Correlates of Diversification in the Plant Clade Dipsacales: Geographic Movement and Evolutionary Innovations

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ABSTRACT: We explore patterns of diversification in the plant clades Adoxaceae and Valerianaceae (within Dipsacales), evaluating correlations between biogeographic change (i.e., movements into new areas), morphological change (e.g., the origin of putative key innovations associated with vegetative and reproductive characters), and shifts in rates of diversification. Our findings indicate that rates of diversification in these plants tend to be less tightly correlated with the evolution of morphological innovations but instead exhibit a pronounced correlation with movement into new geographic areas, particularly the dispersal of lineages into new mountainous regions. The interdependence among apparent novelties (arising from their nested phylogenetic distribution) and the correlation between morphological and biogeographic change suggests a complex history of diversification in Dipsacales. Overall, these findings highlight the importance of incorporating biogeographic history in studies of diversification rates and in the study of geographic gradients in species richness. Furthermore, these results argue against a simple deterministic relationship between dispersal and diversification: like other factors that may influence the probability of speciation and/or extinction, the impact of dispersal on diversification rates depends on being in the right place at the right time.

Keywords: biogeographic movement, dispersal, diversification rates, key innovation, speciation, extinction.

Differences in species richness among geographic regions ultimately reflect differences in the durations that these areas have been occupied by the organisms of interest (i.e., historical biogeography) and/or differences in rates of diversification (i.e., speciation minus extinction) of the groups in those areas. Our focus here is on shifts in diversification rate as a factor underlying geographic patterns in species diversity. Both the origin of intrinsic traits—including morphological, behavioral, and physiological novelties—and extrinsic events—including episodes of biogeographic or climatic change—have been hypothesized to promote shifts in diversification rate by altering the probability of speciation and/or extinction. A comprehensive understanding of the causes of diversification therefore requires incorporation of both elements. Surprisingly, the relative impact of both biotic and abiotic factors on diversification rates has seldom been evaluated in an explicitly phylogenetic context.

In plants, the search for intrinsic correlates of diversification has tended to focus on a few putative key innovations relating to floral morphology, growth form, and fruit type/dispersal mechanism. The role of extrinsic factors in plant diversification has received less attention; however, an important class of abiotic factors pertains to the impact of biogeography on diversification. Dispersal to new geographic areas could conceivably increase the probability of diversification in several ways. For example, the dispersing species may diversify in response to ecological opportunities afforded by the new area if, for instance, it is well suited to exploit resources in the new area that are underexploited by residents of that community. Alternatively, the new area may provide a measure of "ecological release" for the dispersing species if that area lacks antagonistic elements (competitors, predators, etc.) that inhibit diversification (e.g., via competitive exclusion). Conversely, abiotic aspects of the new area may promote diversification either by increasing the opportunity for allopatric speciation (e.g., owing to greater topographic complexity; Carlquist 1974; von Hagen and Kadereit 2003; Xiang et al. 2004; Hughes and Eastwood 2006) or by decreasing the incidence of extinction (e.g., owing to greater climatic stability/reduced environmental harshness; Cracraft 1985; Qian and Ricklefs 1999).

The relationship between geographic dispersal, morphological change, and shifts in diversification rate can be conceived of as a cube in which the cells delimit the set of possible interactions (fig. 1). Of special interest are outcomes in which shifts in diversification are correlated with geographic movement (which we refer to as dispersifica-

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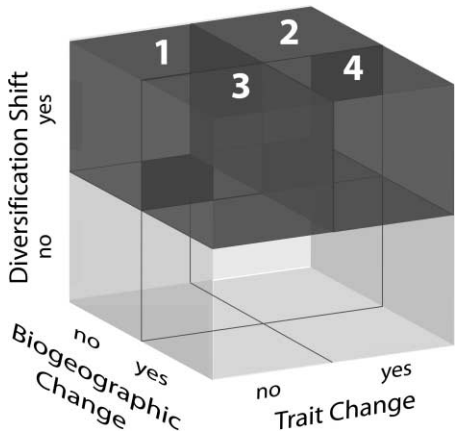


Figure 1: Graphical model of the relationship between morphological and biogeographic variables and diversification rate. The axes of this cube designate change or stasis in morphology, biogeographic distribution, and rates of diversification, such that its cells collectively circumscribe the set of possible correlations between each of the three variables. Our focus is on scenarios restricted to the upper tier of the cube, which entails significant shifts in diversification rate. Within this tier, shifts in diversification rate may occur independent of changes in the other two variables (cell 1, which may be correlated with some unexplored factor), rate shifts may be correlated with the evolution of a morphological trait (cell 2, which is consistent with a key innovation scenario), rate shifts may be correlated with the dispersal to a new biogeographic area (cell 3, which we refer to as a dispersification scenario), or rate shifts may be correlated with both morphological and biogeographic change (cell 4). Our goal is to explore the extent to which inferred diversification rate shifts populate the cells of this cube.

tion), character evolution (key innovation), or changes in both variables. Our goal is to explore how the cells of this cube are occupied. Note that this exercise falls squarely in the realm of data exploration. To the extent that we are testing hypotheses, they are fairly prosaic: the null hypotheses under evaluation are that rates of diversification are stochastically constant and that any shifts in diversification rate are not significantly correlated with morphological or biogeographic change. We hope to show that an exploratory approach to studying the patterns and processes of differential diversification rates may provide insights into what remains one of the most complex and poorly understood problems in evolutionary biology.

We focus here on the plant clade Dipsacales (specifically on Adoxaceae and Valerianaceae), attempting to assign inferred diversification rate shifts to the scenarios circumscribed by the cube. Of general interest is whether shifts in diversification tend to be correlated with movement into new areas, with morphological change, or with changes in both factors. In the spirit of the symposium that stimulated this study, we also consider the broader implications of our findings for the study of geographic patterns of species richness. Overall, we hope to illustrate how such studies are likely to benefit from the adoption of an explicitly historical perspective.

Two Experiments in Dipsacales: Adoxaceae and Valerianaceae

Dipsacales is a clade of campanulid asterid angiosperms with approximately 1,000 species that are largely distributed in temperate or high-elevation areas around the Northern Hemisphere but that also extend into the mountains of Southeast Asia and Latin America (Donoghue et al. 2003). These plants have been the subject of phylogenetic studies based on morphological characters (Donoghue 1985; Judd et al. 1994; Backlund and Donoghue 1996) and molecular data (e.g., Bell et al. 2001; Donoghue et al. 2001, 2003; Zhang et al. 2002), and they are well known from the standpoint of their diverse morphology (e.g., Weberling 1957; Fukuoka 1972; Hara 1983; Verlaque 1984; Donoghue 1985; Backlund and Donoghue 1996; Roels and Smets 1996; Mayer and Ehrendorfer 1999; Donoghue et al. 2003) and complex historical biogeography (e.g., Tang and Li 1994; Bell 2004; Bell and Donoghue 2005*a*, 2005*b*; Winkworth and Donoghue 2005). The fossil record and divergence times of this group have also been studied (Manchester and Donoghue 1995; Bell and Donoghue 2005*a*). These plants therefore provide fertile ground for examining the relationship between shifts in diversification rate, morphological evolution, and biogeographic movements.

Specifically, we focus here on two major clades within Dipsacales: Adoxaceae, with ~190 species, and Valerianaceae, with ~300 species. Within Adoxaceae, recent phylogenetic studies have focused on *Viburnum* (Donoghue et al. 2004; Winkworth and Donoghue 2004, 2005) and *Sambucus* (Eriksson and Donoghue 1997). Similarly, Valerianaceae has been the subject of recent molecular analyses (Bell 2004; Bell and Donoghue 2005*b*). Adoxaceae is comprised of mainly woody plants (shrubs and small trees, although approximately eight species are herbaceous) with fleshy fruits (berries or drupes) dispersed by birds. By contrast, Valerianaceae is comprised of herbaceous plants with dry, single-seeded (achene) fruits dispersed mainly by wind (but in some cases by animal fur or water). Members of each clade also exhibit major differences in flower morphology that might conceivably have influenced probabilities of speciation and/or extinction (Donoghue et al. 2003; Howarth and Donoghue 2005), such as the evolution of enlarged sterile flowers within *Viburnum* (Adoxaceae) and nectar spurs within Valerianaceae. Both clades are inferred to have experienced broadly similar biogeographic histories (Bell 2004; Bell and Donoghue 2005*b*; Winkworth and Donoghue 2005): each group appears to have origi-

nated and diversified in Asia in the early Tertiary, moved from Asia into areas of the Northern Hemisphere on several occasions, and more recently entered the mountains of Mexico and Central America and the Andean region of South America.

Analysis Pipeline

The analytical design used to evaluate correlates of diversification in Dipsacales involves four main steps (fig. 2). The first step entails a series of analyses to estimate phylogenies (with or without estimated divergence times) for the two study groups, Adoxaceae and Valerianaceae. Subsequent analyses involve complementary topological and temporal methods to locate significant shifts in diversification rate, to evaluate morphological correlates of diversification rate, and to identify episodes of dispersal.

Phylogenetic Analyses and Divergence Time Estimation

Preliminary Analyses. We conducted a series of analyses to estimate relationships and divergence times in both Adoxaceae and Valerianaceae. Accession numbers for all sequences are listed in the appendix. Sequences for each group were aligned using Muscle (Edgar 2004) and adjusted manually as necessary; the resulting alignments can be obtained at http://www.phylodiversity.net/brian/resources.html. Various properties of these sequence alignments are summarized in table 1. We performed an exhaustive series of pairwise partition homogeneity tests to identify potential conflict among the set of markers available for each study group. Each pairwise partition homogeneity test entailed 10^3 replications, with each replicate involving a heuristic search with 10^3 random taxon addition starting trees that were subjected to TBR branch swapping using PAUP* (ver. 4.0; Swofford 2000). The results of these tests (table 2) were used to inform a strategy for linking parameters that were shared among the set of partition-specific models used for phylogeny/divergence time estimation (see below). Model selection for each data partition was based on ΔAIC scores for the set of substitution models evaluated by Modeltest (ver. 3.7; Posada and Crandall 1998). Models selected for each partition are listed in table 1. The degree of substitution rate variation among lineages was investigated by means of likelihood ratio tests using PAUP*; we obtained the likelihood score for each partition under the selected model both with and without enforcing substitution rate constancy and then compared the likelihood ratio test statistic to a χ^2 distribution with $2 - N$ degrees of freedom, where N is the number of taxa (Felsenstein 1988). These molecular clock tests detected high levels of substitution rate variation in all data partitions (table 1).

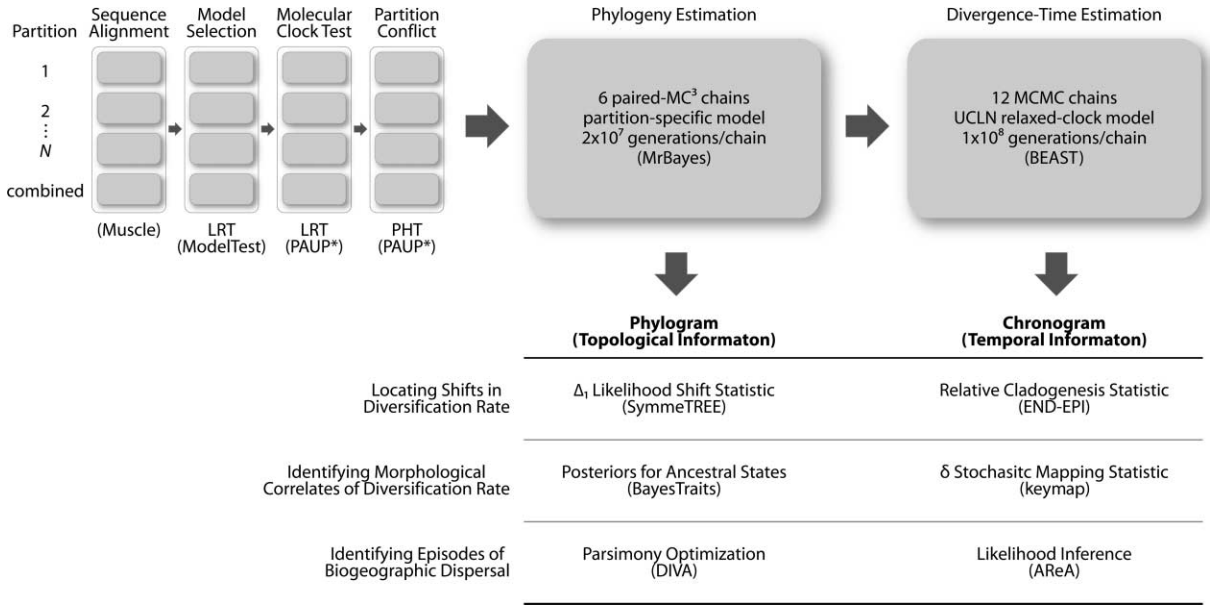


Figure 2: Schematic of the data analysis pipeline used to explore correlates of diversification rate shifts. An initial stage of analyses provides estimates of the phylogeny and divergence times for each study group. Subsequent analyses entail complementary topological and temporal methods to locate significant shifts in diversification rate (the second step), estimate character evolution and evaluate morphological correlates of diversification rate (the third step), and identify episodes of biogeographic dispersal (the final step).

