Phylogenetic Inference of Reciprocal Effects between Geographic Range Evolution and Diversification

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Abstract.—Geographic characters—traits relating to the spatial distribution of a species—may both affect and be affected by processes associated with lineage birth and death. This is potentially confounding to comparative analyses of species distributions because current models do not allow reciprocal interactions between the evolution of ranges and the growth of phylogenetic trees. Here we introduce a likelihood-based approach to estimating region-dependent rates of speciation, extinction, and range evolution from a phylogeny, using a new model in which these processes are interdependent. We demonstrate the method with simulation tests that accurately recover parameters relating to the mode of speciation and source-sink dynamics. We then apply it to the evolution of habitat occupancy in Californian plant communities, where we find higher rates of speciation in chaparral than in forests and evidence for expanding habitat tolerances.

Keywords: diversification, comparative methods, biogeography, macroevolution

The influence of species' traits on lineage diversification is an active area of macroevolutionary research, and recent advances have improved methods for detecting the phylogenetic signature of state-dependent speciation and extinction. In particular, hypotheses of trait acquisition leading to higher rates of species accumulation can now be tested for binary and quantitative characters using models that also allow for asymmetry in the direction of trait evolution (Maddison et al. 2007; FitzJohn 2010b). However, not all traits are well served by current methods, and in this paper, we draw attention to one particularly interesting class: characters whose states can be directly transformed by the processes of lineage birth and death. The concept that trait evolution cannot only affect lineage diversification but also be affected by it is not new (e.g., Eldredge and Gould's (1972) picture of rapid state changes associated with speciation), but it has not previously been modeled in a way that permits hypothesis testing from comparative data.

We illustrate this idea of reciprocal evolutionary interactions with "geographic" characters whose states are defined by spatial distributions. Consider geographic range and habitat preference, two traits likely to influence speciation and extinction (e.g., McKinney 1997; Ribera et al. 2001; Jablonski and Roy 2003; Cardillo et al. 2005). For geographic range, imagine a widespread ancestral species split by allopatric divergence into two daughter species, each confined to a smaller range. For habitat preference, imagine an ancestral generalist species able to tolerate multiple habitat types, in which local adaptation of a population to one habitat leads to its isolation and divergence as a new specialist species. In each of these examples, speciation results in the origin of at least one daughter lineage having a state different from its immediate ancestor.

This possibility of a change in character state at a splitting event has significant consequences for models of trait-dependent lineage diversification, in which speciation is a stochastic process generating discrete events through time. If the rate of speciation is mode-dependent (e.g., if divergence in allopatry is more rapid than divergence in sympatry or parapatry) and the mode of speciation is state-dependent (e.g., if allopatric divergence is more likely in widespread species than in small-ranged endemics), then reciprocal feedback ensues between the evolution of traits and the rate and mode by which lineages proliferate. Character evolution is thus a function of rates of change along phylogenetic branches (anagenesis) and rates of change associated with speciation events (cladogenesis), while the rate of speciation is likewise affected by trait values and modes of divergence.

This feedback loop between diversification and state changes also includes extinction. In the case of geographic range, species with larger ranges are commonly considered less prone to extinction than those with smaller ranges (McKinney 1997). Range contraction events will therefore increase the rate of extinction, and they may have causes that are anagenetic (stochastic extirpation of local populations) or cladogenetic (speciation fragmenting an ancestral range into smaller descendant ranges). These effects are counterbalanced by range expansion, achieved through dispersal events that establish new populations. Increases in range size may have a variety of effects on speciation rates (Rosenzweig 1995; Chown 1997; Gaston and Chown 1999).

Dynamic, reciprocal interactions between state transitions (range expansion and con-

traction) and rates of lineage birth and death are an intrinsic feature of many evolutionary and ecological hypotheses. For example, are regional differences in species richness and endemism driven by spatial asymmetries in speciation and extinction rates, or by asymmetries in the direction of lineage dispersal (i.e., centers of origin and accumulation; Stebbins 1974; Chown and Gaston 2000; Mora et al. 2003)? How do range size and range evolution affect speciation rate (Wagner and Erwin 1995; Gaston and Chown 1999; Jablonski and Roy 2003; Pigot et al. 2010)? What are the most common modes by which speciation divides ancestral ranges, in terms of range size or degree of sympatry (Anderson 1985; Gaston 1998; Barraclough and Vogler 2000; Phillimore et al. 2008; Pigot et al. 2010)? How do speciation rates compare on the mainland, within an island, and directly after dispersal to the island (Gillespie and Roderick 2002; Ricklefs and Bermingham 2007)? Are specialists more likely to arise from generalist ancestors, or directly from other specialists (Simpson 1953; Nosil and Mooers 2005)?

The need for phylogenetic models to infer these interactions has been raised previously, in the context of biogeographic frameworks that lack parameters for stochastic speciation and extinction and hence allow consideration of geographic characters only on a static tree (Ree and Smith 2008; Lamm and Redelings 2009; Ree and Sanmartín 2009). Here, we develop a model for geographic traits that encapsulates the basic concepts introduced above. It uses the mathematical framework of Maddison et al. (2007), modified to include biogeographic parameters and to allow state changes at speciation and through local extinction. We demonstrate with simulations how parameter estimation can be used to test hypotheses about the tempo and mode of lineage diversification in the context of range evolution. We then apply the model to an empirical case study, quantifying the contributions of diversification and range shifts to diversity in Californian chaparral plant communities.

The GeoSSE Model

Our model of "geographic-state speciation and extinction," GeoSSE, differs from the "binary-state speciation and extinction" model (BiSSE, Maddison et al. 2007) in three specific ways. First, the character states are defined so that a single, wide-ranging species may occupy more than one area or region simultaneously. Second, the transitions between states are explicitly parameterized in terms of range expansion through dispersal and range contraction through local extirpation. And third, rates of speciation, extinction, and dispersal are tied to the regions themselves rather than to the character states, causing the dynamics of wider-ranging species to be determined by the cumulative effects of the areas they inhabit.

The mechanisms and assumptions of GeoSSE are the same as the model of Goldberg et al. (2005), with the addition of between-region speciation (from Ree et al. (2005); see below). The two models differ in the type of data they are designed to fit: the first was developed for the ages of extant species as determined from the fossil record, while GeoSSE works with reconstructed phylogenies estimating relationships among extant species. Of existing phylogenetic biogeographic models, the closest is the dispersal-extinction-cladogenesis model of Ree and Smith (2008, DEC); GeoSSE differs in treating speciation and global extinction

as a stochastic process rather than assuming a fixed phylogenetic history.

Conceptualization

The regions.—We greatly simplify spatial structure by modeling a system with only two regions, denoted A and B, in each of which a species may be present (having one or more populations) or absent. Coding ranges in this way yields three possible extant states: A, B (species endemic to a single region), and AB (species widespread, in both regions). We assume that the carrying capacities of both regions are unbounded and that the diversity dynamics are not affected by species interactions, as in the basic birth-death framework.

It is simplest to interpret each region as a continuous portion of space, but our model applies equally to regions consisting of a collection of disjoint areas under the interpretation that the processes within each region are averaged across the individual areas. Consequently, although we will present the model in terms of geographic regions, it is also relevant to other range-related traits such as habitat type or the host type of parasites. Regions cannot, however, be defined by the species within them; such systems may instead require models with clade-specific rates or interaction effects between lineages.

Dispersal and extinction.—Range evolution along a phylogenetic branch (anagenesis) is composed of two processes: range expansion via dispersal and range contraction via local extirpation. Over an infinitesimal time interval, ranges can evolve only by single events. In this two region model, range expansion consists of transitions from A or B to AB, occurring with per-lineage rates d_A and d_B respectively. We assume that these and all other rates of the model are constant over time and across lineages. The reverse process, range contraction from AB to A or B, occurs with per-lineage rates x_B and x_A respectively. We assume that extinction from a region is independent of presence in the other region, so global extinction of species from states A and B also occurs at per-lineage rates x_A and x_B respectively. Lineage extinction in the GeoSSE model thus depends on range size as well as location, since more events are required for extinction of a wider-ranging species. We do not allow instantaneous transitions between A and B or immediate global extinction of AB since each of these requires two events.

Speciation.—In the model, speciation of an endemic lineage always produces two daughter lineages with the same range: an A parent produces two A daughters, and similarly for B. A widespread AB species may also undergo speciation within a single region, yielding one endemic and one wide-ranging daughter, i.e., the daughters have states A and AB if speciation was in region A, or B and AB. The region-specific per-lineage rates for this within-region mode of speciation are s_A and s_B. Alternatively, an AB species may diverge along the boundary that separates the regions, yielding one A and one B daughter. The rate of this between-region mode of speciation is s_{AB}. Because widespread lineages are subject to both the between- and within-region modes of cladogenesis, their effective rate of speciation is greater than that of endemics; it is the sum of s_A, s_B, and s_{AB}.

Identical inheritance of geographic distribution is likely impossible when examined on a fine spatial scale, but we ignore structure inside regions. Therefore, although the two daughter ranges of an endemic parent are equal in our model, we do not specify whether

within-region speciation is allopatric, parapatric, or sympatric. Between-region speciation events in GeoSSE are not traditional vicariance events (a physical change in the connectivity of the regions which affects all species), but allow different species to respond individually to their environment.

Formulation

Because the mathematical description of the GeoSSE model is similar to BiSSE (Maddison et al. 2007), we present the formulation only briefly here; a full derivation can be found in online Appendix 1 (*http://www.sysbio.oxfordjournals.org*). A schematic comparison of GeoSSE and BiSSE is shown in Figure 1.

Like BiSSE, GeoSSE assumes a fully-resolved, dated phylogeny of the group in question. Although BiSSE can in principle allow for ancestral nodes with hard polytomies (via modification of Eq. 4 in Maddison et al. 2007), the possibility of character state changes at nodes makes this unwieldy for GeoSSE. Phylogenetic uncertainty can better be incorporated by performing analyses across a posterior set of bifurcating trees, as we illustrate in our empirical case study below.

Geographic ranges of extant species should be known with sufficient precision to say whether each species is present in region A only, region B only, or both regions. Incomplete sampling, either randomly distributed across the tree or in the form of unresolved clades, can be incorporated as in FitzJohn et al. (2009), as can uncertain tip state information. Such incomplete information, of course, reduces the power of the analysis.

Likelihood of tree and character states (D).—The likelihood $D_{Ni}(t)$ is proportional to the probability of a lineage beginning at time t in state i (i = A, B, or AB) evolving into a clade with identical branching structure and character states as the (sub)tree actually observed to descend from N. The branching process will be viewed as proceeding forward in time, though time is defined to increase towards the root of the tree (Fig. A1-1).

Changes in the D_{Ni} over time within a branch are described by

$$\frac{dD_{NA}}{dt} = -(s_A + d_A + x_A)D_{NA}(t) + d_A D_{NAB}(t) + 2s_A D_{NA}(t)E_A(t) \tag{1a}$$

$$\frac{dD_{NB}}{dt} = -(s_B + d_B + x_B)D_{NB}(t) + d_B D_{NAB}(t) + 2s_B D_{NB}(t)E_B(t) \tag{1b}$$

$$\frac{dD_{NAB}}{dt} = -(s_A + s_B + s_{AB} + x_A + x_B)D_{NAB}(t) + x_A D_{NB}(t) + x_B D_{NA}(t)$$
$$+ s_A[E_A(t)D_{NAB}(t) + E_{AB}(t)D_{NA}(t)] + s_B[E_B(t)D_{NAB}(t) + E_{AB}(t)D_{NB}(t)]$$
$$+ s_{AB}[E_A(t)D_{NB}(t) + E_B(t)D_{NA}(t)], \tag{1c}$$

where $E_i(t)$ is the likelihood that a lineage in state i goes extinct before the present time, described in more detail below.

