Ruxton 1997; Mathias et al. 2001), distance (Heinz et al. 2009), and kernel shape (Hovestadt et al. 2001; Bolker 2010) would also be worthwhile; these factors might interact with complex spatial heterogeneity in interesting ways, perhaps modifying the dynamics of the refugium effect with an effect of the dispersal kernel shape. Steep environmental gradients have previously been shown to promote the evolution of short dispersal distance (Heinz et al. 2009), and we expect that the same would likely apply to other types of heterogeneity, but this might inhibit branching on some landscapes, if it means that the refugium effect is diminished by decreased dispersal into refugia.

Our results indicate that branching, when it occurs, typically occurs immediately; however, some landscapes promote branching in a delayed fashion, perhaps because the population first has to attain a favorable spatial configuration on the landscape before branching can occur (see "Distribution of Branching Times" and "Correlations with Branching Times"). This result underscores the need for a theory linking spatial structure to the expected waiting time to branching, a question that has barely begun to be explored (Orr and Orr 1996; Gavrillets et al. 2000*b*).

Allowing temporal environmental heterogeneity, in ad-

dition to spatial environmental heterogeneity, would connect this work to earlier studies related to environmental change (e.g., Pease et al. 1989; Bürger and Lynch 1995; Kopp and Hermisson 2007; North et al. 2011), with particular relevance for predicting the effects of climate change for species occupying realistically heterogeneous landscapes. Finally, only one ecological dimension has been examined in this work; an exploration of the consequences of complex spatial heterogeneity in multiple ecological dimensions is needed (Nosil and Harmon 2009; Guillaume 2011; Birand et al. 2012). We hope to pursue these topics in future research.

Spatial heterogeneity, by producing divergent selective regimes that promote diversification, is an important driver of speciation. A complete understanding of the effects of complex, realistic patterns of spatial heterogeneity is therefore fundamental to an understanding of the origins of biodiversity. The model and results we have presented here represent a step toward that goal.

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