Table 1: Properties of the gene regions used to estimate phylogenies for Adoxaceae and Valerianaceae

Taxa and marker	Source	*N* taxa	*N* sites	Model selection[a]	Substitution rate variation		Substitution rate autocorrelation[d]
					LRT[b]	PP[c]	
Adoxaceae:							
Combined		63	4,263	GTR I Γ	≪.001	.364	-2.99×10^{-2}
ITS	Donoghue et al. 2004; this study	63	575	GTR I Γ	≪.001	…	…
matK	Donoghue et al. 2004; this study	63	1,146	TVM Γ	≪.001	…	…
trnS-trnG	This study	63	655	F81 Γ	≪.001	…	…
WAXY 1	Winkworth and Donoghue 2005; this study	51	994	HKY Γ	≪.001	…	…
WAXY 2	Winkworth and Donoghue 2005; this study	45	894	HKY Γ	≪.001	…	…
Valerianaceae:							
Combined		103	2,873	GTR Γ	≪.001	.743	-1.68×10^{-2}
ITS	Bell and Donoghue 2005*b*	103	623	GTR Γ	≪.001	…	…
matK	Bell and Donoghue 2005*b*	86	1,058	TVM Γ	≪.001	…	…
psbA	Bell and Donoghue 2005*b*	100	304	K81uf Γ	≪.001	…	…
trnL-trnF	Bell and Donoghue 2005*b*	103	889	TVM Γ	≪.001	…	…

[a] Based on ΔAIC values calculated for the set of molecular substitution models evaluated in ModelTest (Posada and Crandall 1998).
[b] Based on likelihood ratio test of log likelihood scores obtained with and without enforcing substitution rate constancy.
[c] Based on marginal posterior probability of the coefficient of variation in substitution rate for the combined data set estimated with BEAST.
[d] Based on marginal posterior probability of the covariance of substitution rate variation estimated with BEAST.

Phylogeny Estimation. The posterior probability distribution of trees for each group was approximated using the Metropolis-coupled Markov chain Monte Carlo (MC^3) algorithm implemented in MrBayes (ver. 3.1.2; Ronquist and Huelsenbeck 2003). Each MC^3 analysis employed partition-specific substitution models and comprised four incrementally heated chains ($\Delta T = 0.2$–0.1) initiated from random starting trees. Convergence to the stationary distribution was monitored by running paired-MC^3 analyses and evaluating the similarity of trees visited by their respective cold chains (i.e., by observing the average standard deviation of split frequencies reported by MrBayes). Once each chain converged to the stationary distribution, samples were drawn every 10^3 steps until 10^4 samples were obtained. As an additional measure, six replicate paired-MC^3 analyses were performed to confirm that inferences made from independent runs were effectively identical. Finally, the adequacy of sampling intensity was assessed by means of the potential scale reduction factor (PSRF) and estimated sample size (ESS) diagnostics. For each group, we combined the post-burn-in trees sampled by the 12 independent analyses and summarized the collective posterior probability distribution of trees using majority rule consensus.

Results. Samples drawn during the first 10^7 generations of all MC^3 analyses were discarded as burn-in. Average standard deviation of split frequencies suggested that each of the six paired-MC^3 chains converged to the target distribution (values for the paired runs ranged from 0.001 to 0.002), and examination of the trees inferred by each independent run confirmed that these estimates were essentially identical. Diagnostics indicated adequate sampling of all estimated parameters in all runs for both groups (i.e., the PSRF estimates approximated unity, and the ESS values were much greater than 10^3 for all parameters). Accordingly, the 10^4 post-burn-in samples from each of the 12 independent analyses were combined and summarized by majority rule consensus (figs. 3, 4 for Adoxaceae and Valerianaceae, respectively). These phylogenies (and corresponding alignments) have been deposited in TreeBASE (http://treebase.org/treebase/index.html; accession no. SN3284). The estimated marginal log likelihood of the combined runs was −16,565.57 for Adoxaceae and −41,161.87 for Valerianaceae. The 95% highest posterior density (HPD) comprised 12,059 unique trees for Adoxaceae and 18,924 for Valerianaceae, reflecting a comparable degree of phylogenetic uncertainty in both estimates. The results of the current analyses correspond closely to those of recently published studies based on more limited samples of taxa and/or markers (e.g., Bell 2004; Donoghue et al. 2004; Winkworth and Donoghue 2004, 2005; Bell and Donoghue 2005*b*).

Divergence Time Estimation. Owing to the high level of substitution rate variation, divergence times were estimated under a relaxed molecular clock. In contrast to most relaxed clock divergence time estimation methods—which presuppose the autocorrelation of molecular rate variation between ancestral and descendant branches—the uncor-

Table 2: Pairwise tests of conflict among the Adoxaceae and Valerianaceae data partitions

	Valerianaceae						
Partitions	ITS	*matK*	*trnS-G*	*WAXY* 1	*WAXY* 2	*psbA*	*trnL-F*
Adoxaceae:							
ITS	…	.01[a]	NA	NA	NA	.01[a]	.01[a]
matK	.61	…	NA	NA	NA	.01[a]	.01[a]
trnS-G	.97	.09	…	NA	NA	NA	NA
WAXY 1	.01[a]	.04[a]	.34	…	NA	NA	NA
WAXY 2	.49	.40	.51	.01[a]	…	NA	NA
psbA	NA	NA	NA	NA	NA	…	.01[a]
trnL-F	NA	NA	NA	NA	NA	NA	…

Note: *P* values are based on partition homogeneity test implemented in PAUP*; values below the diagonal reflect tests among Adoxaceae data partitions, and those above the diagonal reflect tests among Valerianaceae data partitions. NA = not applicable.

[a] Significant conflict.

related lognormal (UCLN) model (Drummond et al. 2006) assumes that substitution rates on adjacent branches are independently sampled from an underlying lognormal distribution. That is, autocorrelation of substitution rate variation is allowed, but it is not assumed a priori. The estimation of absolute divergence times requires calibrating (or constraining) the age of one or more nodes. The implementation of the UCLN model in BEAST (ver. 1.4.1; Drummond and Rambaut 2003) enables uncertainty in the age of calibrations to be represented as prior distributions rather than committing to point estimates. We therefore constrained one or more nodes in each study tree (which had posterior probabilities of 1.0 in all of the preliminary phylogenetic analyses) to prior probability distributions (table 3).

The rather extensive Tertiary record of Dipsacales will require detailed studies to elucidate the phylogenetic placement of the many macrofossils attributed to this group (see Bell and Donoghue 2005*a*). Accordingly, we chose relatively broad constraints in order to reflect this level of paleontological uncertainty. The crown group of Adoxaceae was constrained to a lognormal distribution with an upper bound of 86 million years and a lower bound of 45 million years, on the basis of the earliest macrofossil occurrence (reviewed by Baskin et al. [2006]) and palynological record (e.g., Muller 1981) for this group. Within Adoxaceae, the crown group of *Viburnum* was constrained to a similarly conservative lognormal distribution with an upper bound of 85 million years and a lower bound of 45 million years (on the basis of the oldest fossil unambiguously assignable to the crown group of *Viburnum*; Gruas-Cavagnetto 1978). The crown group of Valerianaceae was constrained to a lognormal distribution with an upper bound of 60 million years and a lower bound of 45 million years (on the basis of fossil fruits assignable to the stem group of *Patrinia*; Lancucka-Srodoniowa 1967; see also Bell and Donoghue 2005*a*; Baskin et al. 2006). Within Valerianaceae, the crown group of *Valeriana* was constrained to a lognormal distribution with an upper bound of 25 million years and a lower bound of 15 million years (Baskin et al. 2006).

We estimated the posterior probability density of divergence times under the substitution model selected for the combined set of markers for each of the two study groups (table 1) and assumed that substitution rates evolved under the UCLN model and that the branching process evolved according to a Yule prior (i.e., the prior distribution of divergence times was generated by a pure birth stochastic branching process). For each group, we initiated 12 independent Markov chain Monte Carlo (MCMC) analyses from starting trees that satisfied the respective priors on divergence times described above (table 3). Convergence of each chain to the target distribution was inferred by plotting time series of the marginal probabilities of sampled parameter values using Tracer (ver. 1.3; Rambaut and Drummond 2003). After achieving convergence, each chain was sampled every 10^3 steps until 10^5 samples were obtained, and the adequacy of sampling intensity was assessed by means of the PSRF and ESS diagnostics.

Results. The UCLN analyses corroborated findings of the likelihood ratio test of substitution rate constancy (table 1): the estimated coefficient of variation identified substantial levels of substitution rate variation in both groups (Adoxaceae $\sigma = 0.364$, 95% HPD: [0.271, 0.463]; Valerianaceae $\sigma = 0.743$, 95% HPD: [0.641, 0.848]). Substitution rates across ancestor-descendant lineages appeared to be effectively uncorrelated in both groups (table 1; Adoxaceae covariance = 0.0299, 95% HPD: [−0.139, 0.201]; Valerianaceae covariance = 0.0169, 95% HPD: [−0.115, 0.153]). Accordingly, these data are likely to be

Table 3: Temporal constraints used to estimate divergence times for Adoxaceae and Valerianaceae

Taxa and node	Prior distribution	Upper bound	Lower bound	$\bar{x}/\sigma^a$
Adoxaceae:				
1	Lognormal	86.0	46.0	1.1/1.1
2	Lognormal	84.0	45.0	1.1/1.1
Valerianaceae:				
1	Lognormal	25.0	15.0	.0/1.0
2	Lognormal	65.0	45.0	.9/.9

Note: Node numbers correspond to those depicted in figures 3 and 4.

[a] The mean and standard deviation of the lognormal distribution.

ill suited to divergence time estimators that presuppose the phylogenetic autocorrelation of substitution rate variation. We note, however, that the covariance statistic implemented in BEAST may have limited power to detect substitution rate autocorrelation (A. Rambaut, personal communication). For each group, we combined the post-burn-in samples from the 12 independent MCMC analyses to provide a composite posterior of 1.2×10^5 samples. The PSRF values of ~1.0 and large ESS values ($\gg 10^3$) for all parameters for both groups suggest adequate sampling intensity. The composite posterior probability density for Adoxaceae had a mean of −16,887.136 (95% HPD: [−16,915.623, −16,861.762]), and that for Valerianaceae had a mean of −41,688.905 (95% HPD: [−41,724.087, −41,655.125]). The posterior probability density of each group was summarized using TreeAnnotator (ver. 1.4.1; Drummond and Rambaut 2003); the resulting chronograms for Adoxaceae and Valerianaceae (figs. 3, 4, respectively) largely agree with previous studies of divergence times in Dipsacales (e.g., Bell and Donoghue 2005*a*, 2005*b*).

Locating Diversification Rate Shifts

We surveyed the Adoxaceae and Valerianaceae trees for significant shifts in diversification rate using both topological methods (which exploit the topological distribution of species diversity across the tree) and temporal methods (which exploit the temporal distribution of waiting times between branching events).

Relative Cladogenesis Statistic Analyses. The relative cladogenesis statistic relies on temporal information to circumscribe a set of lineages that are of equal age (e.g., Nee et al. 1992, 1996; Purvis et al. 1995). We can arbitrarily draw a line through the tree at some point in the past, t_k, to identify a set of k contemporary ancestral lineages that all survive to the present and collectively give rise to N extant descendants, such that the ith ancestral lineage leaves n_i extant species (where $n_i \geq 1$ and the n_i sum to N). If the k lineages have diversified at the same stochastic rate, then all vectors of descendant species diversities (n_1, n_2, n_3, …, n_k) are equiprobable (e.g., Harding 1971; Chan and Moore 1999, 2002). This expectation can be used to calculate the probability that one of the ancestral lineages will realize more than r descendants, given a total of N species descended from the set of k ancestral lineages. A significant result indicates that the clade in question is anomalously diverse and has therefore diversified under a significantly higher rate than its contemporaries. The relative cladogenesis statistic can be evaluated over the entire duration of the tree (i.e., by integrating t_k over the interval from the first to the last branching event) to assess the probability of a diversification rate shift along all internal branches. The chronograms for Adoxaceae and Valerianaceae were evaluated for significant diversification rate shifts under the relative cladogenesis statistic using End-Epi (Rambaut et al. 1997).