Comparing Eq. 1 with Eq. 3 of Maddison et al. (2007), the description for states A and B (Eq. 1a and 1b) is quite similar to that for BiSSE's two states. A lineage remains unbranched and in state A, for example, if it does not speciate, disperse, or go extinct (first

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term in Eq. 1a); it changes state by dispersing (second term in Eq. 1a); and if speciation does occur, one daughter lineage goes extinct before the time of observation in order for the branch to appear without a node in the reconstructed tree (third term in Eq. 1a). The AB state operates differently, however. Dispersal is not an option for a species already present in both regions, so d_A and d_B do not appear in Eq. 1c. Local extinction causes a change of state out of AB (second and third terms in Eq. 1c). Speciation can occur in any of three ways (last three terms of Eq. 1c), but if it does, one of the daughter lineages must go extinct before the present.

When N is a tip, the $D_{Ni}(0)$ are the initial conditions, equal to the probability of finding state i at that tip. This value is one for the observed state i (or f_i if only a proportion f_i of tips of state i are included in the tree (FitzJohn et al. 2009)) and zero for the others.

Likelihoods from sister branches (denoted N and M) must be combined at the node of their immediate ancestor (denoted C; see Fig. A1-1) with a speciation event. The likelihood of a lineage just below the ancestral node, $D_{Ci}(t_C)$, is

$$D_{CA}(t_C) = D_{NA}(t_C)D_{MA}(t_C)s_A \tag{2a}$$

$$D_{CB}(t_C) = D_{NB}(t_C)D_{MB}(t_C)s_B \tag{2b}$$

$$D_{CAB}(t_C) = \frac{1}{2} \left[D_{NAB}(t_C)D_{MA}(t_C) + D_{NA}(t_C)D_{MAB}(t_C) \right] s_A$$

$$+ \frac{1}{2} \left[D_{NAB}(t_C)D_{MB}(t_C) + D_{NB}(t_C)D_{MAB}(t_C) \right] s_B$$

$$+ \frac{1}{2} \left[D_{NA}(t_C)D_{MB}(t_C) + D_{NB}(t_C)D_{MA}(t_C) \right] s_{AB}. \tag{2c}$$

Comparing Eq. 2 with Eq. 4 of Maddison et al. (2007), the node join for states A and B is as simple as in BiSSE because a species endemic to a single region can only produce daughters that are themselves only in that region. A parent species in AB, however, can produce three possible pairs of daughters: AB and A, AB and B, or A and B (terms one to three, respectively, of Eq. 2c).

When the ancestral node is the root of the tree ($C = R$), the conditional likelihoods $D_{Ri}(t_R)$ must be summed with an appropriate weighting to obtain the likelihood of the entire tree given the parameter values. Equal or equilibrium frequencies of the three geographic states can be used as the weights, but this is not always appropriate (Goldberg and Igić 2008). A more robust solution is to weight each state by its likelihood of giving rise to the observed data (FitzJohn et al. 2009), which we do in all analyses below.

Likelihood of extinction (E).—The probability that a lineage in state i at time t goes extinct by the present time ($t = 0$) is denoted $E_i(t)$. Changes in E_i over time are described

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by

$$\frac{dE_A}{dt} = -(s_A + d_A + x_A)E_A(t) + x_A + d_A E_{AB}(t) + s_A E_A(t)^2 \qquad (3a)$$

$$\frac{dE_B}{dt} = -(s_B + d_B + x_B)E_B(t) + x_B + d_B E_{AB}(t) + s_B E_B(t)^2 \qquad (3b)$$

$$\frac{dE_{AB}}{dt} = -(s_A + s_B + s_{AB} + x_A + x_B)E_{AB}(t) + x_A E_B(t) + x_B E_A(t)$$
$$+ s_A E_{AB}(t)E_A(t) + s_B E_{AB}(t)E_B(t) + s_{AB}E_A(t)E_B(t). \qquad (3c)$$

Eq. 3 is analogous to Eq. 7 of Maddison et al. (2007) for species endemic to regions A or B, and slightly more complicated for AB species because of the additional modes of speciation. The possible ways in which a lineage can eventually go extinct are: no events at this particular time but later extinction (first term of each of Eq. 3abc); immediate extinction (only possible for endemics, second term of Eq. 3a and 3b); a state change at this time, via dispersal for endemics (third term of Eq. 3a and 3b) or extinction for widespread species (second and third terms of Eq. 3c), followed by eventual extinction from the new state; or speciation at this time followed by eventual extinction of both daughter lineages (final terms of each of Eq. 3abc).

Extinction can only occur if some amount of time has passed, so the initial condition is $E_i(0) = 0$ when taxon sampling is complete, or $E_i(0) = 1 - f_i$ if only a proportion f_i of tips of state i are included in the tree (FitzJohn et al. 2009). As in BiSSE, the extinction probability equations (Eq. 3) can be solved numerically. Their solutions can then be used to obtain solutions to Eq. 1, which, together with the procedure for combining branch likelihoods at nodes (Eq. 2), allows the tree likelihood to be computed for a specified set of parameter values. Maximum likelihood estimates or posterior probability distributions of regional speciation, extinction, and dispersal rates can then be obtained.

SIMULATION TESTS

We used simulation tests to assess the accuracy and power of the GeoSSE model under a collection of scenarios for generating spatial structure in diversity and endemism.

Methods

We simulated trees using a continuous-time birth-death process under a variety of parameter values, summarized in Table 1. Each simulation started with a single lineage in state AB, and each scenario was tested with a batch of 500 trees. The tree sizes varied because the simulations were run for a fixed period of time rather than to a fixed number of tips, but we selected time periods such that the expected number of tips was 200. In order to consider a tree for analysis, we required a minimum of 20 tips and the existence of at least two of the three possible tip states. Acquisition bias (Lewis 2001) is therefore a possible artifact that may reduce estimation accuracy, but we did not find any obvious signs of bias in our results.

We obtained maximum likelihood parameter estimates to assess accuracy across a batch of trees. Rates were constrained to be non-negative, and the subplex algorithm was used to search the sometimes-tricky likelihood space. To test power in discerning differences between rates, we used likelihood ratio tests for which the critical log-likelihood difference was determined from simulated trees with symmetric rate parameters.

To test model selection performance, we compared scores of the Akaike information criterion (AIC), equal to twice the difference between the number of free parameters in a model and its maximum log-likelihood. The best model is the one with the lowest AIC score, but models scoring no more than two units higher still have "substantial" support (Burnham and Anderson 2002). The parameter combinations compared under this procedure were chosen to yield similar equilibrium distributions of tip states when possible, so as to give a fair and conservative test of the model's ability to distinguish between alternative explanations for the same pattern.

To assess precision and power for individual trees, we additionally carried out a Bayesian analysis on 100 trees chosen randomly from batch 8. Each tree was subjected to 5000 post-burn-in iterations of Markov chain Monte Carlo under broad priors (slice sampling algorithm, exponential priors with rate 0.5). We formed credible intervals for the differences between relevant parameter pairs by computing quantiles of the MCMC samples.

Finally, to assess correlations between model parameters, we performed similar MCMC analyses on trees from batches 5–9. Ten trees of approximately 200 tips were taken from each batch. A cross-correlation matrix was computed for the posterior samples from each tree.

Code for simulating trees under the GeoSSE model is available in the C program *SimTreeSDD*, available as Supplementary Material and from *http://tigger.uic.edu/~eeg/code/code.html*. Code for estimating parameters is available in the R package *diversitree* (FitzJohn 2010a), available as Supplementary Material and from *http://cran.r-project.org/web/packages/diversitree/*, which was also used for the maximum likelihood and Bayesian analyses. Analysis scripts are in the Dryad database at *doi:10.5061/dryad.8343*.

<center>Scenario-specific results</center>

Regional differences in a single process.—We first apply our model to test the separate contributions of speciation, extinction, and dispersal to diversity differences between regions. Under the center of origin hypothesis (Croizat et al. 1974), a region with high diversity has a high speciation rate. Wallace (1878) argued that low diversity in some areas is due primarily to extinctions there driven by climate fluctuations. The center of accumulation hypothesis (Mora et al. 2003) suggests that high diversity in a region comes through immigration.

We used likelihood ratio tests to assess the power of the GeoSSE model to recover each of these three scenarios (fixing s_{AB} to 0). Using trees simulated with symmetric parameter values (batch 1; see Table 1), we fit a six-parameter model and three constrained five-parameter models ($s_A = s_B$, $x_A = x_B$, or $d_A = d_B$) to obtain the log-likelihood differences below which 95% of the trees fell. These critical values were 2.07 for the equal-speciation model, 1.80 for the equal-extinction model, and 1.78 for the equal-dispersal model. Then

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we performed likelihood ratio tests, using those critical values, on trees simulated with asymmetric rates. We found that 95% of the trees correctly rejected equal speciation rates (batch 2), 26% correctly rejected equal extinction rates (batch 3), and 29% correctly rejected equal dispersal rates (batch 4).

For each of batches 1–4, we fit the four models corresponding to those scenarios (i.e., one three-parameter model and three four-parameter models). With the three processes symmetric (batch 1), the correct model had the lowest AIC score on 71% of the trees, but it was never substantially preferred (i.e., in no case did all the other models score more than two AIC units worse). Under the three asymmetric scenarios, the correct model was substantially preferred on 95% of trees under asymmetric speciation (batch 2), 45% of trees under asymmetric extinction (batch 3), and 46% of trees under asymmetric dispersal (batch 4). When the full six-parameter model was added to the set of those considered, it frequently scored well, lowering the selection of the correct model to 35% and 33% of trees for batches 3 and 4, respectively, and always scoring comparably to or better than the correct model for batch 2. These results are consistent with the known tendency of AIC to favor parameter-rich models (Kass and Raftery 1995), and we therefore prefer to conduct our subsequent inference by comparing parameter estimates rather than by selecting models.

Figure 2 shows the effects of tree size and correlations between corresponding parameters in batches 1–4. The median rate estimates under the six-parameter model across each batch of 500 trees were close to the values used in the simulations. The handful of outlier points were mostly small trees. Asymmetry in speciation rate could be identified more reliably across trees than could asymmetry in dispersal or extinction, though the parameter clouds for even those quantities show moderate separation (keep in mind the high density of points near the true values).

Geographic mode of speciation.—The GeoSSE model allows us to ask whether speciation occurs mainly within regions (s_A and/or s_B dominate) or if it involves reproductive isolation across the border between the regions (s_{AB} dominates). We consider three scenarios relating to the geographic mode of speciation: both within- and between-region speciation (batch 5), within-region only ($s_{AB} = 0$, batch 6), and between-region only ($s_A = s_B = 0$, batch 7). Parameter values are given in Table 1 and histograms of maximum likelihood estimates of the three speciation rates are shown in Figure 3.