Likelihood Analyses. The likelihood-based diversification rate shift statistics, Δ_i (Moore et al. 2004), are topology-based methods that evaluate the probability of a shift along the lone internal branch of a three-taxon tree comprised of a local outgroup clade and the two basalmost subclades of the local ingroup clade. The probability of a diversification rate shift along the internal branch is returned by a shift statistic, which is calculated as a function of two likelihood ratios. The first likelihood ratio is calculated at the root of the three-taxon tree (involving the diversity partition between the outgroup and ingroup clades), and the other is calculated at the root of the ingroup clade (involving the diversity partition between the left and right ingroup subclades). Each likelihood ratio compares the likelihood of realizing the observed diversity partition under a homogeneous (one-rate parameter) model, in which both groups have the same branching rate, with that under a heterogeneous (two-rate parameter) model, in which the two groups have different branching rates.

In order to address the so-called trickle-down problem—the tendency for a diversification rate shift along a given branch to create illusory shifts at more inclusive nodes in the tree (Moore et al. 2004)—the shift statistic

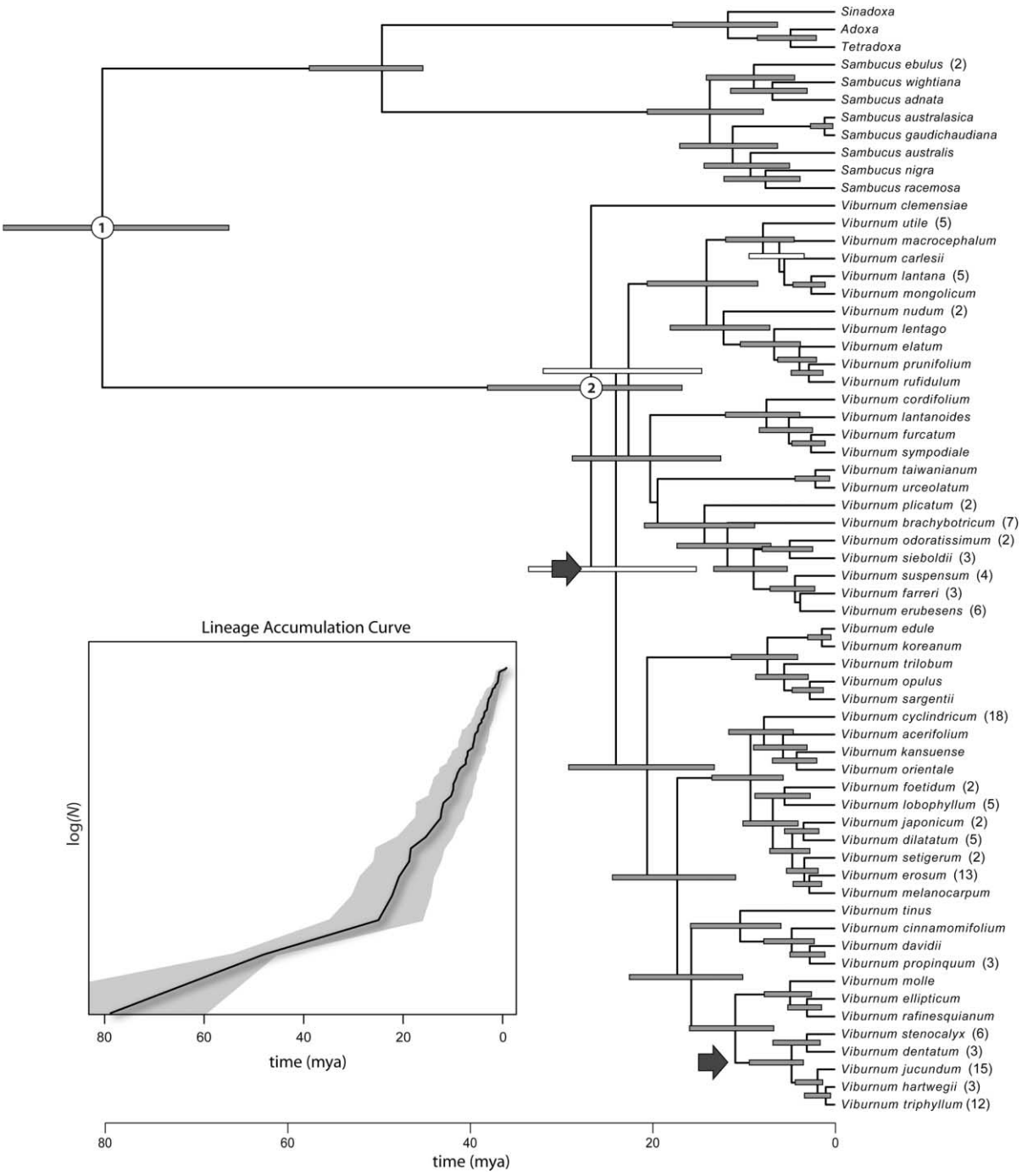


Figure 3: Dated phylogeny for Adoxaceae based on a Bayesian analysis of the combined data set. Uncertainty in the tree topology and divergence times are indicated by bars on internal nodes; their length corresponds to the 95% highest posterior density (HPD) of node ages, and their shading reflects the posterior probabilities of nodes (*shaded bars*, ≥0.90; *open bars*, <0.90). Numbered internal nodes correspond to the fossil constraints used to estimate divergence times (listed in table 3). Arrows adjacent to internal nodes indicate the locations of shifts in diversification rate identified by both the temporal and topological methods. The inset graph depicts the semilogarithmic trace of lineage accumulation through time (i.e., the so-called lineage-through-time plot); the solid line corresponds to the mean of the posterior probability density, and the shaded area reflects the 95% HPD credible region. Numbers in parentheses next to terminal taxa indicate the species diversity of their respective clades.

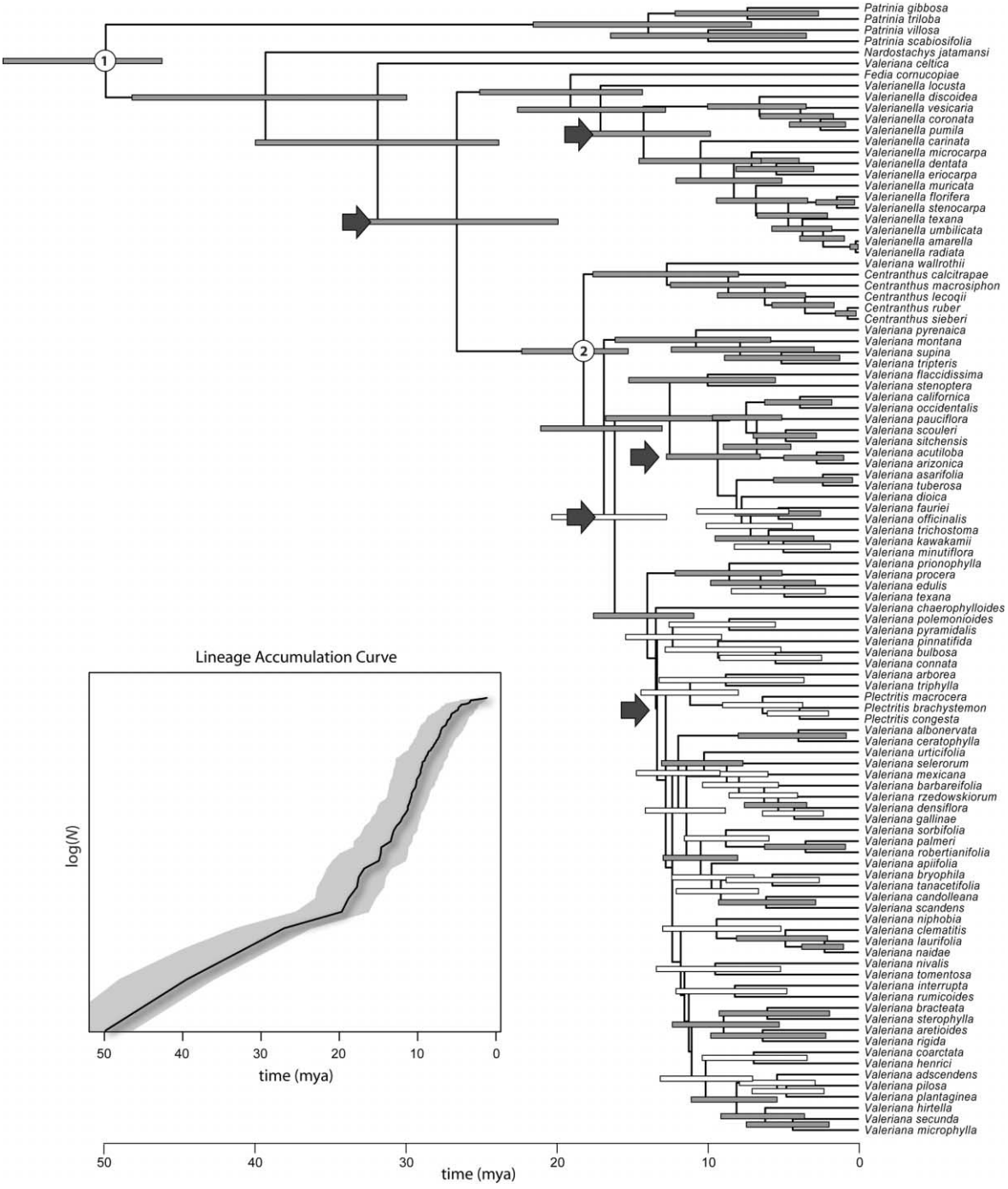


Figure 4: Dated phylogeny for Valerianaceae based on a Bayesian analysis of the combined data set. Uncertainty in the tree topology and divergence times are indicated by bars on internal nodes; their length corresponds to the 95% highest posterior density (HPD) of node ages, and their shading reflects the posterior probabilities of nodes (*shaded bars*, ≥0.90; *open bars*, <0.90). Numbered internal nodes correspond to the fossil constraints used to estimate divergence times (listed in table 3). Arrows adjacent to internal nodes indicate the locations of shifts in diversification rate identified by both the temporal and topological methods. The inset graph depicts the semilogarithmic trace of lineage accumulation through time (i.e., the so-called lineage-through-time plot); the solid line corresponds to the mean of the posterior probability density, and the shaded area reflects the 95% HPD credible region.

conditions the likelihood of a diversification rate shift along the internal branch of the three-taxon tree by the likelihood of a shift within the ingroup clade. Specifically, the Δ_1 diversification rate shift statistic simply takes the difference in the values of the likelihood ratios assessed at the inclusive and nested nodes of the three-taxon tree (i.e., that bracket the internal node under evaluation). These three-taxon evaluations are iterated in a postorder traversal over the tree to effectively survey all internal branches for diversification rate shifts, and significance is assessed by generating a null distribution by Monte Carlo simulation under a pure birth (Yule) stochastic branching process.

Analyses using the Δ_1 shift statistic were performed using SymmeTREE (ver. 1.0; Chan and Moore 2005). The null distribution of the test statistic was approximated by Monte Carlo simulation by generating 10^6 trees equal in size to the study tree (simulated via equal-rates Markov stochastic branching process). Because sampled species in the Adoxaceae phylogeny are placeholders for monophyletic supraspecific taxa, we assessed the influence of incomplete taxon sampling using the taxon substitution approach (Moore and Chan 2005). This entails grafting omitted species to their respective terminal taxa and then evaluating diversification rates over a distribution of random resolutions of the resulting terminal polytomies. Specifically, we assessed uncertainty associated with the resulting terminal polytomies by generating 10^6 random resolutions under all three taxon addition algorithms (i.e., proportional-to-distinguishable arrangements, and size-insensitive and size-sensitive ERM taxon addition algorithms; Moore and Chan 2005), providing the upper and lower bounds on the confidence interval on inferred diversification rate shifts. Although taxon sampling for Valerianaceae is similarly incomplete, uncertainty regarding the distribution of unsampled species among the tips precluded use of the taxon substitution approach.

Results. A total of seven significant diversification rate shifts were identified by both the temporal and topological methods, including two shifts in Adoxaceae and five shifts in Valerianaceae (figs. 3, 4, respectively). Although the two methods identified identical diversification rate shifts in Adoxaceae, the Δ_1 statistic identified a subset of the shifts inferred by the relative cladogenesis statistic in Valerianaceae. Specifically, the relative cladogenesis statistic inferred a cascade of shifts along the backbone of the Valerianaceae tree (i.e., along all adjacent internal nodes from the root of the tree to the lowermost arrow depicted in fig. 4). However, all but three of these shifts appear to be artifacts of the trickle-down effect (Moore et al. 2004). Accordingly, we focus only on those diversification rate shifts identified by both methods.