When speciation happens only within regions, s_{AB} is usually correctly estimated to be near zero, and different values for s_A and s_B can easily be distinguished (Fig. 3b). When speciation is only between regions, s_A and s_B are correctly estimated near zero and the positive value of s_{AB} is correctly found (Fig. 3c). When speciation occurs both within and between regions, the three speciation rates can on average be recovered, but their distributions across trees are broader and overlapping (Fig. 3a). When between-region speciation occurs but is ignored, estimates of s_A and s_B are correctly ordered and distinguished but are biased substantially upward (by more than 40% with the batch 5 parameter values; results not shown).

In likelihood ratio tests, using critical values determined from batches 6 and 7 (1.21 and 1.29, respectively), we found that 85% of trees in batch 5 correctly rejected $s_{AB} = 0$ and

100% correctly rejected $s_A = s_B = 0$.

Macroevolutionary sinks.—Dispersal or range expansion of species can play an important role in determining regional diversity (Roy and Goldberg 2007). This is particularly evident in "macroevolutionary sinks," regions in which the speciation rate is low and richness is maintained by immigration. We consider two such scenarios. In the source-sink case (batch 8, Table 1), all species in the system arise in one region (the source), but they may expand their ranges, so diversity in the other region (the sink) increases through immigration. For simplicity, dispersal from the sink to the source does not occur, and extinction occurs at the same rate in both regions. In the sink-sink scenario (batch 9, Table 1), both regions have speciation rates lower then their extinction rates, so without dispersal, diversity would fall to zero in each area. Because extinction in each region is an independent event, however, sufficiently frequent dispersal can maintain positive diversity in the system, allowing each region to serve as a refuge for the other.

Despite the difficulties in estimating extinction and dispersal rates, the GeoSSE model is able to recover both source-sink and sink-sink dynamics (Fig. 4). Net diversification is nearly always estimated as positive in the source (Fig. 4a) and negative in the sinks (Fig. 4bcd). Dispersal rate estimates show more variation, but immigration is clearly recovered as greater than diversification in the sinks and less in the source.

To better reflect how real-world analysis of a single dataset would proceed, results from the posterior probability distributions of 100 trees from the source-sink scenario (batch 8) are shown separately (Fig. 5). Precision increases markedly with tree size and is lowest for dispersal. Accuracy is generally good for extinction and within-region speciation rates, and it improves with tree size for dispersal and between-region speciation rates. There is a slight bias toward underestimating the speciation difference between the regions (Fig. 5a; likely because s_B and s_{AB} can be given values greater than but not less than their true values of zero), which causes underestimation of the dispersal difference (Fig. 5d).

Of the 100 trees, 98% confidently show a difference in the source and sink speciation rates (i.e., a difference of zero falls outside the 90% credibility interval); this increases to 100% when considering only the 57 trees with more than 200 tips (Fig. 5a). 93% of trees (89% of trees with more than 200 tips) show a speciation rate difference that is consistent with the value used in the simulations (Fig. 5a). All trees correctly find no extinction rate difference between the two regions, and this is not due solely to large credibility intervals, at least on the large trees (Fig. 5c). The between-region speciation rate was zero in the simulations and was estimated to be very small on the large trees (Fig. 5b). On the smallest trees, however, some of the diversity in the sink region was incorrectly attributed to between-region speciation (Fig. 5b; also to speciation within the sink to a lesser extent, results not shown) rather than to immigration. 74% of trees (96% of trees with more than 200 tips) confidently show a difference between the dispersal rates, and 79% of trees (75% of trees with more than 200 tips) find a dispersal difference consistent with the value used in the simulations (Fig. 5d).

General conclusions

Parameter correlations.—We found that the posterior distribution in multi-dimensional parameter space is considerably more constrained than is represented by the marginal parameter distributions. Some parameter correlations persisted across much of parameter space and all individual trees, while others were more localized or intermittent. All scenarios except the source-sink (batch 8) showed consistent correlation between net diversification rate within a region and immigration into that region ($s_A - x_A$ and d_B; $s_B - x_B$ and d_A). This was generally driven by higher correlations between extinction and dispersal than between speciation and dispersal. Correlation between d_B and x_A was slightly weaker in the source-sink scenario, likely because dispersal into the source is low. Correlation between speciation and extinction within a region was common only when speciation was relatively high (region A of batches 5, 6, and 8). There was little correlation between the two (or three) speciation rates or between the two extinction rates (see also Fig. 2). Correlation between the two dispersal rates was common only in batch 5. The overall strength of correlations was greatest in the sink-sink scenario (batch 9).

Analysis recommendations.— Due to the complex likelihood surfaces that arise under GeoSSE (as revealed by parameter correlation study and trial usage of a variety of optimization algorithms), working with more than point estimates of parameters is important. The MCMC-based approach we illustrate in the source-sink scenario above and the empirical application below provided a relatively straightforward basis for examining parameter uncertainties and correlations, and for hypothesis testing without the complications of model selection procedures.

Such investigations will be an important part of any empirical analysis, although some patterns are likely to emerge in all applications. Based on our simulation tests, the signature of speciation, particularly the within-region mode, appears to be written most clearly on a phylogeny, followed by those of extinction and dispersal. The strongest parameter correlations are typically between extinction and immigration, and accounting for those can allow more powerful inference than can the marginal parameter distributions alone.

APPLICATION TO CALIFORNIA CHAPARRAL

We applied GeoSSE to the problem of diversification and historical habitat shifts in the California flora. The California Floristic Province (CA-FP) is one of five Mediterranean biodiversity hotspots on the planet, all of which are characterized by a diversity of habitat types that turn over rapidly at short spatial scales, thus supporting multiple niches for diversification and species persistence (de Castri and Mooney 1973). Mediterranean regions are also all characterized by unique sclerophyllous shrubland communities, which are rare or absent outside of these temperate hotspots (Verdú et al. 2003). One or both of these features of Mediterranean biomes may critically affect the currently high diversity in those regions.

Two California-native shrub genera, *Arctostaphylos* Adans. (manzanita, Family: Ericaceae) and *Ceanothus* L. (California lilac, Family: Rhamnaceae), are key indicator species of the chaparral, California's version of unique Mediterranean shrubland (24% of *Arctostaphylos*

spp. and 30% of *Ceanothus* spp. are chaparral-endemics). However, both genera also contain forest/woodland-restricted species (7% and 29%, respectively), and generalist species inhabiting both chaparral and wooded habitats (69% and 41%, respectively), making these genera excellent candidates for examining how a unique habitat (chaparral) and shifts in habitat occupancy have interacted to produce extant diversity and distributions in California.

Because of the ubiquity of sclerophyllous shrublands in Mediterranean biodiversity hot-spots, we predicted that the chaparral habitat may promote speciation, leading to a higher speciation rate in the chaparral than in forested regions ($s_C > s_F$). Consequently, we expected to see greater habitat expansion out of chaparral than into it ($d_C > d_F$). We also investigated historical expansion and contraction of habitat tolerance in these genera. Like other Mediterranean hotspots, California features many, highly interdigitated plant communities. Therefore, species have ample opportunity to enter and adapt to alternative habitats. Because of this, we predicted that expansion in habitat tolerance would be more common than habitat specialization (i.e., net range expansion is positive; $d_C - x_F > 0$ and $d_F - x_C > 0$).

We further expected the interdigitated nature of California's habitats to preclude between-region speciation: barriers to gene flow that separate all habitat patches by type are uncommon, so it is unlikely that a generalist species would produce one chaparral-specialist daughter and one forest-specialist daughter ($s_{CF} = 0$). This would mean that habitat specialization is more likely to occur via extirpation (anagenic specialization) or local speciation (cladogenic specialization) than via allopatric divergence. We therefore asked which of anagenic of cladogenic specialization has been more important (comparing x_F with s_C and x_C with s_F).

Methods

We generated time-calibrated phylogenies for each of *Arctostaphylos* and *Ceanothus* using sequences for internal transcribed spacer regions of 18s-26s rDNA retrieved from GenBank (*http://www.ncbi.nlm.nih.gov*) and fossil calibration dates retrieved from the Paleobiology Database (*http://paleodb.org*). Phylogenies were constructed with the Bayesian MCMC method implemented in BEAST (Drummond and Rambaut 2007), using a lognormally distributed relaxed molecular clock model (Drummond et al. 2006) and a birth-death prior. Habitat states for extant species were obtained from the Jepson Manual (Hickman 1993), the CalFlora database (*http://www.calflora.org*), and other sources (Fig. 6). We fit the GeoSSE model to *Arctostaphylos* and *Ceanothus* jointly by approximating the genera as independent; joint fitting increased power without qualitatively changing the results from estimates derived from each genus separately. Model parameters were estimated via MCMC over 1000 trees per genus, and results are reported as the proportion of samples from the posterior distribution for which a statement is true. Models with and without the between-habitat speciation parameter (s_{CF}) were compared with the Bayes factor (Kass and Raftery 1995). Full methods are provided in online Appendix 2, and data files and analysis scripts are available in the Dryad database at *doi:10.5061/dryad.8343*.

Results

We found "positive" evidence in favor of the 6-parameter over the 7-parameter model ($2 \ln[BF_{67}] = 3.0$; Kass and Raftery 1995). Based on this moderate statistical support and the spatial structure of the system, we present results only for the model that excludes (sets to zero) s_{CF}. Parameter estimates are reported in Table 2, and their posterior distributions are shown in Fig. 7a–c.

We inferred a higher rate of speciation in chaparral than in forested regions in California ($s_C - s_F = 0.11 \pm 0.003$, positive with posterior probability 0.82; Fig. 7a,d). Comparing directions of range expansion and contraction, we find indications of more rapid dispersal out of chaparral than into it ($d_C - d_F = 0.420 \pm 0.019$, positive with posterior probability 0.72; Fig. 7c) and of more frequent reduction to chaparral habitat than to forest ($x_F - x_C = 0.187 \pm 0.0051$, positive with posterior probability 0.76; Fig. 7b,d).

We also found that expansion in habitat tolerance has been more common than habitat specialization in the history of these genera (Fig. 7e). Net range expansion (i.e., expansion exceeds contraction) out of chaparral-covered regions and into forested habitat was strongly supported ($d_C - x_F = 0.812 \pm 0.017$, positive with posterior probability 0.97). Support for net range expansion in the opposite direction was milder ($d_F - x_C = 0.579 \pm 0.015$, positive with posterior probability 0.75).

Finally, we find that the production of range-limited species (i.e., species inhabiting chaparral or forest but not both) has occurred predominantly via anagenesis, rather than via cladogenesis, in these genera (Fig. 7f). (For specialization on or range limitation to chaparral-covered regions, $x_F - s_C = 0.287 \pm 0.0086$ and was positive with posterior probability 0.90. For forested regions, $x_C - s_F = 0.214 \pm 0.0054$ and was positive with posterior probability 0.96.)

Correlations between parameters are reported in Table 2. As in the simulation tests, the strongest correlations were between the extinction/extirpation and range expansion parameters. Next strongest, for these data, were the correlations between speciation in and range expansion out of each habitat; this is likely driven by the tie between extinction and dispersal. The combination of these two factors leads to very strong negative correlations between net diversification within a region and immigration into that region. Correlations between speciation and extinction in the same habitat type were relatively low.

Imprecision in the parameter estimates, as displayed in Fig. 7, reflects contributions from both phylogenetic uncertainty (in topology and branch lengths, as captured by the posterior set of trees) and uncertainty from the parameter estimation process on each tree. Using coefficients of variation for each parameter to compare average within-tree variability, tree-to-tree variation in median estimates, and overall variability, we find that phylogenetic uncertainty contributes approximately 50% of the variation seen in each speciation rate, 40% for each extinction rate, and 35% for each dispersal rate. More precise phylogenetic inference would hence provide moderate improvement in our results, particularly for speciation, the process to which the model is most sensitive.

Interpretation

Our results indicate that chaparral is a key site of speciation in California, at least for the two shrub genera under consideration here. Future examination of additional groups in more regions will test whether sclerophyllous shrublands consistently foster speciation across all five Mediterranean biodiversity hotspots. We also found evidence that habitat tolerance is more likely to expand than to contract in these California genera. The spatially fine-grained, and hence readily accessible patches of alternative habitat types in California and other Mediterranean regions may promote habitat generalization and may therefore support species richness if habitat-generalist lineages have lower extinction probability than specialists (as assumed by GeoSSE). We further found that the net direction of range expansion was in the direction of forested habitats; similarly, other forest lineages in California and other Mediterranean regions may have shrubland origins. As predicted, we found no evidence of vicariant speciation between forest and chaparral habitat types, likely because barriers to gene flow between these habitat types are rare. However, we did estimate moderate rates of anagenic habitat specialization, perhaps due to trade-offs between adaptation to drier, fire-prone shrublands, and moister, shaded forest habitats.

Habitat preference is often thought of as a labile trait, with transitions potentially occurring on ecological rather than macroevolutionary timescales, and this could limit GeoSSE's power (see below). However, recent evidence indicates that plant community membership is in fact quite conserved, with $> 96\%$ of sister species in one study occupying the same plant community type as their most recent shared ancestor (Crisp et al. 2009). This indicates that adaptation to a new plant community is a significant and relatively rare event in a plant lineage, and one that is therefore tractable at macroevolutionary timescales.

Directly comparing the success of generalist and specialist species is not possible with GeoSSE since the same rates apply to each (though in different combinations). Possible re-parameterizations to address this are discussed below, but a different approach is to apply the existing model to additional clades spanning various combinations of habitat types. Resulting associations between habitat breadth and speciation or extinction rates may reveal the extent to which habitat generalization enhances speciation rates or reduces global extinction probability.

Discussion

Biogeographic Significance

The GeoSSE model advances existing biogeographic inference methods by integrating processes that have previously been treated separately (Lamm and Redelings 2009; Ree and Sanmartín 2009). Range and habitat evolution have been inferred on phylogenies using models for discrete characters that do not include parameters for the tempo, mode, or regional dependence of lineage diversification (e.g., Nepokroeff et al. 2003; Fine et al. 2005; Sanmartín et al. 2008; Weir et al. 2009; Bastida et al. 2010; Pirie et al. 2010). The dispersal-extinction-cladogenesis (DEC) model of range evolution considers mode, but not tempo or

regional dependence (Ree et al. 2005; Ree and Smith 2008). Such models have been used to test for lineage movement as a key innovation (e.g., Moore and Donoghue 2007, 2009), but since separate analyses are required to first reconstruct ancestral states and then estimate their effect on diversification, this approach may sacrifice power or be subject to confounding model interactions (Maddison 2006).

Studies of regional effects on diversification, largely in the context of latitudinal diversity gradients or centers of origin, typically employ sister-group or -species comparisons or regressions on lineage or clade size or age (Gaston and Blackburn 1996; Cardillo et al. 2005; Ricklefs 2006; Weir and Schluter 2007; Wiens 2007). However, these do not consider the effect of change in species' ranges through time (Roy and Goldberg 2007). Methods for distinguishing the geographic mode of speciation are similarly hampered by post-speciational range shifts (Chesser and Zink 1994; Losos and Glor 2003; Fitzpatrick and Turelli 2006).

Application of BiSSE (Maddison et al. 2007) to a geographic character (Valente et al. 2009; Rabosky and Glor 2010) does allow consideration of both diversification differences and range changes. Geographic mode of speciation is not considered, though, so it does not cleanly extract the signal of region-specific effects from widespread species. The different parameterizations of BiSSE and GeoSSE may, however, be combined to give complementary perspectives on the dynamics of a system (cf. Anacker et al. in press).

Model Limitations and Extensions

As mathematical models of character evolution on a phylogeny become more elaborate, an obvious question is, how much data is necessary for confident inferences? The answer certainly depends on the model, the details of the data, and the strength of the signal being sought, but our simulation and empirical results indicate that roughly one or two hundred tip species may be sufficient for GeoSSE to uncover significant differences between parameters. The continuing rapid increase in availability of large phylogenies makes this a reasonable demand, and we have also illustrated how separate, smaller trees can be combined into a single analysis (subject to assumptions or justifications of independence; e.g., Anacker et al. in press).

A potential liability of requiring a moderately large set of species is the assumption that rates of diversification and trait evolution are constant across the phylogeny, which may become more tenuous with broader and deeper clades. Allowing rates to vary across time and between clades is certainly possible, and it could be useful to represent, for example, the effects of an unmodeled trait that appears in one or a few instances, or changes in spatial connectivity such as appearance of a dispersal corridor or a vicariance event. This technique must be applied judiciously (e.g., Alfaro et al. 2009; Weir et al. 2009; FitzJohn 2010b), however, to prevent an explosion in the number of parameters to be estimated. Diversification that depends on species richness presents a different form of time-dependent rates. Phylogenetic models in which speciation and extinction are affected by species interactions will be considerably more complicated to develop, but they may be necessary to distinguish truly density-dependent diversification from the more general pattern of slowdowns in diversification (Pybus and Harvey 2000; Rabosky and Lovette 2008). Including a biogeographic

context is especially relevant here (Rabosky 2009) since species interactions depend on their spatial distributions. Successfully tying rate heterogeneity to particular conditions, events, or trait changes will greatly improve the extent to which relatively simple models fit real data, and it will enhance our understanding of the forces shaping diversification and trait macroevolution.

As with related macroevolutionary models of character evolution, GeoSSE's utility will be limited when state changes are very rapid or very slow relative to diversification and/or the age of the clade being studied. This will affect the spatial scale of regions that can be effectively treated, since, for example, range changes between continents occur on a different temporal scale than those within local landscapes. A small set of simulations (not shown) indicated that when extinction and especially dispersal rates are very high relative to speciation and elapsed time, speciation rates are still accurately estimated and dispersal rates are correctly found to be much larger, but pronounced correlations can cause dispersal-driven diversity differences to be mis-attributed to extinction. Further tests of this limitation will require separating the rates of range contraction or extirpation from those of global extinction (see below). It may well be that rates of range expansion and contraction can be correctly inferred as large relative to speciation and extinction, but that ancestral ranges (see below) cannot then be reconstructed with any confidence.

One difficulty with this model's structure is the inevitable correlations between some parameters. We cannot reduce parameter number by combining processes because each has its own unique behavior. Incomplete independence of the parameters is, however, evidenced by pervasive correlations, especially between dispersal and extinction. This is intuitively expected because immigration and extirpation "undo" each other in their effects on species richness. It is perhaps surprising that correlations between speciation and extinction are less strong, but we attribute this to speciation effects being directly written on tree shape while dispersal effects are not. Strong correlations do not necessarily prevent useful inference, however, and understanding their structure will improve the precision of conclusions.

All else being equal, GeoSSE may have greater statistical power than BiSSE because it has the same number of rate parameters but a larger number of character states. Further work is needed to determine whether additional states generally improve power in the BiSSE family of models, or if the benefits of increased resolution may be offset by the reduction in number of tips in each state and the greater number of parameters generally required to describe transitions between the states. When feasible, however, multi-state characters may allow finer-grained questions to be addressed.

GeoSSE requires only six rate parameters with its three states by making constraining assumptions about several processes, e.g., rates of local and global extinction are equal within each region, and endemics and wide-ranging species share common regional rates of speciation. This strategy can be retained to maintain a reasonable number of parameters when extending the model to allow more than two regions (online Appendix 3). Constraints of this nature may not always be desired, however. For example, further study of diversification and range shifts in California chaparral communities would benefit from separating the parameters describing local extirpation and global extinction. This would enable tests of

habitat shift directionality that are not directly affected by lineage extinction and facilitate comparisons between habitat specialists and generalists. In other systems, hypotheses of interest might involve state transitions not allowed by GeoSSE, e.g., A changing directly to B, an ancestral AB species yielding two AB daughters at a speciation event, or global extinction of AB species.

A general framework would allow an arbitrary number of states, all possible transitions between them along phylogenetic branches, and all possible modes of state segregation at cladogenesis events. This general model could then be constrained as needed, by disallowing certain events and assuming that some processes share parameters. For example, such constraints might set northward dispersal to be constant across regions, speciation rates to vary linearly with latitude, or extinction rates to scale with region size. Such a framework would allow flexible handling of a variety of discrete characters and provide a natural means for testing hypotheses about anagenetic versus cladogenetic change. It could also facilitate tests of the errors incurred by fitting models with parameterizations that misrepresent the true processes acting in a system.

Analysis of non-geographic characters could also benefit from models that link state change to speciation and extinction. For example, the breakdown of self-incompatibility can accelerate speciation because self-fertilization will rapidly isolate a new lineage from its parent stock (Foxe et al. 2009); this mating system trait can also affect extinction and net diversification rates (Goldberg et al. 2010). Polyploidization can cause immediate speciation (Ramsey and Schemske 1998), and this process could be built into a model of chromosome number evolution (Mayrose et al. 2010).

These examples recall punctuated character evolution, in the sense that speciation events can be a direct and immediate outcome of anagenetic transitions. A biogeographic process that might be modeled in this way is long-distance or "jump" dispersal, in which rare migration events establish new populations that are effectively isolated by geographic barriers from the rest of the species. In GeoSSE, this phenomenon translates to a high value of s_{AB}, the allopatric speciation parameter, which accelerates divergence following dispersal. However, one might imagine the need for a model in which state transitions and speciation events are exactly coincident in time. In general, tests of punctuated change are preferably performed using methods that explicitly model the process of character change (e.g., Bokma 2008), rather than indirect strategies such as setting all branches of the phylogeny to equal length (Pagel 1994, 1999a).

In addition to rate estimation, reconstruction of ancestral states is an appealing class of inference due to its nominally more concrete view of changes in character states. Implementation with GeoSSE would require an extension of existing approaches (Schluter et al. 1997; Pagel 1999b; Bollback 2006) to allow for state changes during speciation. This could be approached by considering triplets of parent and daughter states at each node. It may well be that ancestral states can be more confidently reconstructed under BiSSE and GeoSSE when diversification is strongly state-dependent. Testing is required, however, to determine accuracy and power.

Beyond the more general parameterization of GeoSSE described above, a useful extension

would be to multiple, correlated characters. This would allow tests of, for example, ties between life history or morphology and geographic distribution. Another, perhaps more technically difficult possibility is to treat range as a continuous character and work with more spatially explicit functions of speciation and extinction rates; this could begin with the framework of FitzJohn (2010b).

Evidence for macroevolutionary and biogeographic dynamics may come from a variety of sources, employing data and methods spanning population biology, comparative analyses, and the fossil record. Further modeling of the reciprocal effects of speciation and character change on phylogenetic trees may enable a new, complementary suite of tests for questions typically addressed on other spatial or temporal scales.