Evaluating Patterns of Morphological Evolution and Correlations with Diversification Rate

To explore the relationship between morphological evolution and diversification rates in Adoxaceae and Valerianaceae, we evaluated several traits that represent plausible key innovations in these groups. We first briefly discuss our choice of traits and then describe the analyses used to infer the history and estimate the correlation of these traits with rates of diversification.

Selection of Putative Evolutionary Novelties. Previous studies have posited several putative key innovations of flowering plants, largely related to floral morphology, growth form, and fruit type/dispersal mechanism. For example, novel floral morphologies have been hypothesized to increase the probability of speciation by enhancing pollinator fidelity, which may confer increased population structure on the affected plant populations and promote their exposure to novel selection pressures associated with pollinator preference (e.g., Hodges and Arnold 1994*a*, 1994*b*, 1995; Hodges 1997; Waser 1998; Sargent 2004; Ree 2005). Similarly, novel fruit types have been proposed to enhance opportunities for dispersal, which may foster the foundation of small isolated populations in new areas that rapidly diverge in response to novel selection pressures and/or the stochastic effects of genetic drift (e.g., Herrara 1989; Eriksson and Bremer 1991, 1992; Dodd et al. 1999; Schemske and Bradshaw 1999; Smith 2001). On the basis of this literature and the availability of relevant morphological variation in the two study groups, we selected a total of nine discrete morphological traits as putative key innovations. Specifically, we examined five traits in Adoxaceae—(1) growth form (woody/herbaceous), (2) fruit color at maturity (purple/red), (3) fruit type (>1 seed/1 seed), (4) inflorescence form (umbel/panicle), and (5) enlarged sterile flowers (absent/present)—and four traits in Valerianaceae—(6) stamen number (even/odd), (7) fruit type (not plumose/plumose), (8) anther lobe number (four/two), and (9) nectar spurs (absent/present).

Inferring Patterns of Morphological Evolution. The evolutionary histories of the various traits in Adoxaceae and Valerianaceae were inferred by estimating the marginal posterior probability of ancestral states under a Bayesian model-averaging approach (Pagel et al. 2004; Pagel and Meade 2006). Like other methods based on stochastic mutational mapping (e.g., Huelsenbeck and Bollback 2001; Nielsen 2002; Huelsenbeck et al. 2003), this is a fully hierarchical Bayesian approach for inferring ancestral character states that exploits MCMC sampling to integrate over uncertainty in the phylogeny and parameters of a stochastic model of trait evolution. However, rather than con-

ditioning inferences on a specific model of trait evolution, the approach developed by Pagel and Meade (2006) uses reversible jump (RJ) MCMC to integrate over the set of plausible models (see also Huelsenbeck et al. 2004). The evolution of binary traits (i.e., discrete characters that occur in one of two states, *i* and *j*) invokes five continuous-time Markov models that differ with respect to the parameters describing the instantaneous rate of change between states, q_{ij} and q_{ji}. These include three one-rate parameter models: the first, *00*, constrains the rate of forward and backward change to be equal (i.e., $q_{ij} = q_{ji}$; equivalent to the *Mk*1 model described in Lewis 2001); the other two one-rate models, *Z0* and *0Z*, constrain the forward or backward rate to be zero (i.e., $q_{ij} = 0$ $q_{ji} > 0$ and $q_{ij} > 0$ $q_{ji} = 0$, respectively). The two-rate parameter models allow an asymmetry in the rate of forward and backward change: the *10* model assumes a higher rate of forward change (i.e., $q_{ij} > q_{ji}$), whereas the *01* model assumes an opposite bias in rate (i.e., change; i.e., $q_{ij} < q_{ji}$). At stationarity, these five models will be visited by the RJ chain in proportion to their posterior probabilities, effectively selecting among (or averaging over) the models of trait evolution while simultaneously accommodating uncertainty in the phylogeny and rate parameters of the models.

Ancestral states were estimated using BayesTraits (ver. 1.0; Pagel and Meade 2007). Posterior probabilities of rate coefficients and ancestral states for each of the nine traits were estimated individually using the posterior probability distributions of phylogenies for Adoxaceae and Valerianaceae. Inferences were integrated over the composite post-burn-in sample of trees, which were thinned to reduce the autocorrelation of successive samples: 10^3 trees were drawn from the distribution of 1.2×10^5 trees, which equates to sampling every ~120,000th generation of the chains used in the phylogenetic analyses. Ancestral states for nodes with posterior probabilities <1.0 were estimated using the MRCA approach (Pagel et al. 2004). We used a uniform prior on models of trait evolution and an exponential prior on the rate coefficients. Because there is little information on the mean of the exponential prior, we chose to seed this parameter from a uniform hyperprior, which allows the values of the prior to be estimated from the data. Nevertheless, a range for the uniform hyperprior must be specified, for which we adopted an "empirical hyperprior" approach. Specifically, we used BayesMultistate (Pagel and Meade 2007) to estimate the rate coefficients for each of the nine traits on each of the 10^3 trees under maximum likelihood. The maximum likelihood parameter estimates of the rate coefficients for each trait were used to inform the range of the respective hyperprior. To ensure adequate mixing, we ran a series of preliminary chains for each trait, iteratively adjusting the magnitude of the rate coefficient proposals (i.e., the value of the "ratedev" parameter) until acceptance rates achieved 20%–40%. We then ran two independent RJ MCMC analyses for each trait. Convergence of each chain to the target distribution was inferred by plotting time series of the marginal posterior probability of sampled parameter values using Tracer (ver. 1.3; Rambaut and Drummond 2003). After achieving convergence, each chain was sampled every 10^4 steps until 10^4 samples were obtained, and the adequacy of sampling intensity was assessed by means of the ESS diagnostic.

Typically, inferences of ancestral states are made from molecular phylogenies in which the branch lengths are proportional to the expected number of substitutions per site. This approach implicitly assumes that the rate of trait evolution is proportional to the rate of sequence evolution, an assumption that has received little empirical scrutiny (but see Omland 1997 and Bromham et al. 2002 for contradictory results). Accordingly, we repeated the series of analyses described above using the posterior probability distribution of chronograms for Adoxaceae and Valerianaceae to explore the implications of an explicitly gradualistic model in which rates of morphological evolution are assumed to be proportional to absolute time.

Evaluating Correlations between Morphological Evolution and Diversification Rate. We evaluated the correlation between changes in the selected morphological traits and diversification rates using a Bayesian method for testing key innovations (Ree 2005). This method works as follows: given a tree with estimated divergence times and observed states of a binary trait across its tips (with states *i* and *j*), a character history is generated by means of stochastic mapping. In essence, this procedure uses the *Mk*1 model of character evolution to paint segments of the study tree according to the inferred character states. The diversification rate, λ, of the lineages with each character state is simply calculated as the number of branching events, *n*, that occurred in the part of the tree inferred to be in a given state divided by the duration of time spent in that state; for example, $\lambda_i = n_i/t_i$. The difference in diversification rate under the two state-specific rates is given by $\Delta = \lambda_i - \lambda_j$. To accommodate for uncertainty in the estimate of character evolution, this process is repeated many times, and the average of the resulting Δ values provides the test statistic, $\bar{\Delta}$. The value of the test statistic is compared with a null distribution that is generated by Monte Carlo simulation as follows: the topology of the study tree is held constant, while divergence times are sampled from a constant-rate, pure birth stochastic branching (Yule) process. The $\bar{\Delta}$ statistic is calculated for each simulated tree, and the values from the set of simulated trees collectively comprise the null distribution against which the

observed value is compared to determine its cumulative probability (i.e., the posterior predictive *P* value).

Analyses of the correlation between each of the selected traits and diversification rate were performed using keymap (ver. 0.1; Smith 2006*b*; implements the method of Ree 2005) and were conditioned on the majority rule consensus chronograms for Adoxaceae and Valerianaceae (figs. 3, 4, respectively). For each of the nine traits, the observed value of the $\bar{\Delta}$ statistic was estimated as the average of 10^4 stochastic mappings, and the null distribution was approximated by generating a sample of 10^5 simulated chronograms that were derived by perturbing branching times in each study tree using a pure birth Yule stochastic branching process. For each simulated tree, the value of the statistic was estimated as the average of 10^4 stochastic mappings.

Results. The inferred phylogenetic histories of the various traits in Adoxaceae and Valerianaceae are depicted in figures 5 and 6, respectively, and the corresponding marginal log likelihoods and posterior probabilities of parameter estimates are summarized in table 4. In general, estimates based on the posterior probability distributions of chronograms and phylograms were quite similar, which reflects the fact that the former are effectively a UCLN transformation of the latter (i.e., both are ultimately derived from a common set of branch length estimates). However, the two sets of inferences differed in consistent ways. For example, rate coefficients estimated from the posterior probability distribution of phylograms tended to exceed those based on chronograms (table 4). This stems from the differential scale of the two sets of branch lengths/durations: continuous-time Markov models allow multiple changes per branch and so will adopt higher rates when branches are relatively short and changes across branches are implied (e.g., Pagel 1994). As a consequence of these higher rate estimates, inferences based on phylograms tended to be associated with greater uncertainty. Finally, posterior probabilities under various models suggest that the *00* (i.e., *Mk*1) model is inappropriate for several of the traits under consideration.

Visual comparison of the estimated locations of character state change to the inferred locations of diversification rate shifts suggests that morphological evolution and diversification rate are largely decoupled in Adoxaceae and Valerianaceae. These impressions are corroborated by the tests of correlation between these traits and diversification rate: none of the five traits in Adoxaceae are inferred to be significantly correlated with diversification rate, and only stamen number in Valerianaceae is inferred to exhibit a significant correlation with diversification rate (figs. 5, 6, respectively). The behavior of the key innovation test (Ree 2005) is presently unclear, since simulation studies have not yet characterized its statistical properties. We note that this test assumes that traits evolved under the *Mk*1 model of character evolution, which is evidently inappropriate for several of the traits evaluated in this study (table 4). We comment further on the behavior of this method in the "Discussion."

Identifying Geographic Dispersal Events

To evaluate the influence of movement between geographic areas on rates of diversification in Adoxaceae and Valerianaceae, we estimated the biogeographic history of each group using recently developed likelihood methods. We first briefly describe this approach and then detail how we parameterized the biogeographic model for the present analysis.

Likelihood Estimation of Biogeographic History. To locate dispersal events in Adoxaceae and Valerianaceae, we used a likelihood approach (Ree et al. 2005; Moore et al. 2007) for inferring the evolution of geographic range that models the persistence, dispersal, and extinction of lineages through time. The objective of this method is to identify the biogeographic history that maximizes the likelihood of realizing the observed geographic distributions of extant and fossil taxa under the specified biogeographic model. Biogeographic history here refers to both the set of ancestral areas and the scenarios by which those ranges are subdivided during speciation and subsequently inherited by descendant species. The biogeographic model comprises two main components. The phylogenetic component specifies the tree topology, the vector of branches with estimated durations/divergence times, and the intrinsic probabilities of lineage dispersal between areas and extinction within an area. The paleogeographic component includes the set of areas that encompass the ranges of the study species and their ancestors, the set of pairwise connections between those areas, and the corresponding set of dispersal functions that specify the probability of successful migration across each connection through time. Our analysis is based on an extension of this likelihood method that incorporates information on the spatial and temporal occurrence of lineages in the fossil record (Moore et al. 2007).