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batch	s_A	s_B	s_{AB}	x_A	x_B	d_A	d_B	T	scenario	results
1	2.0	2.0	0.	1.9	1.9	2.0	2.0	4.2	symmetric parameters	Fig. 2abc
2	0.5	2.0	0.	1.9	1.9	2.0	2.0	9.2	asymmetric speciation	Fig. 2a
3	2.0	2.0	0.	1.9	0.4	2.0	2.0	2.5	asymmetric extinction	Fig. 2b
4	2.0	2.0	0.	1.9	1.9	2.0	0.8	5.4	asymmetric dispersal	Fig. 2c
5	1.5	0.5	1.0	0.7	0.7	1.5	1.5	4.1	both speciation modes	Fig. 3a
6	1.5	0.5	0.	0.7	0.7	1.5	1.5	4.7	within-region speciation	Fig. 3b
7	0.	0.	1.0	0.1	0.1	1.5	1.5	12.0	between-region speciation	Fig. 3c
8	1.5	0.	0.	0.5	0.5	2.0	0.	5.1	source-sink system	Fig. 4ab, 5
9	0.5	0.5	0.2	1.0	1.0	3.0	4.0	11.3	sink-sink system	Fig. 4cd

Table 1: Parameter values used in the simulation tests. s_A is speciation within region A, s_B is speciation within region B, s_{AB} is between-region speciation, x_A is extinction in region A, x_B is extinction in region B, d_A is dispersal from A to B, d_B is dispersal from B to A, and T is elapsed time. In all cases, the expected number of tips per tree is approximately 200.

parameter	mean ± s.e.	correlations					
		s_C	s_F	x_C	x_F	d_C	d_F
s_C	0.194 ± 0.0032	—					
s_F	0.080 ± 0.0020	-0.436	—				
x_C	0.294 ± 0.0067	0.322	0.503	—			
x_F	0.481 ± 0.011	0.485	0.195	0.280	—		
d_C	1.293 ± 0.028	0.515	-0.025	0.175	0.887	—	
d_F	0.873 ± 0.021	-0.106	0.653	0.837	0.101	-0.018	—

Table 2: For the California plants, mean parameter estimates, their standard errors, and their correlations. C denotes chaparral habitat and F denotes forest habitat. Stronger correlations (approximately -0.9) were found between $s_C - x_C$ and d_F, and between $s_F - x_F$ and d_C.
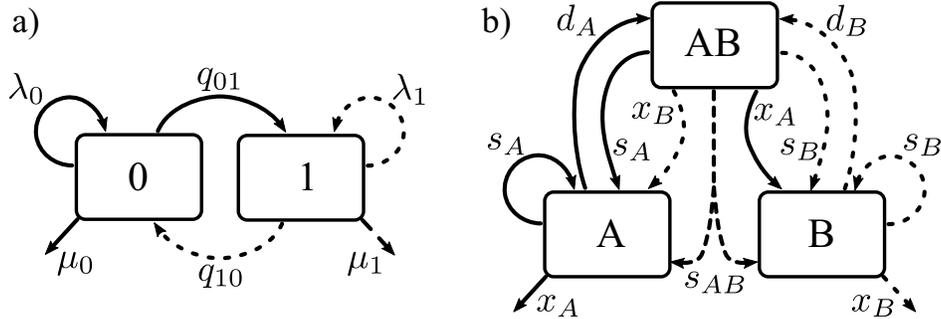
Figure 1: The states and allowed transitions in (a) BiSSE and (b) GeoSSE. Both models have six rate parameters and allow state-dependent speciation (λ or s) and extinction (μ or x), and anagenetic state changes (q, d, x). GeoSSE additionally allows state changes during speciation in association with the third (AB) character state.
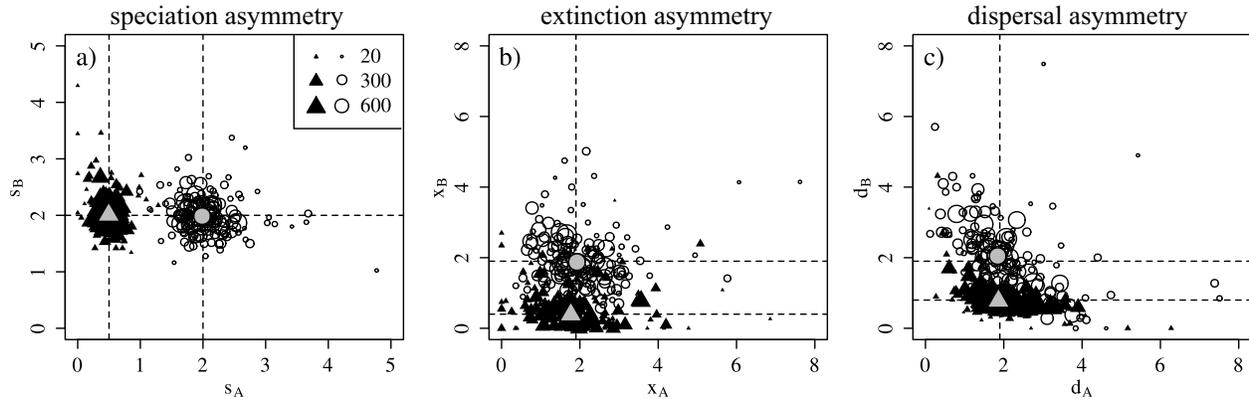

Figure 2: Maximum likelihood parameter estimates under asymmetries in each of (a) speciation, (b) extinction, and (c) dispersal. Of the 500 trees per batch, a representative 150 are shown. The symmetric parameter values (batch 1 in Table 1) are shown by open circles, and the asymmetric parameter values (batches 2–4 for panels (a)–(c), respectively) are shown by filled triangles. Large gray symbols show the median parameter estimates for all trees in each batch, and dashed lines show the values used in the simulations. Symbol sizes indicate the number of tips per tree, with the scale shown in the panel (a) legend.
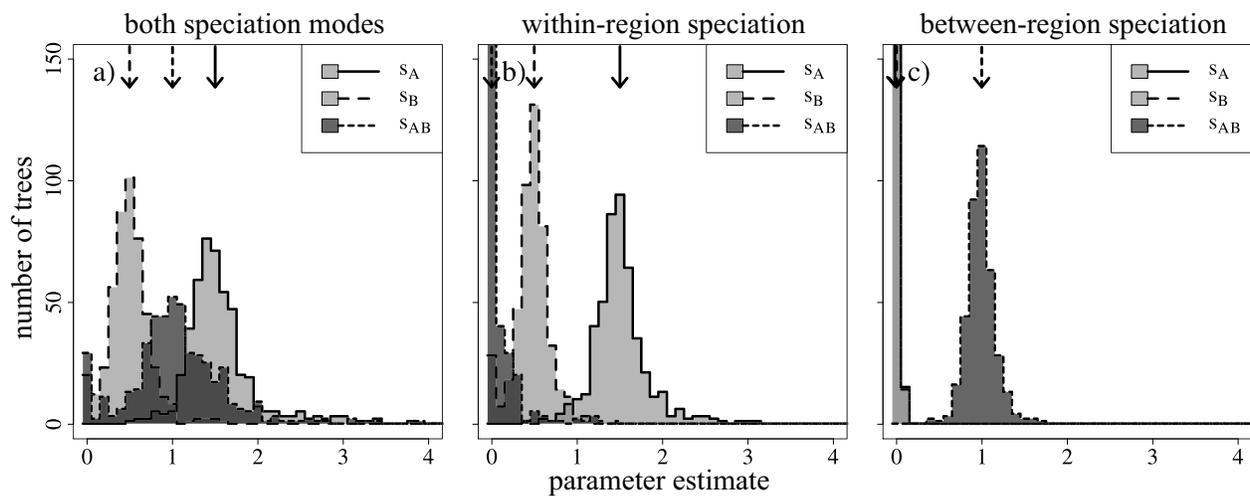
Figure 3: Histograms of maximum likelihood parameter estimates, with emphasis on geographic mode of speciation. Panels (a)–(c) are for batches 5–7, respectively (Table 1). Arrows indicate the parameter values used in the simulations. In panel (c), the results for s_A and s_B are nearly identical thus overwrite each other.
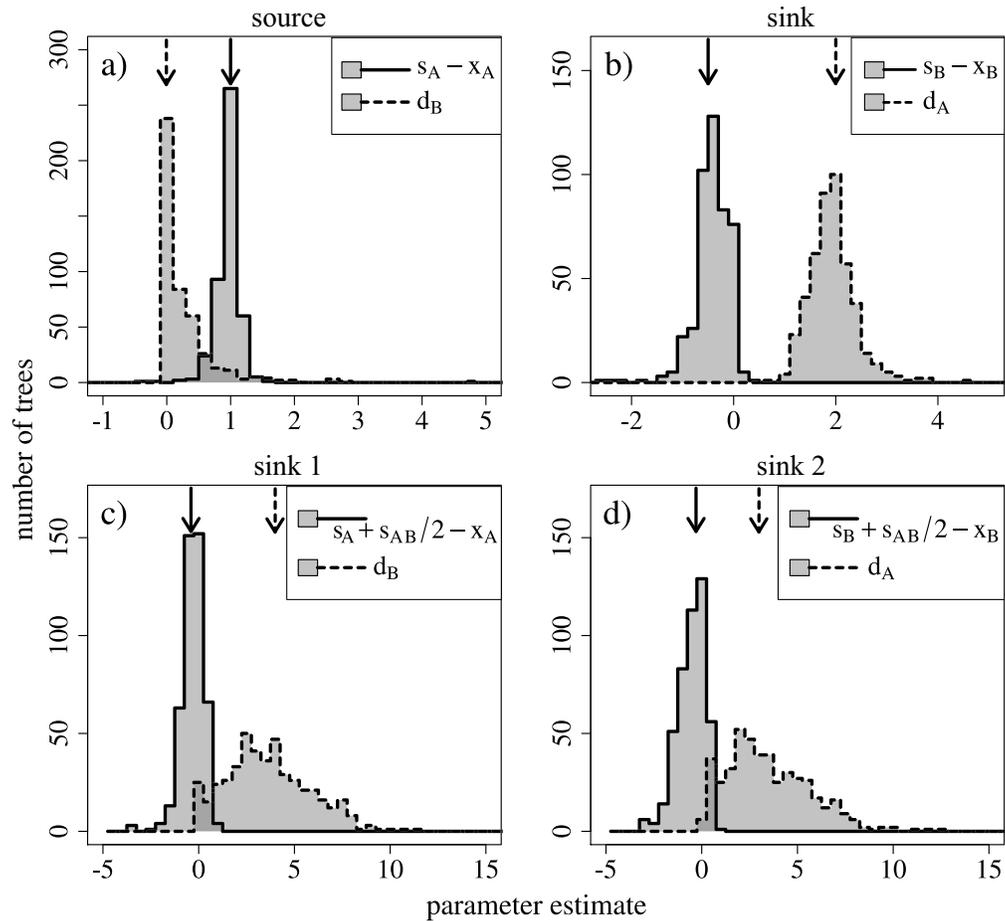
Figure 4: Histograms of maximum likelihood parameter estimates, with emphasis on dispersal maintaining diversity. Panels (a) and (b) are for the source and sink regions in batch 8, and panels (c) and (d) are for the two sink regions in batch 9. Net diversification rates of and immigration rates into each region are shown. Arrows indicate the parameter values used in the simulations.
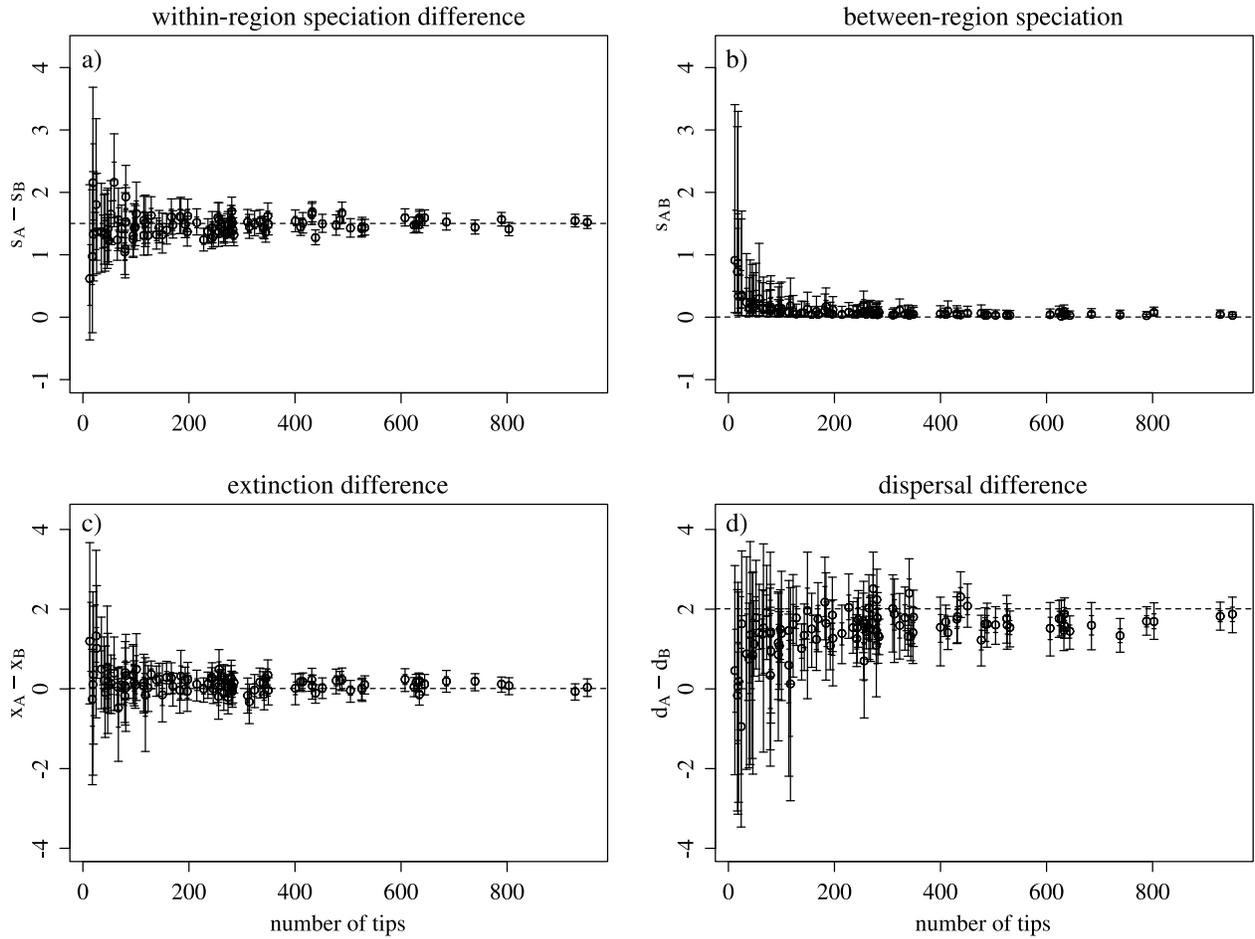
Figure 5: Credible intervals for diversity differences driven by source-sink dynamics (batch 8). Each point shows results for a single tree, ordered on the horizontal axis by tree size. Open circles show the median value of the quantity written on the vertical axis, and inner and outer whiskers mark the 50% and 90% credible intervals, respectively. Horizontal dashed lines indicate the values used in the simulations.
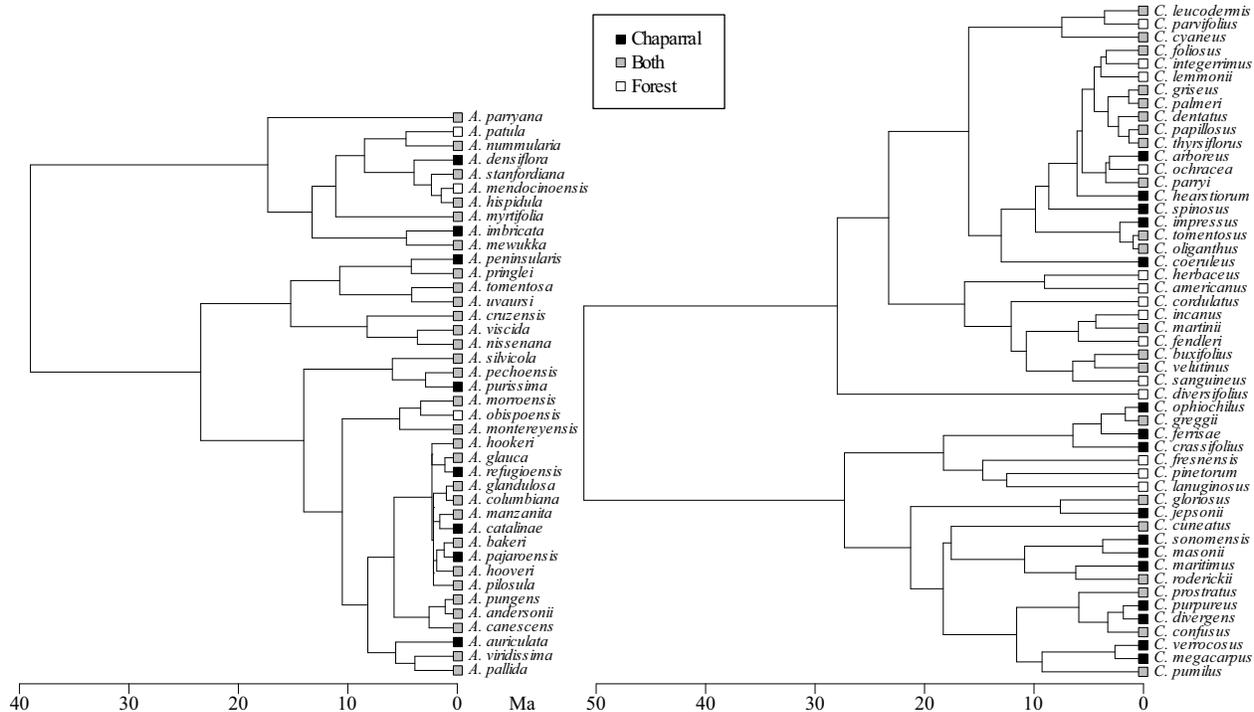
Figure 6: Summary phylogenies with tip states for *Arctostaphylos* and *Ceanothus*. These are the maximum clade credibility trees with mean node heights; the full posterior set of trees was used in the analysis.
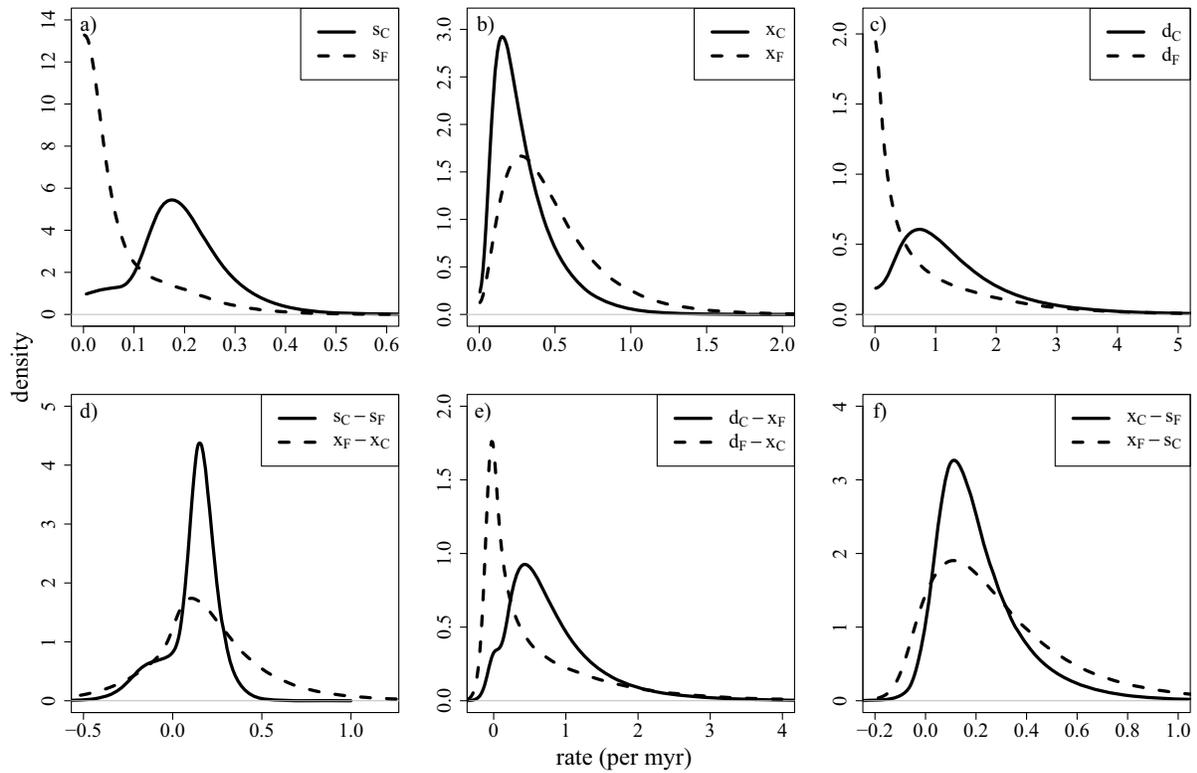
Figure 7: Posterior probability distributions of GeoSSE parameters for California plants. Rates of (a) speciation, (b) extinction, and (c) dispersal were estimated for chaparral (solid lines) and forest (dashed lines) habitats. Differences in (d) speciation and extinction rates between habitats, (e) range contraction versus expansion, and (f) mechanism of specialization were computed from the six estimated parameters.

The final form of the GeoSSE model is given in the main text. Here we provide a more detailed derivation of Eq. 1–3. We use the notation of Maddison et al. (2007) as much as possible, and similarly take time to be 0 at the tips and increasing towards the root. Much of the notation used is summarized in Fig. A1-1.

Likelihood of tree and character states (D)

The quantity $D_{Ni}(t)$ is the conditional likelihood that a lineage beginning at time t in state i (i = A, B, or AB) evolves into a clade with identical branching structure and character states as the (sub)tree actually observed to descend from N, given a set of rate parameters.