Parameterization of the Biogeographic Model. The biogeographic model for Adoxaceae and Valerianaceae comprises six areas (fig. 7): eastern Asia (EAS), Europe (EUR), Australia (AUS), eastern North America (ENA), western North America (WNA), and Latin America (LAM). There are six corresponding connections between these areas: the Bering land bridge (BLB) links WNA to EAS, the North Atlantic land bridge (NALB) links ENA to EUR, the Meso-

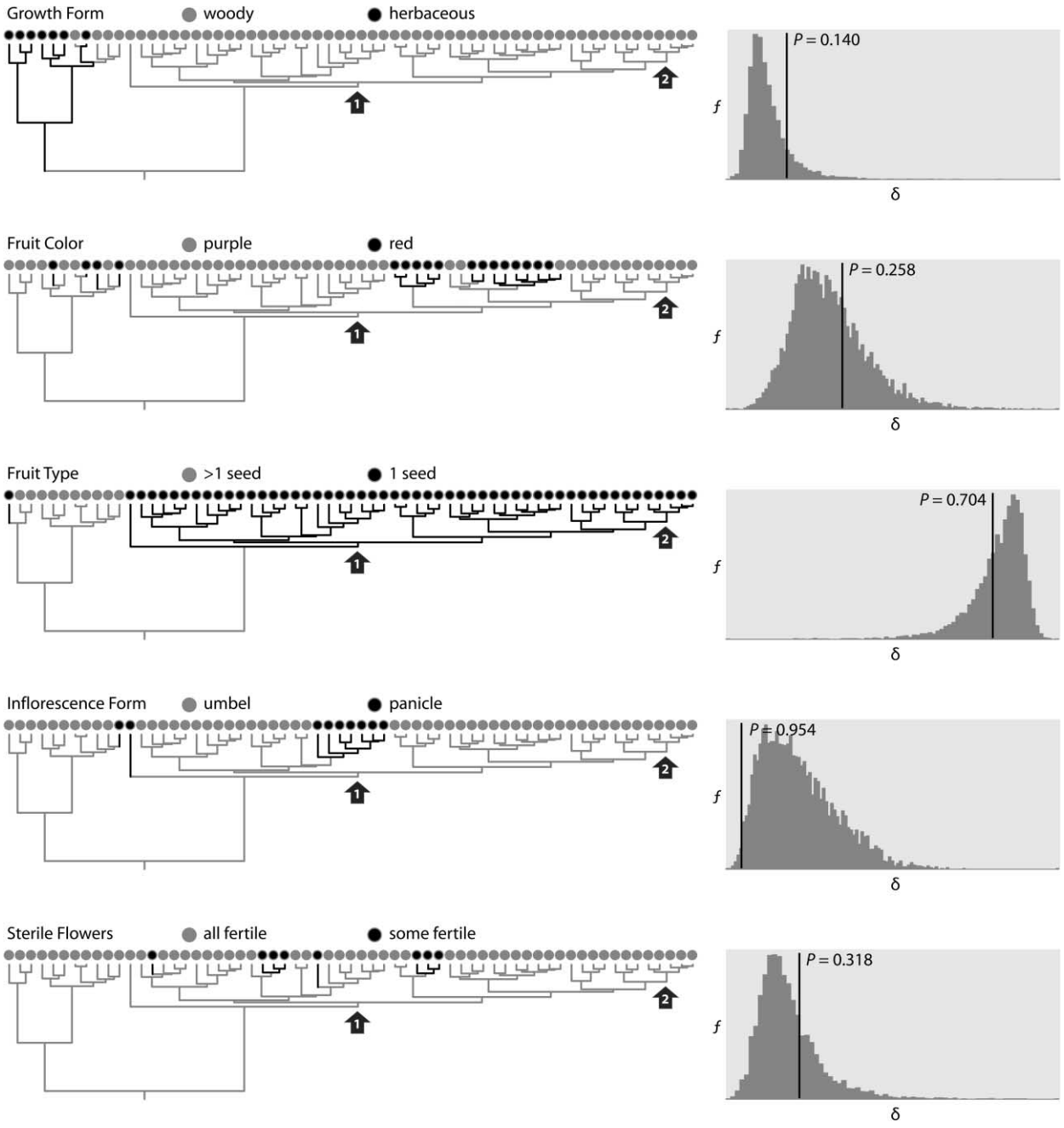
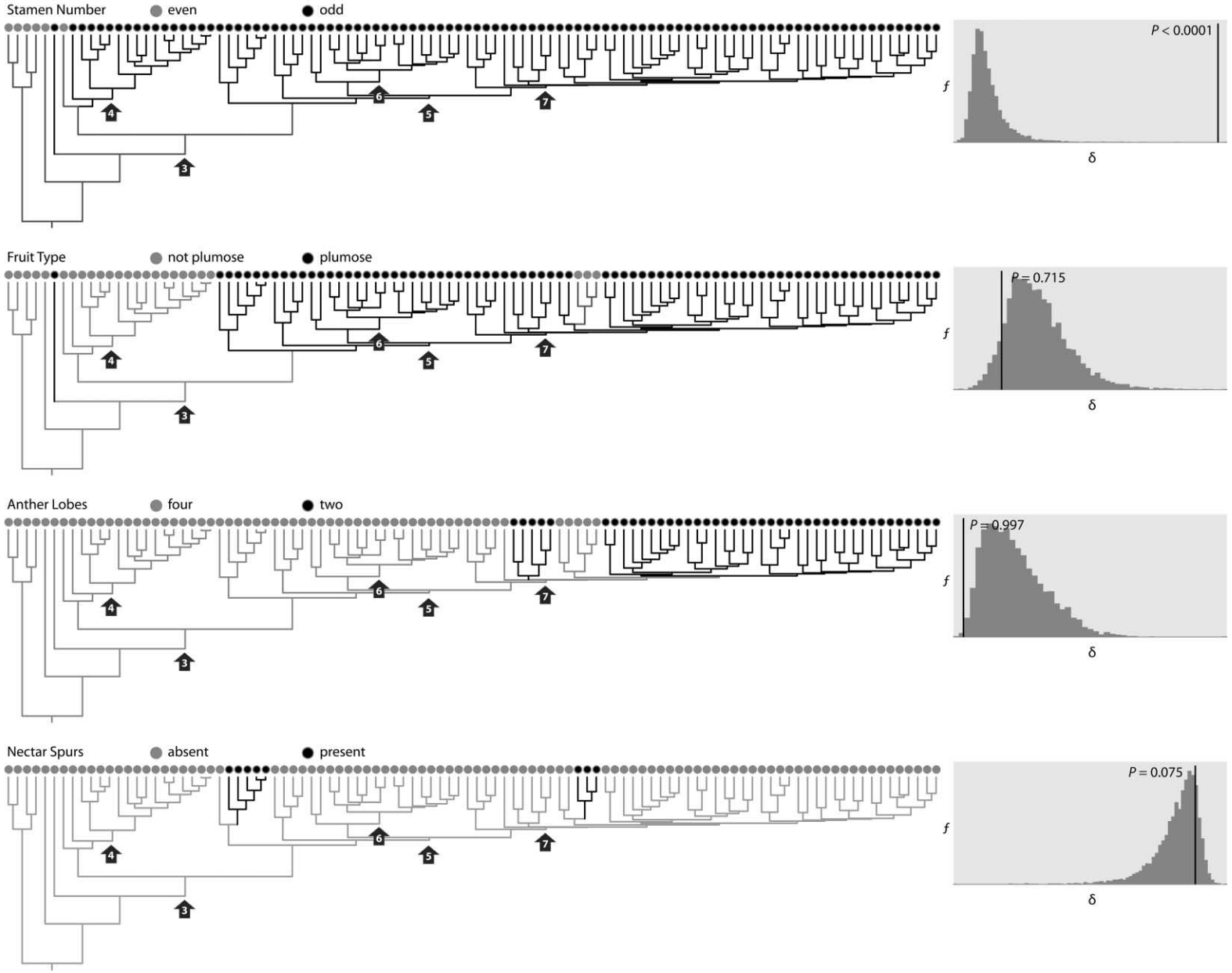


Figure 5: Estimates of the evolution of five morphological traits and their correlation with diversification rates in Adoxaceae. The tree topology and divergence times are identical to those depicted in figure 3, but the species names have been removed for clarity. Circles adjacent to the tips of each tree are shaded to indicate the observed states of the respective species, and branches of the tree have been shaded to correspond to the posterior probability estimates for ancestral states. Arrows adjacent to internal nodes indicate the inferred locations of shifts in diversification rate, with numbers that correspond to discussion of these events in the text. The graphs to the right of each tree summarize the inferred correlation between diversification rate and the corresponding character history; each histogram depicts the null distribution of the test statistic, $\bar{\Delta}$; the vertical line indicates the observed value of the test statistic, with the corresponding posterior-predictive probability. These tests indicate that none of the five traits examined are significantly correlated with diversification rate.


Stamen Number
even
odd
4
3
6
5
7
P < 0.0001
f
δ
Fruit Type
not plumose
plumose
4
3
6
5
7
P = 0.715
f
δ
Anther Lobes
four
two
4
3
6
5
7
P = 0.997
f
δ
Nectar Spurs
absent
present
4
3
6
5
7
P = 0.075
f
δ

american connection links ENA and WNA to LAM, the Indo-Pacific connection links EAS to AUS, and two intracontinental connections link ENA to WNA within North America and EAS to EUR within Eurasia. Dispersal functions specifying the probability of successful migration across each connection are primarily based on the synthesis of paleogeographical and paleoclimatological evidence presented by Tiffney and Manchester (2001). Specifically, the probability of dispersal success at any given time is given by the unweighted average of three factors: physical connection, precipitation, and temperature. However, our parameterization of the BLB deviates slightly from that by Tiffney and Manchester (2001) in that we specify a nonzero probability ($P = .1$) of successful dispersal across this connection over the last ~5 million years (from the Pliocene onward). Although not discernible within the granularity of their study, we allow for the possibility that this generally unfavorable period was interrupted by geologically brief episodes (on the order of 1,000 years) in which conditions were favorable to dispersal across the BLB. Because Tiffney and Manchester (2001) restricted their consideration to connections within the Northern Hemisphere, we based our parameterization of connections between the Northern and Southern Hemispheres on the paleogeographic reconstructions of Scotese (2001). The probability of successful migration across all six connections was assumed to be independent of direction (i.e., the dispersal functions are symmetric).

Episodes of biogeographic movement in Adoxaceae and Valerianaceae were inferred using AReA (ver. 2.1; Smith 2006*a*). The most likely dispersal scenarios at all internal nodes of the study phylogenies were estimated using the maximum likelihood estimates for lineage dispersal and extinction parameters and the branch-specific geographic range transition probability matrices that were approximated via Monte Carlo simulation using 10^5 simulations/matrix (Ree et al. 2005; Moore et al. 2007).

Results. A total of 23 episodes of biogeographic dispersal were inferred, including 14 in Adoxaceae and nine in Valerianaceae (figs. 8, 9, respectively). The maximum likelihood estimates for Adoxaceae ($\ln L = -155.064$) and Valerianaceae ($\ln L = -165.361$) were obtained under equal rates of dispersal and extinction (values for both parameters = 0.1). Biogeographic diagrams adjacent to internal nodes depict the details of the dispersal event inferred to have occurred along the corresponding branch (figs. 8, 9). The DIVA analyses (Ronquist 1996, 1997) inferred 24 and 12 dispersal events for Adoxaceae and Valerianaceae, respectively (results not shown). The differences in these results apparently reflect the fact that DIVA does not incorporate information on divergence times (Donoghue and Moore 2003), paleogeography (Ree et al. 2005), or the fossil record (Moore et al. 2007). Visual comparison suggests that several of the inferred locations of dispersal events coincide with the inferred locations of diversification rate shifts (see "Discussion"). In Adoxaceae, one of the two rate shifts coincides closely with biogeographic movement from ENA into LAM (fig. 8). In Valerianaceae, two of the five significant diversification rate shifts coincide with episodes of biogeographic dispersal: one from EUR to EAS and one from EAS to WNA. We note that the inferred dispersal event from EUR to ENA also coincides with a diversification rate shift inferred to be significant under the relative cladogenesis statistic but not under the Δ likelihood diversification rate shift statistic (fig. 9).

Discussion

Our findings reveal a complex pattern of morphological evolution, biogeographic movement, and shifts in diversification rate in Adoxaceae and Valerianaceae. The seven significant diversification rate shifts identified in these groups can be assigned to the cells of the cube model (fig. 1) as follows: three shifts correspond to a dispersification scenario, and the four remaining shifts could not be attributed to either morphological or biogeographic changes. We found no diversification rate shifts to be directly correlated with a morphological change (key innovation). We first briefly discuss each of these seven diversification rate shifts, presented in order of their corresponding numbers in figures 5 and 8 (shifts 1 and 2 in Adoxaceae) and figures 6 and 9 (shifts 3–7 in Valerianaceae). We then consider the more general implications of our results for studies of diversification and conclude with some thoughts on how

Figure 6: Estimates of the evolution of four morphological traits and their correlation with diversification rates in Valerianaceae. The tree topology and divergence times are identical to those depicted in figure 4, but the species names have been removed for clarity. Circles adjacent to the tips of each tree are shaded to indicate the observed states of the respective species, and branches of the tree have been shaded to correspond to the posterior probability estimates for ancestral states. Arrows adjacent to internal nodes indicate the inferred locations of shifts in diversification rate, with numbers that correspond to discussion of these events in the text. The graphs to the right of each tree summarize the inferred correlation between diversification rate and the corresponding character history; each histogram depicts the null distribution of the test statistic, $\bar{\Delta}$; the vertical line indicates the observed value of the test statistic, with the corresponding posterior-predictive probability. These tests indicate that only the first trait, stamen number, is significantly correlated with diversification rate.