If $D_{Ni}(t)$ is assumed to be known, the probability a very short time before, $D_{Ni}(t + \Delta t)$, can be calculated from the assumptions of the model. Following Maddison et al. (2007), we show these calculations first in the case where the time interval Δt does not encompass a node, and then in the case where it does. We assume that the time interval is very short, so that only one event can occur in it, and then we shrink Δt to an infinitesimal interval to derive differential equations. These derivations include the functions $E_i(t)$, which are the likelihoods that a lineage in state i at time t goes extinct by time 0. These extinction probabilities are derived in a subsequent section.

Calculations within a branch.—First, we consider moving a time step down a branch of the tree, landing in state A to obtain $D_{NA}(t + \Delta t)$. Because at most one event can occur in this interval, there are three possible paths: the lineage may remain in state A throughout Δt, the lineage may transition from state A to state AB by dispersal in Δt, or the lineage may speciate in Δt with one of the daughter lineages (which are both in state A) eventually going extinct by the present time.

$$
\begin{aligned}
D_{NA}(t + \Delta t) = {}&(1 - s_A\Delta t)(1 - d_A\Delta t)(1 - x_A\Delta t)D_{NA}(t) &&\text{no events} \\
&+ (d_A\Delta t)D_{NAB}(t) &&\text{dispersal} \\
&+ 2(s_A\Delta t)E_A(t)D_{NA}(t) &&\text{speciation, eventual extinction} \\
& &&\text{of either daughter}
\end{aligned}
$$

Discarding terms of order Δt^2 and higher yields

$$D_{NA}(t+\Delta t) = [1-(s_A+d_A+x_A)\Delta t]D_{NA}(t)+(d_A\Delta t)D_{NAB}(t)+2(s_A\Delta t)E_A(t)D_{NA}(t). \quad \text{(A1-1)}$$

The analogous equation for state B endemics is

$$D_{NB}(t + \Delta t) = [1 - (s_B + d_B + x_B)\Delta t]D_{NB}(t) + (d_B\Delta t)D_{NAB}(t) + 2(s_B\Delta t)E_B(t)D_{NB}(t). \quad \text{(A1-2)}$$

The likelihood for state AB is somewhat more complicated. Such species may go extinct from either region without going globally extinct, and a state change occurs during speciation. If speciation occurs within region A or B, one daughter species is in state AB but the other daughter is in either state A or state B, respectively. If speciation is between regions, one daughter species is in A and the other is in B. Dispersal need not be considered for species already present in both regions.

1

$$D_{NAB}(t + \Delta t) = (1 - s_A\Delta t)(1 - s_B\Delta t)(1 - s_{AB}\Delta t)(1 - x_A\Delta t)(1 - x_B\Delta t)D_{NAB}(t)$$

no events

$$+ (x_A\Delta t)D_{NB}(t) + (x_B\Delta t)D_{NA}(t)$$

extinction in A or B

$$+ (s_A\Delta t)[E_A(t)D_{NAB}(t) + E_{AB}(t)D_{NA}(t)]$$

speciation in A and eventual extinction of either daughter

$$+ (s_B\Delta t)[E_B(t)D_{NAB}(t) + E_{AB}(t)D_{NB}(t)]$$

speciation in B and eventual extinction of either daughter

$$+ (s_{AB}\Delta t)[E_B(t)D_{NA}(t) + E_A(t)D_{NB}(t)]$$

between-region speciation and eventual extinction of either daughter

Terms of order Δt^2 and higher can again be discarded, leaving

$$\begin{aligned}
D_{NAB}(t + \Delta t) = {}& [1 - (s_A + s_B + s_{AB} + x_A + x_B)\Delta t]D_{NAB}(t) \\
& + (x_A\Delta t)D_{NB}(t) + (x_B\Delta t)D_{NA}(t) \\
& + (s_A\Delta t)[E_2(t)D_{NAB}(t) + E_1(t)D_{NA}(t)] \qquad \text{(A1-3)} \\
& + (s_B\Delta t)[E_3(t)D_{NAB}(t) + E_1(t)D_{NB}(t)] \\
& + (s_{AB}\Delta t)[E_3(t)D_{NA}(t) + E_2(t)D_{NB}(t)].
\end{aligned}$$

Finally, letting $\Delta t \to 0$, Eq. A1-1–A1-3 become the set of coupled differential equations given in Eq. 1.

Initial conditions.—States of the tips are assumed to be known, so for each tip N, the initial condition is

$$D_{Ni}(0) = \begin{cases} f_i & \text{if the tip is in state } i, \\ 0 & \text{otherwise.} \end{cases} \qquad \text{(A1-4)}$$

where f_i is the proportion of species in state i that are sampled in the phylogeny, assuming that sampling within a tip state is uniform across the tree. Further detail on dealing with incomplete sampling and unresolved clades is given in FitzJohn et al. (2009), and those methods are also applicable to GeoSSE.

Calculations at nodes.—When computing the likelihood of a tree by working from the tips toward the root, likelihoods from sister branches (denoted N and M) must be combined at the node of their immediate ancestor (denoted C since A is used to label a region; see Fig. A1-1). The likelihood of the C clade is the product of the daughter lineage likelihoods and the chance of speciating at the node time (denoted t_C). When the parent lineage is in state A, both daughters are in state A, and similarly for state B. For parental state AB, either one daughter will be in state AB and one in state A or B, or one daughter will be in state A and the other in state B, as discussed above. Therefore, the likelihoods of the lineage just before the ancestral node are given in Eq. 2.

At the root.—When the ancestral node is the root of the tree ($C = R$), the conditional likelihoods $D_{Ri}(t_R)$ must be summed with an appropriate weighting. Possibilities include equal weights for each state, the equilibrium frequencies of each state, or likelihoods determined from the data. We use the last of these, $D_{Ri}/\sum_i D_{Ri}$ (FitzJohn et al. 2009).

The probability that a lineage in state i at time t goes extinct by the present time ($t = 0$) is denoted $E_i(t)$. Extinction can only occur if some amount of time has passed, so the initial condition is $E_i(0) = 0$. (For randomly-incomplete sampling, the initial condition is $E_i(0) = 1 - f_i$ (FitzJohn et al. 2009).) If $E_i(t)$ is assumed known, $E_i(t + \Delta t)$ can be calculated by enumerating the possible paths to extinction.

Recalling that at most one event can happen in the small time step Δt, extinction by the present time of a lineage endemic to region A can occur through extinction in Δt, no event in Δt but extinction afterwards, dispersal in Δt followed by eventual extinction, or speciation in Δt followed by eventual extinction of both daughter lineages:

$$
\begin{aligned}
E_A(t + \Delta t) = (1 - s_A \Delta t)(1 - d_A \Delta t)(1 - x_A \Delta t) E_A(t) \quad & \text{no events, eventual extinction} \\
+ \, x_A \Delta t \quad & \text{immediate extinction} \\
+ \, (d_A \Delta t) E_{AB}(t) \quad & \text{dispersal, eventual extinction} \\
+ \, (s_A \Delta t) E_A(t)^2 \quad & \text{speciation, eventual extinction}
\end{aligned}
$$

Dropping higher order terms in Δt yields

$$
E_A(t + \Delta t) = \left[1 - (s_A + d_A + x_A)\Delta t\right] E_A(t) + x_A \Delta t + (d_A \Delta t) E_{AB}(t) + (s_A \Delta t) E_A(t)^2, \quad \text{(A1-5)}
$$

and similarly for the extinction probability of lineages endemic to B,

$$
E_B(t + \Delta t) = \left[1 - (s_B + d_B + x_B)\Delta t\right] E_B(t) + x_B \Delta t + (d_B \Delta t) E_{AB}(t) + (s_B \Delta t) E_B(t)^2. \quad \text{(A1-6)}
$$

For lineages present in both regions, dispersal in Δt can be ignored. Total extinction (from both A and B) cannot occur in Δt, but extinction in either region is possible. A speciation event leaves daughters in different states, as described above. We therefore have:

$$
\begin{aligned}
E_{AB}(t + \Delta t) = (1 - s_A \Delta t)(1 - s_B \Delta t)(1 - s_{AB}\Delta t)(1 - x_A \Delta t)(1 - x_B \Delta t) E_{AB}(t) \\
\text{no events, eventual extinction} \\
+ (x_A \Delta t) E_B(t) + (x_B \Delta t) E_A(t) \\
\text{immediate extinction in one region, eventual extinction from the other} \\
+ (s_A \Delta t) E_{AB}(t) E_A(t) + (s_B \Delta t) E_{AB}(t) E_B(t) + (s_{AB}\Delta t) E_A(t) E_B(t) \\
\text{speciation, eventual extinction of both daughters}
\end{aligned}
$$

Dropping higher order terms in Δt yields

$$
\begin{aligned}
E_{AB}(t + \Delta t) = \left[1 - (s_A + s_B + s_{AB} + x_A + x_B)\Delta t\right] E_{AB}(t) + (x_A \Delta t) E_B(t) + (x_B \Delta t) E_A(t) \\
+ (s_A \Delta t) E_{AB}(t) E_A(t) + (s_B \Delta t) E_{AB}(t) E_B(t) + (s_{AB}\Delta t) E_A(t) E_B(t).
\end{aligned}
$$
$$\text{(A1-7)}$$

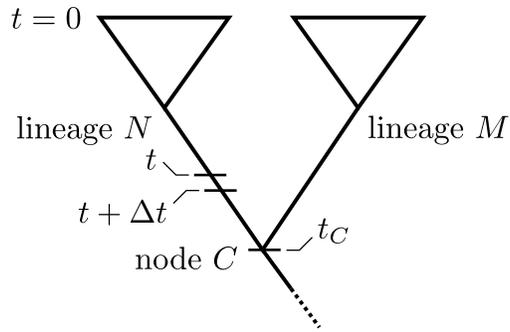Taking the $\Delta t \to 0$ limit in Eq. A1-5–A1-7 yields Eq. 3.

Figure A1-1: A portion of a phylogenetic tree, illustrating notation used in the likelihood derivation.

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FitzJohn, R. G., W. P. Maddison, and S. P. Otto. 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. Systematic Biology 58:595–611.

Maddison, W. P., P. E. Midford, and S. P. Otto. 2007. Estimating a binary character's effect on speciation and extinction. Systematic Biology 56:701–710.

Phylogeny Construction and Molecular Clock Calibration

To construct phylogenies, we obtained sequences for the internal transcribed spacer regions of 18s–26s nuclear ribosomal DNA (ITS-1 and ITS-2) from GenBank (*http://www.ncbi.nlm.nih.gov*). ITS sequences are commonly used in phylogenetic studies at the species level (Baldwin et al. 1995) and were available for most *Arctostaphylos* and *Ceanothus* species. In addition, we obtained outgroup sequences, which were used for dating the ingroup divergence time but were later clipped from the final trees.

For *Arctostaphylos* (Ericaceae), we initially included, but later pruned, all available sequences within subfamily Arbutoideae, to take advantage of fossil data for this more inclusive clade. The age of *Arctostaphylos* was estimated using a lognormal prior with a hard minimum bound of 37.2 Ma, based on the age of an *A. elliptica* fossil from Wyoming, USA, estimated to be 48.6–37.2 Ma (Knowlton 1899; this and several other dates obtained from the Paleobiology Database, *http://paleodb.org*). The age of *Comarostaphylos* was also estimated using a lognormal prior, with an 11.61 Ma minimum bound based on fossilized *C. globula* in Germany, estimated to be 15.97–11.61 Ma in age (Mai 2001).

For *Ceanothus* (Rhamnaceae), the age of the genus was estimated using a lognormal prior with a 48.6 Ma minimum bound, based on fossilized *C. chaneyi* found in the 55.8–48.6 Ma Eocene Germer Basin Flora of Idaho, USA (Edelman 1975). The split between *C. cuneatus* and *C. roderickii* (reported as sister species by Hardig et al. (2000) but not constrained to be monophyletic here) was estimated using a lognormal prior with 15.97 Ma minimum bound, based on fossilized *C. precuneatus* (cuneatus) 20.43–15.97 Ma (Axelrod 1975). The split between *C. spinosus* and *C. dentatus* (grouping also from Hardig et al. (2000), here not constrained as monophyletic) was estimated using a lognormal prior with 5.33 Ma minimum bound, based on fossil age of *C. prespinosus* (spinosus), 23.03–5.33 Ma (Becker 1969).

ITS sequences were aligned separately for each clade in MUSCLE v. 3.7 (Edgar 2004) using default parameters, with non-aligning regions evaluated by eye and removed. The GTR+I+G model of nucleotide substitution was determined to be appropriate for each clade using AIC and hLRT in MrModeltest v2.3 (Nylander 2004). We then constructed the phylogenies with the Bayesian Markov chain Monte-Carlo (MCMC) method implemented in BEAST v4.8 and 5.0 (Drummond and Rambaut 2007), using a lognormally distributed relaxed molecular clock model (Drummond et al. 2006), birth-death tree prior, and the fossil- and vicariance-derived clade age priors described above. The MCMC chain length was set to 50,000,000 for each tree for sufficient effective sample sizes to be reached to confidently estimate tree parameters from their posterior probabilities. Multiple BEAST runs were compared (for parameter convergence) and combined to generate a final set of 1000 trees for each clade, after removing a 10% burnin from each run.

GenBank accession numbers, BEAST files for each genus, and posterior sets of trees are deposited in the Dryad database at *doi:10.5061/dryad.8343*. Alignments and maximum clade credibility trees with mean node heights are also deposited in TreeBASE under submission number 11157.

Habitat Coding and Sampling Frequency

For each species of *Arctostaphylos* and *Ceanothus*, habitat information was obtained from the Jepson Manual (Hickman 1993), the CalFlora database (*http://www.calflora.org*), and several other government and botanical garden plant databases. (Habitat states are listed with references in the Dryad database at *doi:10.5061/dryad.8343*.) Species found in chaparral and/or coastal scrub communities, but not in woodland or forest habitats, were designated chaparral-specialists (C). Species found in woodland or forest habitats, but not found in chaparral, were designated forest-specialists (F). Species found in both chaparral/scrub and forest/woodland were designated habitat-generalists (CF). No species in either genus was absent from both forest and chaparral habitats. Following habitat coding, we determined the sampled proportions of C, F, and CF species in each genus; they were 0.71, 0.64, and 0.67 for *Arctostaphylos*, and 0.89, 0.95, and 0.91 for *Ceanothus*. The correction for randomly incomplete sampling (FitzJohn et al. 2009) was applied during rate estimation.

Habitat-Dependent Diversification Rate Estimation under GeoSSE

We fit the GeoSSE model to *Arctostaphylos* and *Ceanothus* jointly. Trees from the posterior set for each genus were paired randomly, and the joint likelihood of each pair was computed as the product of the likelihoods for each genus. This procedure assumes that the genera are independent of each other: they of course share an ancestor, but they belong to separate eudicot radiations (*Ceanothus* is a Rosid, while *Arctostaphylos* is an Asterid), which diverged approximately 120 Ma (Wikstrom et al. 2001). We also attempted parameter estimation for each genus separately. The results were comparable for the two genera but showed insufficient power for meaningful conclusions (results not shown).

We used Markov chain Monte Carlo to estimate the GeoSSE model parameters, running 10,000 steps under the slice sampling algorithm implemented in *diversitree*'s (FitzJohn 2010) *mcmc()* function with broad exponential priors (rate = 0.1) for each of 1000 pairs of trees. After removing burn-in for each tree and keeping every tenth sample, a total of 990,000 MCMC samples were used in the analysis. Analysis scripts are deposited in the Dryad database at *doi:10.5061/dryad.8343*.

We report results from the MCMC analysis as the proportion of samples from the posterior distribution, or probability, for which a statement is true, and as the mean value of a quantity with its standard error computed from a time-series analysis as implemented in the *R* package *coda* (Plummer et al. 2010). Models without and with the between-habitat speciation parameter (s_{CF}) were compared with the Bayes factor, approximated with the harmonic mean of the posterior samples for each model, trimmed to the 50% highest posterior density region (Robert and Wraith 2009; a nearly identical result came from anything between the 95% to the 10% HPD).

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The GeoSSE model processes and assumptions can be extended to more than two regions.

Preliminaries

Denote the regions A, B, ... and use indices i and j to refer to arbitrary single regions. Let R denote the set of all regions, and let r be a non-null subset of regions. To reduce clutter, time dependence (t) is not written out.

Speciation within region i is at per-lineage rate s_i, extinction is x_i, and dispersal from i to j is d_{ij}. Dispersal expands ranges one region at a time, and all pairwise dispersal patterns are allowed.

Between-region speciation is restricted to a single rate, s, to avoid a rapid proliferation of variables. The two daughter ranges under this mode of speciation may each consist of any set of regions as long as they sum to the parent's range ($r_1 \cup r_2 = r$ and $r_1 \cap r_2 = \varnothing$, or equivalently $r_2 = r \smallsetminus r_1$, for parental range r and daughter ranges r_1 and r_2). The interpretation is that vicariance is equally likely to occur between any sets of regions. Larger ranges have more possible subdivisions and are therefore subject to a higher rate of between-region speciation. If desired, different speciation rates for different divisions of the parent range could instead be specified. These might be functions of the identity of the regions in a range or of the size of a range.

For a parental range r, let $\mathcal{Q}_r$ be the set of all possible ranges for one daughter under between-region speciation. Using $\wp(r)$ to denote the power set of r (the set of all possible subsets of r), $\mathcal{Q}_r = \wp(r) \smallsetminus \{\varnothing, r\}$ since each daughter must have a non-zero range. The number of possible daughter ranges, the cardinality of $\mathcal{Q}_r$, is $|\mathcal{Q}_r| = 2^{|r|} - 2$.

If the regions have an explicit spatial arrangement, it may be appropriate to constrain the types of between-region speciation events allowed (e.g., requiring a daughter range to consist of contiguous regions) and/or to constrain the dispersal events (e.g., only between neighboring regions, or rates declining as a function of distance). Rates of speciation and extinction could similarly be made functions of the region's location in space.

Likelihood of tree and character states (D)

Calculations within a branch.—The general case of Eq. 1 is

$$
\frac{dD_{Nr}}{dt} = -\underbrace{\left[\sum_{i \in r}\left(s_i + x_i + \sum_{j \in R \smallsetminus r} d_{ij}\right) + (2^{|r|-1}-1)s\right]D_{Nr}}_{\text{no events}} + \underbrace{\sum_{i \in r} x_i D_{Nr \smallsetminus \{i\}}}_{\text{extinction}} + \underbrace{\sum_{i \in r}\sum_{j \in R \smallsetminus r} d_{ij} D_{Nr \cup \{j\}}}_{\text{dispersal}}
$$

$$
+ \underbrace{\sum_{i \in r} s_i \left(E_{\{i\}} D_{Nr} + E_r D_{N\{i\}}\right)}_{\text{within-region speciation}} + \underbrace{(2^{|r|}-2)s \sum_{r_i \in \mathcal{Q}_r} E_{r \smallsetminus r_i} D_{Nr_i}}_{\text{between-region speciation}} .
$$

(A3-1)

The "extinction" term in Eq. A3-1 includes extinction in any region i within r followed by survival of the observed clade from the reduced range $r \smallsetminus \{i\}$. This term vanishes for a

lineage in only one region (Eq. 1ab), $D_{N\varnothing} = 0$, because a clade that doesn't exist can't be observed.

The "dispersal" term in Eq. A3-1 covers dispersal from any region within the range r to any other region outside of it. For a lineage present in all regions, this term vanishes (Eq. 1c), via $R \smallsetminus R = \varnothing$, because there is nowhere else to disperse to.

The "within-region speciation" term in analogous to those in Eq. 1c and easily reduces to those in Eq. 1ab when r consists of a single region. The "between-region speciation" term similarly incorporates the extinction of one daughter and the survival of the other daughter. Here, however, the daughter ranges can be any subdivision of the parent range. The ordering of daughters doesn't matter, so the factor here is half of $|\mathcal{Q}_r|$. When the parent range is a single region, between-region speciation vanishes via $\mathcal{Q}_r = \varnothing$.

Calculations at nodes.—The general case of Eq. 2 is

$$D_{Cr} = \frac{1}{2}\sum_{i\in r}\left(D_{Nr}D_{M\{i\}} + D_{N\{i\}}D_{Mr}\right)s_i + \frac{1}{2}\sum_{r_i\in\mathcal{Q}_r}\left(D_{Nr_i}D_{Mr\smallsetminus r_i} + D_{Nr\smallsetminus r_i}D_{Mr_i}\right)s. \qquad \text{(A3-2)}$$

The first summation covers within-region speciation, in which one daughter retains the parental range r and the other has a range of a single region. The second summation covers between-region speciation, where the sum of the two daughters' ranges is the parental range. The $2^{|r|} - 2$ factors of s could be pulled out of the second summation, as was done in the final terms of Eq. A3-1 and Eq. A3-3.

At the root.—Conditional likelihoods can be weighted by the likelihood of the observed data. Alternatively, equilibrium frequencies can be computed from the (large) transition matrix.

<center>*Likelihood of extinction (E)*</center>

The general case of Eq. 3 is

$$\frac{dE_r}{dt} = -\underbrace{\left[\sum_{i\in r}\left(s_i + x_i + \sum_{j\in R\smallsetminus r}d_{ij}\right) + (2^{|r|-1}-1)s\right]E_r}_{\text{no events}} + \underbrace{\sum_{i\in r}x_i E_{r\smallsetminus\{i\}}}_{\text{extinction}} + \underbrace{\sum_{i\in r}\sum_{j\in R\smallsetminus r}d_{ij}E_{r\cup\{j\}}}_{\text{dispersal}}$$

$$+ \underbrace{\sum_{i\in r}s_i E_i E_r}_{\text{between-region speciation}} + \underbrace{(2^{|r|-1}-1)s\sum_{r_i\in\mathcal{Q}_r}E_{r_i}E_{r\smallsetminus r_i}}_{\text{within-region speciation}}. \qquad \text{(A3-3)}$$

The "extinction" term in Eq. A3-3 contains immediate extinction from one region followed by eventual extinction from the remaining regions. For a lineage in a single region i, this simplifies to x_i because $E_\varnothing = 1$, i.e., a species with no range is already extinct. The "dispersal" term in Eq. A3-3 operates as in Eq. A3-1 and similarly drops out for a species already present in all regions. The "within-region speciation" and "between-region speciation" terms in Eq. A3-3 each incorporate the eventual extinction of the two daughters from their allowable states.

<center>2</center>