Table 4: Bayesian inference of trait evolution and model parameters in Adoxaceae and Valerianaceae by reversible jump Markov chain Monte Carlo

Taxa and trait	ln(*L*)[a]	Pr(q_{01}) $\bar{x}/\sigma$[b]	Pr(q_{10}) $\bar{x}/\sigma$[c]	Pr(model)[d]				
				0Z	*01*	*00*	*10*	*Z0*
Adoxaceae:								
Growth form:								
Phylograms	−10.290	.055/.354	3.831/.011	.00	.00	.03	.00	.97
Chronograms	−11.621	.065/.3470	3.483/.015	.00	.00	.01	.00	.99
Fruit color:								
Phylograms	−45.221	9.444/2.945	9.443/.011	.00	.00	1.00	.00	.00
Chronograms	−38.828	.581/.546	1.095/.011	.00	.34	.34	.33	.00
Fruit type:								
Phylograms	−6.160	1.975/1.300	.143/.011	.85	.00	.15	.00	.00
Chronograms	−6.124	.014/.009	.0004/.011	.94	.00	.06	.00	.00
Inflorescence form:								
Phylograms	−35.579	5.358/2.242	10.186/.011	.02	.12	.74	.12	.00
Chronograms	−25.972	.293/.213	1.561/.011	.00	.40	.00	.60	.00
Sterile marginal flowers:								
Phylograms	−28.019	5.866/3.812	12.611/.011	.06	.12	.68	.12	.01
Chronograms	−25.516	.073/.077	.393/.011	.05	.31	.31	.32	.01
Valerianaceae:								
Stamen number:								
Phylograms	−9.182	5.686/4.640	.340/.584	.65	.00	.33	.00	.01
Chronograms	−9.357	.094/.070	.005/.011	.75	.00	.17	.00	.07
Fruit type:								
Phylograms	−12.767	1.277/.790	1.399/.755	.00	.00	.93	.00	.06
Chronograms	−11.556	.055/.063	.017/.011	.00	.00	.70	.00	.30
Anther lobes:								
Phylograms	−9.440	.016/.305	.999/.0003	.66	.00	.47	.00	.00
Chronograms	−9.950	.055/.063	.005/.011	.69	.00	.30	.00	.00
Nectar spurs:								
Phylograms	−10.723	.479/.698	.999/.002	.52	.00	.47	.00	.00
Chronograms	−10.672	.055/.063	2.374/.011	.49	.00	.48	.00	.02

Note: Values in the table reflect estimates based on the averaging over the posterior probability density of phylograms or chronograms.

[a] Marginal log likelihood.

[b] The mean and standard deviation of the marginal posterior probability distribution for the instantaneous rate of forward change integrated over all models.

[c] The mean and standard deviation of the marginal posterior probability distribution for the instantaneous rate of backward change integrated over all models.

[d] Posterior probability of models of trait evolution sampled by the RJ MCMC; model abbreviations described in the text.

the study of geographic patterns of species richness might benefit from the adoption of an explicitly historical perspective.

Biogeographic and Morphological Correlates of Diversification in Dipsacales

Shift 1. The diversification rate shift inferred near the root of *Viburnum* has no clear morphological or biogeographic correlates, and so it is assigned to cell 1 of the cube model (fig. 1). We note, however, that the location of this shift occurs in close proximity to one of the two independent origins of single-seeded fruits in Adoxaceae (the evolution of a drupe fruit type in *Viburnum*; fig. 5). Furthermore, there may be a hidden biogeographic correlate, namely, the possible movement of *Viburnum* from Southeast Asia (*Viburnum clemensiae* is endemic to Borneo) northward into more temperate Asia and subsequently around the Northern Hemisphere (Winkworth and Donoghue 2005). This dispersal event is not evident in our scoring of biogeographic areas, in which Southeast Asia and temperate Asia were both coded as East Asia (EAS). Ultimately, however, any such interpretation rests on the precise phylogenetic placement of *V. clemensiae*, which is not yet well established (fig. 3).

Shift 2. The second significant diversification rate shift in

Adoxaceae occurs independently of a change in any of the traits evaluated here (or, in fact, of any morphological trait known to us). Intriguingly, *Viburnum dentatum*, the eastern North American member of this diverse clade, is known to be a polyploid (tetraploid with 36 chromosomes but occasionally with 72; Egolf 1962), and there is evidence that the Latin American species are also tetraploids (Donoghue 1982; Winkworth and Donoghue 2004). It is possible, therefore, that this shift in diversification rate is correlated with an origin of polyploidy. In any case, however, this rate shift corresponds quite directly to movement from North America into the mountains of Latin America (fig. 8) and so appears to represent a case of dispersification (assigned to cell 3 of fig. 1). This appears to be a rapid recent radiation marked by considerable morphological differentiation (e.g., in plant and leaf size, pubescence, and several fruit characteristics; Donoghue 1982) but with little corresponding molecular divergence (Winkworth and Donoghue 2005; M. J. Donoghue, personal observation). For the most part, the Latin American species are also characterized by relatively narrow geographic ranges along separate mountain ranges, implying that diversification in this group has been driven by allopatric speciation (Donoghue 1982).

Shift 3. The diversification rate shift inferred near the root

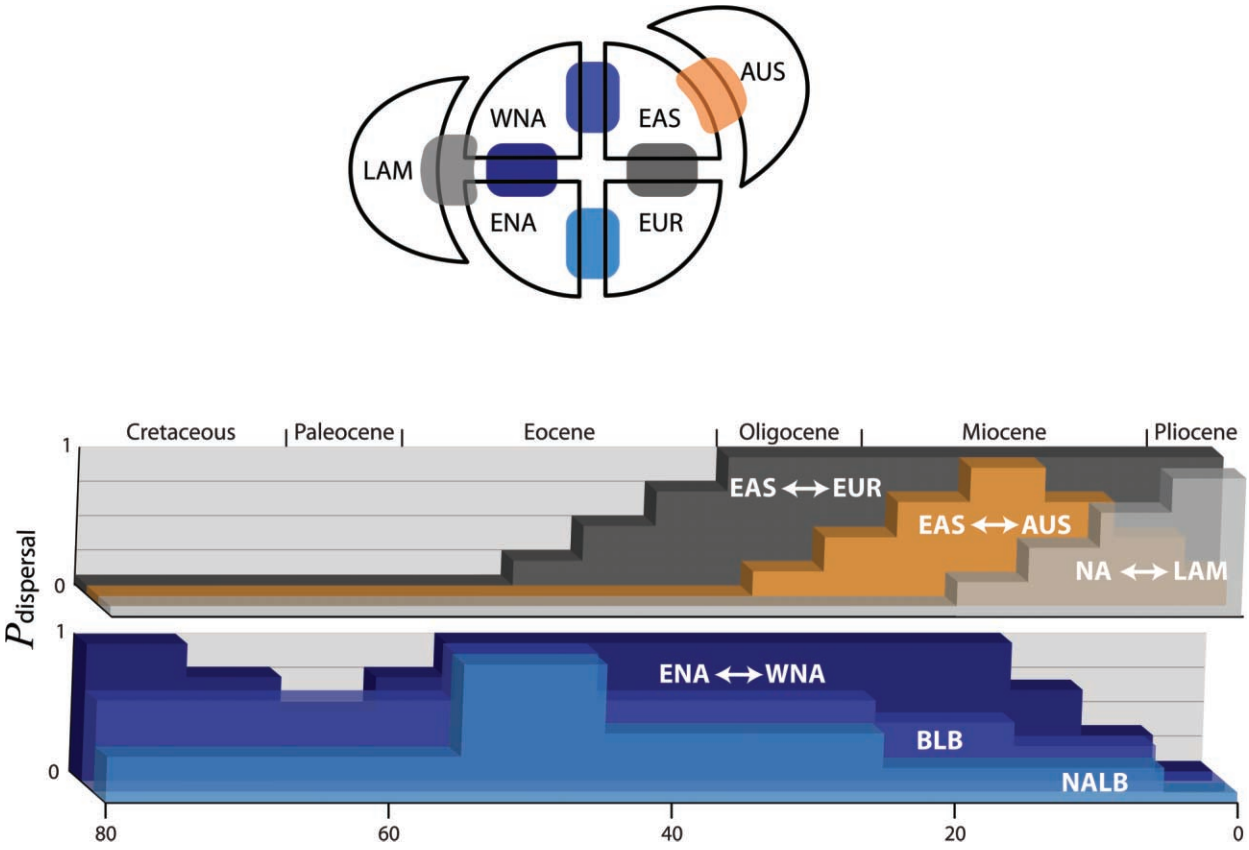


Figure 7: Biogeographic model used to infer episodes of dispersal in Adoxaceae and Valerianaceae. The model comprises six areas: eastern Asia (EAS), Europe (EUR), eastern North America (ENA), western North America (WNA), Latin America (LAM), and Australia (AUS). There are six corresponding connections between these areas: the Bering land bridge (BLB; linking WNA and EAS), the North Atlantic land bridge (NALB; linking ENA and EUR), the Mesoamerican connection (linking North America to LAM), the Indo-Pacific connection (linking EAS and AUS), and two intracontinental links (within North America and Eurasia). The probability of dispersal success across each connection is plotted through time and is symmetrical with respect to direction. Essentially, this biogeographic model specifies the probability that a given lineage will move from one area to another by conditioning the intrinsic rates of lineage dispersal and extinction. For example, paleogeological and paleoclimatic information collectively specifies the probability of dispersal across the NALB connection at various times in the past (the dispersal function depicted in light blue), which influences the probability of a dispersal event between ENA and EUR (across the corresponding light blue connection in the area model). Accordingly, this model suggests that dispersal across this connection was more likely during the mid-Eocene (~50–40 Mya) than during the Pliocene (in the last ~5 million years). Abbreviations: NH = Northern Hemisphere (i.e., EUR + EAS + WNA + ENA); NA = North America (i.e., WNA + ENA).

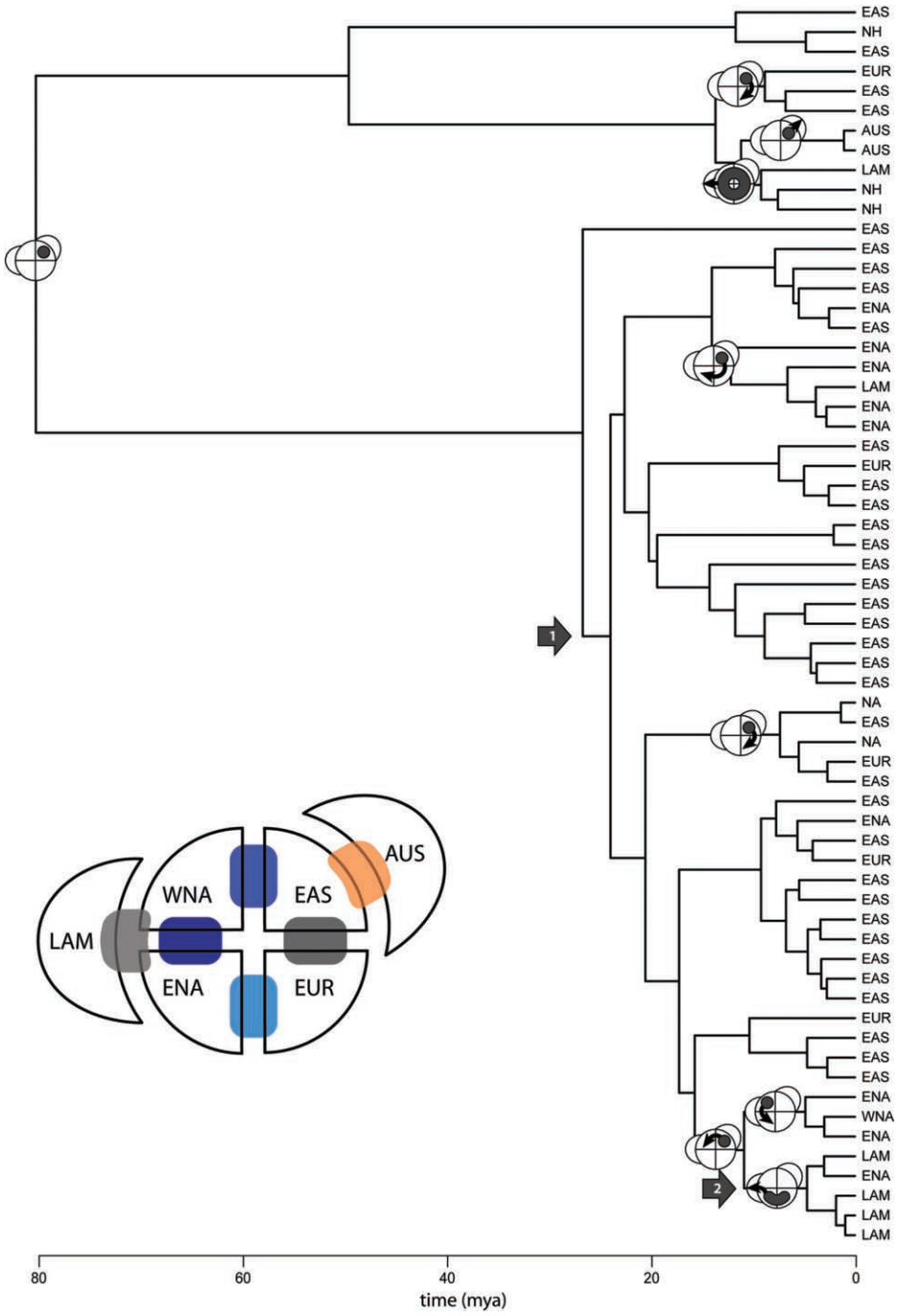


Figure 8: Likelihood inference of biogeographic movement (i.e., dispersal events) in Adoxaceae. The tree topology and divergence times are identical to those depicted in figure 3. Observed species ranges are indicated across the tips of the tree, and the historical relationships among these areas are indicated by the inset biogeographic model (detailed in fig. 7). The maximum likelihood estimate ($\ln L = -155.064$) was obtained under equal rates of dispersal and extinction (both parameters 0.1). Each episode of dispersal is depicted by a biogeographic diagram adjacent to the corresponding internal branch (for clarity, six dispersal events inferred along terminal nodes have been omitted). The inferred biogeographic history of Adoxaceae indicates an origin in EAS and 14 episodes of dispersal, including several among areas in the Northern Hemisphere, one movement into AUS, and two dispersals into LAM. Arrows adjacent to internal nodes indicate the inferred locations of shifts in diversification rate, with numbers that correspond to discussion of these events in the text. Details of the biogeographic model and abbreviations are as described in figure 7.

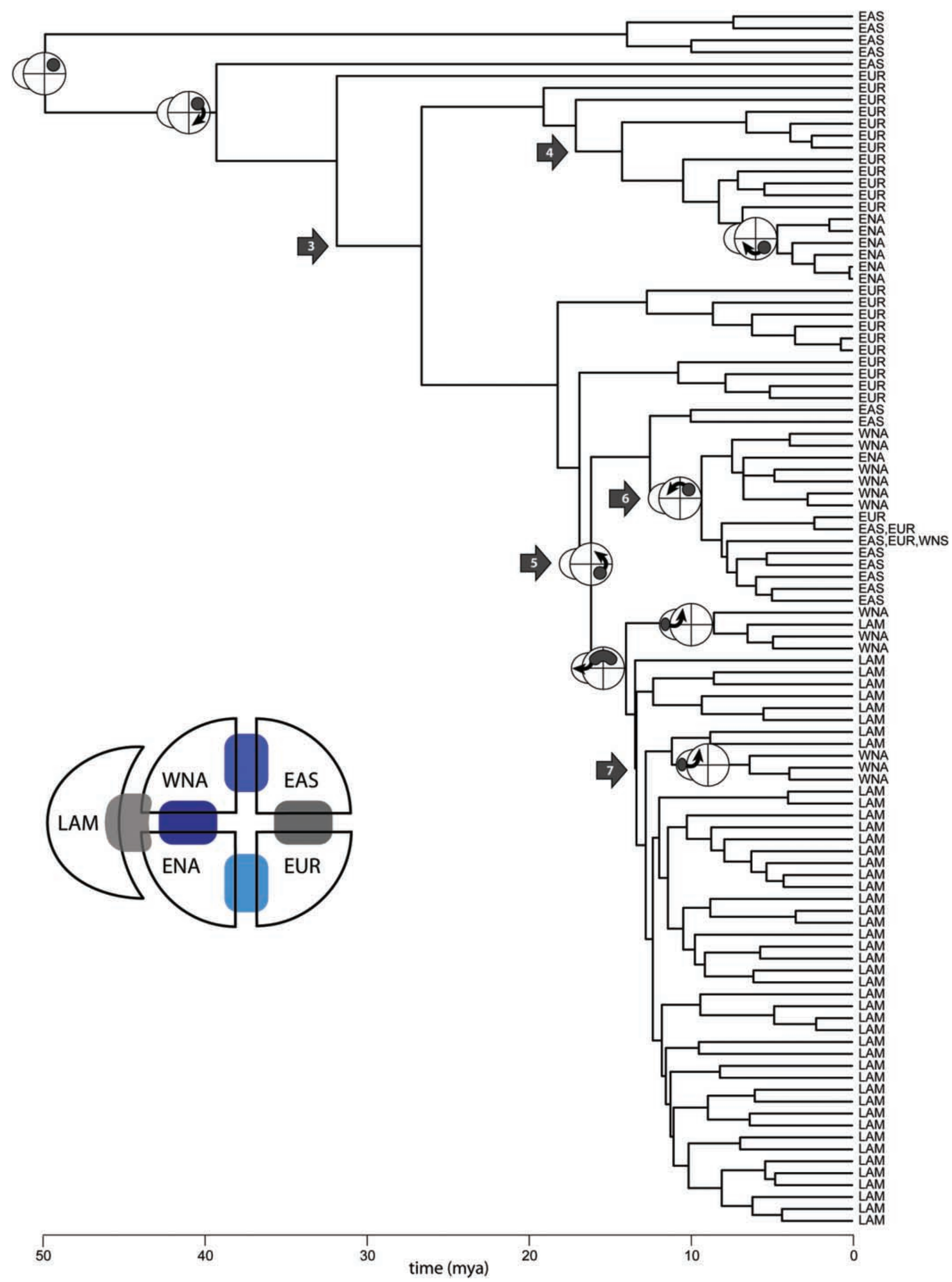


Figure 9: Likelihood inference of biogeographic movement (i.e., dispersal events) in Valerianaceae. The tree topology and divergence times are identical to those depicted in figure 4. Observed species ranges are indicated across the tips of the tree, and the historical relationships among these areas are indicated by the inset biogeographic model (detailed in fig. 7). The maximum likelihood estimate ($\ln L = -165.361$) was obtained under equal rates of dispersal and extinction (both parameters 0.1). Each episode of dispersal is depicted by a biogeographic diagram adjacent to the corresponding internal branch (for clarity, two dispersal events inferred along terminal nodes have been omitted). The inferred biogeographic history of Valerianaceae indicates an origin in EAS, with four dispersal events among areas in the Northern Hemisphere, one dispersal into LAM, and two dispersal events back into WNA. Arrows adjacent to internal nodes indicate the inferred locations of shifts in diversification rate, with numbers that correspond to discussion of these events in the text. Details of the biogeographic model and abbreviations are as described in figure 7.

of Valerianaceae has no direct correspondence with a change in morphology or biogeography; however, there are close calls in both categories. Morphologically, the distribution of species with an odd number of stamens (and therefore asymmetrical flowers) spans the node associated with the diversification rate shift (fig. 6). However, the inferred evolution of this trait suggests that it arose independently in three descendant lineages. From a biogeographic standpoint, the diversification rate shift appears to have occurred soon after the inferred movement of Valerianaceae out of Asia into Europe (fig. 9). Nevertheless, it is most conservative to assign this rate shift to cell 1 of the cube in figure 1.

Shift 4. This shift in diversification rate is inferred to have occurred shortly after the probable reduction in stamen number (and hence the origin of asymmetric flowers) that marked the evolution of *Valerianella* (fig. 6). It does not appear to be associated with a geographic movement. Although it is tempting to argue that the stamen character may have influenced diversification, we conservatively assign this scenario to cell 1 in figure 1.

Shift 5. This diversification rate shift may represent another instance of dispersification, since it coincides directly with an inferred dispersal from Europe back into Asia (fig. 9). However, it also occurs in rather close proximity to two morphological changes (fig. 6): one of the origins of plumose fruits (wind dispersal) and one of the origins of an odd number of stamens (especially the presence of asymmetric flowers with three stamens in *Valeriana*, as compared with asymmetric flowers with just one stamen in *Centranthus*; Donoghue et al. 2003). We assign this case to cell 3 in figure 1.

Shift 6. This shift does not appear to be correlated with any morphological change, but it coincides directly with a geographic movement from Asia into western North America (fig. 9). Accordingly, we score this as a dispersification scenario (cell 3 in fig. 1).

Shift 7. Again, this rate shift has no immediate association with a morphological change, although it occurs in proximity to the change from anthers with four lobes (locules, pollen sacs) to anthers with two lobes. Immediately preceding this diversification shift, we also infer an episode of dispersal from western North America into Latin America (fig. 9). Although this is the most likely biogeographic scenario, it is important to note that it is within the confidence interval for movement into Latin America to coincide precisely with the diversification rate shift, which would support dispersification. For present purposes, we provisionally assign this case to cell 1 in figure 1. The diversification of Valerianaceae in the Andes likely does represent a bona fide adaptive radiation characterized by a remarkable degree of morphological and ecological disparity (Eriksen 1989; Bell 2004; Bell and Donoghue 2005*a*, 2005*b*). Our sense is that this may have been triggered primarily by the colonization of a newly forming, topographically complex, high-elevation mountainous region. But this radiation may well have also been promoted by reduction in flower size and a tendency to self-pollinate, which may both be reflected in the loss of anther lobes.

Summary. Our analyses have failed to identify unequivocal associations between diversification shifts and morphological shifts (key innovations). Some character changes are inferred to occur in close proximity to rate shifts, however, and one can readily imagine causal roles for several of these traits. By contrast, in several cases, our analyses have revealed a direct association between a diversification shift and a biogeographic shift. That is, our results demonstrate several cases of lineages that appear to radiate when entering a new geographic region. More specifically, it appears that the occupation of new mountainous regions may have triggered diversification both within *Viburnum* (Adoxaceae) and within *Valeriana* (Valerianaceae). In some cases, these montane habitats were likely mature and occupied by an established native flora, but in the case of the Andes in particular, these lineages may have entered at a time when high-elevation habitats were just becoming available. The latter cases are marked by the most extreme shifts in diversification in the groups considered in this study.

Implications for the Study of Diversification Rates

Through collaboration with the National Evolutionary Synthesis Center Phytogeography Working Group, we hope to extend the empirical scope of this study to include many more groups of plants. Although derived from a small set of empirical observations, the findings of the current analysis have general implications for studies of diversification.

Explanations of Diversification Patterns Need to Be More Mechanistic. Many factors appear to be rather capricious in their association with rates of diversification. That is, particular variables appear to be strongly correlated with diversification rate shifts in one group but not in others. For example, nectar spurs have been proposed as a key innovation in *Aquilegia* (e.g., Hodges and Arnold 1994*a*, 1994*b*, 1995; Ree 2005) and in flowering plants more generally (e.g., Hodges 1997) but are evidently not correlated with diversification rates in Valerianaceae (see also von Hagen and Kadereit 2003). Similarly, several shifts in di-

versification rate appear to be correlated with the independent dispersal of Adoxaceae and Valerianaceae lineages from North America into Latin America (a pattern also detected in, e.g., *Lupinus*; Hughes and Eastwood 2006); however, other movements between these areas had no discernible influence on diversification rates.

Such findings highlight the potential of a data exploration approach to help inform and refine our causal hypotheses regarding diversification rates. For instance, the observation that only some plant lineages experienced diversification rate shifts when entering Latin America may reflect differences in the degree to which they are confined to higher elevations. For example, *Sambucus* species—which did not experience elevated rates of diversification—occupy somewhat lower elevations in Latin America, whereas the relatively high-elevation *Viburnum* and *Valeriana* clades appear to have diversified rapidly in this region. Similarly, *Viburnum elatum*, which represents a separate entry into Mexico, occurs in generally lower and drier habitats. Although dispersal per se clearly did not invariably lead to elevated rates of diversification in Adoxaceae and Valerianaceae, the dispersal of relatively high-elevation lineages into topographically complex and particularly more recently uplifted areas may have resulted in an increased probability of allopatric speciation via geographic isolation among mountain ranges. Such reciprocal illumination between theoretical predictions and data exploration has the potential to guide the formulation of hypotheses regarding factors that influence rates of diversification.

Furthermore, these findings stress the need to evaluate predictions associated with the mechanism by which the variables under consideration are hypothesized to influence the probability of diversification. For example, if our mechanistic hypothesis specifies that nectar spurs increase the probability of speciation via increased population structure conferred by enhanced pollinator fidelity, several predictions follow: for example, spurred plants should exhibit high pollinator fidelity relative to nonspurred plants, and these plants should also show higher population structure relative to their nonspurred relatives. Evaluating these predictions may reveal that some apparently contradictory instances (i.e., diversification rates not correlated with the evolution of nectar spurs) may arise because one or more conditions required by the putative mechanism have not been met (e.g., perhaps the requisite pollinators are absent). Conversely, testing these mechanistic predictions may reveal instances of spurious correlation (e.g., although the evolution of nectar spurs may be correlated with increased rates of diversification, it may turn out that these spurred species do not exhibit the predicted increase in pollinator fidelity and/or population structure). Ultimately, assigning causality to the relationship between a given factor and rates of diversification will only become compelling when we move beyond the demonstration of simple phylogenetic correlations.

Explanations of Diversification Patterns Need to Be More Integrative. The search for correlates of diversification rate typically focuses on a single (usually morphological) factor. However, our results are rife with interactions among the variables, which highlights the need to adopt a more integrative approach. For example, the three morphological traits closely correlated with diversification rate shifts in Valerianaceae are phylogenetically interdependent: the distribution of the anther lobe trait is nested within the fruit type trait, which in turn is nested within the stamen number trait (fig. 6). In such cases, the degree to which a particular variable influences the probability of diversification (if any) is difficult to ascertain. Imagine, for example, that the probability of diversification in a lineage has been significantly increased by the origin of a given trait and that the phylogenetic distribution of this trait is nested within a second, more widely distributed trait. In this situation, the bona fide causal correlation between diversification rate and the evolution of the first trait may well create an illusory correlation between diversification rate and the evolution of the second trait. This is similar to the trickle-down behavior associated with inferring the location of shifts in diversification rate (Moore et al. 2004). The spurious nature of the second correlation would escape detection if we ignored the potential influence of other factors. Moreover, the evaluation of variables in isolation precludes the discovery of interactions in which the evolution of one trait mediates or facilitates the effects of subsequently evolved features (Donoghue 2005).

The apparent interaction of variables also occurs between the major variable classes, since several inferred diversification rate shifts in our study were closely associated with both morphological and biogeographic change. The existence and nature of such multivariate relationships cannot be revealed under the conventional univariate approach. Specifically, it is conceivable that morphological evolution might drive dispersal and diversification, that a given dispersal event might drive diversification and morphological evolution, that diversification rate might drive dispersal and morphological evolution, or that all three variables might be driven by some fourth variable (fig. 10). Consider, for example, the case of plumose fruits in Valerianaceae. The origin of these wind-dispersed fruits may have increased the probability of dispersal to and isolation within new geographic areas, which in turn increased the probability of allopatric speciation. On the other hand, the chance dispersal of this group to a new geographic area may have been characterized by the formation of small, isolated populations, which then expe-

rienced increased rates of morphological change and increased rates of diversification. Alternatively, increased rates of diversification (associated with some other factor) might have driven expansion of the range of the lineage to new areas and their rate of morphological evolution (e.g., Maddison 2006).

In general, we are struck by how often our analyses indicate that morphological changes and geographic movements occurred in close proximity to shifts in the diversification rate. In some cases, we suspect that such results may reflect genuine causal interactions. As highlighted above, for example, there is reason to suspect an interaction between the entry of *Valeriana* into the mountains of Latin America and the evolution of bilobed anthers (possibly associated with smaller, selfing flowers) that may have acted in concert to collectively promote the rapid Andean radiation of this lineage. It is important to note, however, that the close proximity between shifts in diversification rate and morphological and biogeographic changes also engendered considerable uncertainty in assigning cases to the cells of the cube model (fig. 1). It is likely that our conservative assignment of such cases to cell 1 of the cube overestimates scenarios in which diversification rate shifts were decoupled from biogeographic or morphological change. In other words, the prevalence of scenarios assigned to cell 1 may partly reflect a methodological artifact.

The test that we used to identify morphological correlates of diversification rates (Ree 2005) evaluates the overall association between a given character state and rates of diversification, regardless of the number of times the trait may have independently evolved on the tree. It may be valid to treat independent origins of a trait as equivalent in the context of hypothesis testing, but this aspect of the method may be undesirable in the context of data exploration. Specifically, a trait that evolves multiple times in the study phylogeny may be associated with a significantly higher rate of diversification in one instance but not in others. In a few cases, this test indicated no significant overall correlation between a given trait and rates of diversification, even though there appeared to be a strong correlation between diversification rate and a particular origin of that trait. For example, plumose fruits are inferred to have arisen twice in Valerianaceae (fig. 6); one origin coincides with the inferred location of a diversification rate shift, whereas the second origin occurs in a lineage with an evidently slow rate of diversification (*Valeriana celtica*). Under the Ree (2005) method, these two origins are lumped together, such that no significant correlation is inferred. We see a need for a method that allows greater flexibility in model specification, accommodates uncertainty in divergence time estimates, and is better suited to a data exploration approach (B. R. Moore and M. J. Donoghue, unpublished manuscript). Such a method is likely to resolve the status of diversification rate scenarios and correspondingly decrease the number of cases assigned to cell 1 of the cube model.

Overall, these analyses leave us with the impression that

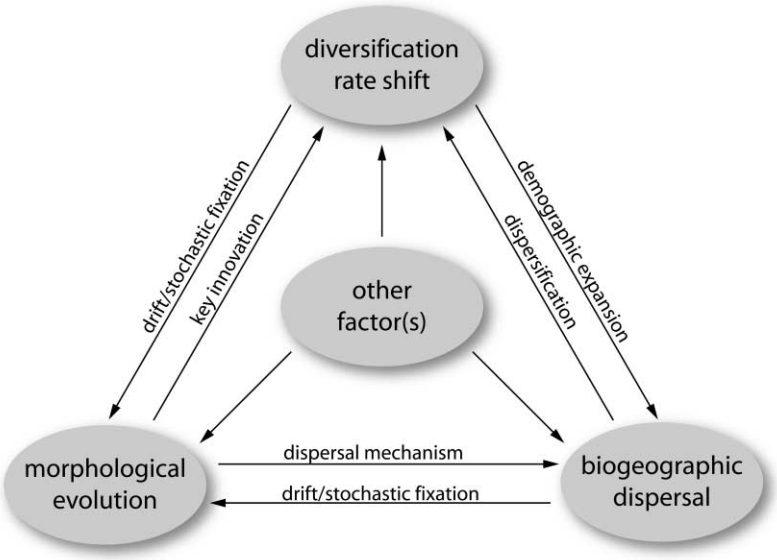


Figure 10: Illustration of the possible causal relationships between diversification rate, morphological evolution, and biogeographic change.

geography is a key factor in understanding diversification. In the cases presented here, geography is more obviously related to diversification shifts than is morphological evolution. Morphological innovation can be important too, of course, but our analyses emphasize the wisdom of evaluating the impact of trait changes in the context of historical biogeography, fully aware of the potentially important interactions between movement and evolutionary change.

Explanations of Geographic Patterns of Species Richness Need to Be More Historical. Our findings also bear on explanations of geographic gradients in species richness. Such studies, we believe, should incorporate not only historical biogeography (Wiens and Donoghue 2004) but also an examination of possible shifts in diversification rate associated with movement between geographic regions. Xiang et al. (2004) highlighted possible differences in species diversity in several plant groups between eastern Asia and eastern North America but did not specifically identify the timing and directionality of movements between these areas. We believe that inferring episodes of biogeographic movement may prove to be crucial in discerning the underlying causes of differences in species diversity among areas.

These comments relate directly to the tropical conservatism hypothesis reviewed by Wiens and Donoghue (2004), wherein relatively high tropical species diversity is attributed to a longer occupation of these areas compared with the more recent residence in temperate habitats. Their basic model assumed that diversification rate remained stochastically constant throughout time and across areas, that is, that the movement of lineages from the tropics into the temperate zones was not associated with shifts in diversification rate. They did note the possibility of higher diversification rates in the tropics, which would accentuate the magnitude of the observed latitudinal diversity gradient, but it also is possible that movement into temperate zones (perhaps associated with attaining the ability to persist in colder, seasonal climates) may have been accompanied by an increase in the rate of diversification in some lineages. This would obscure the picture or could even reverse the direction of the expected diversity gradient. We suspect that this may indeed be the case in some plant lineages, although the analysis of such movements may be confounded by correlated shifts from the woody to the herbaceous habit in many angiosperms (Judd et al. 1994).

Our findings that Adoxaceae and Valerianaceae rapidly radiated in the mountains of Latin America, especially in the Andes, bear directly on the latitudinal species diversity gradient (Mittelbach et al. 2007). The explanation for the preponderance of "tropical" species in our two cases appears to represent the opposite of tropical conservatism (sensu Wiens and Donoghue 2004). The relatively high number of species at tropical latitudes in these two clades is not due to a longer residence time at these latitudes. Instead, these lineages appear to have originated at temperate latitudes and subsequently entered higher elevation habitats within the tropical zone, and their recent occupancy was accompanied by a significant increase in the rate of diversification. If anything, this is a case of temperate conservatism combined with movement into mountainous habitats, which resulted in geographic isolation and rapid divergence in allopatry (cf. Kozak and Wiens 2007). It seems clear that the latitudinal diversity gradient will, in the end, be underlain by a variety of causes that vary among different lineages. Tropical conservatism may well apply in some cases, temperate conservatism in others. In any case, we suspect that the presence and recent formation of the Andes at tropical latitudes will be found to be a key factor in many groups of organisms (e.g., Hughes and Eastwood 2006). More generally, this again emphasizes the importance of adopting a historical perspective that specifically considers the relationship between geographic movements and rates of diversification.

Conclusions

Our exploration of the evolutionary radiation of Adoxaceae and Valerianaceae reveals complex relationships between biotic and abiotic variables and shifts in diversification rate. Although the evolution of several morphological traits associated with pollination and dispersal appears to occur in close proximity to shifts in diversification rate, we see the clearest evidence for a relationship between diversification rate shifts and movement into new geographic regions. The prevalent biogeographic signal in these findings highlights the need to explicitly consider the role of biogeography in studies of diversification. This requires a more mechanistic and integrative approach as well as the development of methods to help identify the relative contribution of—and possible interactions among—multiple biotic and abiotic factors. Finally, the discovery of an important role for geographic movement in promoting rates of diversification highlights the need to develop a richer historical approach to the study of species richness gradients.

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APPENDIX

GenBank Accession Numbers for Sampled Dipsacales Species

Table A1: GenBank accession numbers for Adoxaceae species

Species	ITS	*matK*	*trnS-G*	*WAXY1*	*WAXY2*
Adoxa	U88194.1	EF490235	EF490255	NA	NA
Sambucus adnata	AH006915.1	EF490236	EF490256	NA	NA
Sambucus australasica	U41381.1	EF490237	EF490257	NA	NA
Sambucus australis	U88196.1	EF490238	EF490258	NA	NA
Sambucus ebulus	U88200.1	EF490239	EF490259	NA	NA
Sambucus gaudichaudiana	U41382.1	EF490240	EF490260	NA	NA
Sambucus nigra	U88204.1	EF490241	EF490261	NA	NA
Sambucus racemosa	U88207.1	EF490242	EF490262	NA	NA
Sambucus wightiana	U88208.1	EF490243	NA	NA	NA
Sinadoxa	AF248611.1	AY310458.1	EF490263	NA	NA
Tetradoxa	AJ419710.1	AY265204.1	EF490264	NA	NA
Viburnum acerifolium	AY265114.1	AY265160.1	EF490265	AY596829	AY596876
Viburnum brachybotricum	EF462982	EF490244	NA	EF490292	EF490303
Viburnum carlesii	AY265115.1	AY265161.1	EF490266	AY596830	AY596877
Viburnum cinnamomifolium	AY265116.1	AY265162.1	NA	AY596831	NA
Viburnum clemensiae	AY265117.1	AY265163.1	EF490267	AY596832	AY596878
Viburnum cordifolium	AY265118.1	AY265164.1	EF490268	AY596833	AY596879
Viburnum cyclindricum	AY265119.1	AY265165.1	EF490269	AY596834	AY596880
Viburnum davidii	AY265120.1	AY265166.1	EF490270	AY596835	NA
Viburnum dentatum	AY265121.1	AY265167.1	NA	AY596867	AY596905
Viburnum dilatatum	AY265122.1	AY265168.1	NA	AY596836	AY596881
Viburnum edule	AY265123.1	AY265169.1	EF490271	AY596837	NA
Viburnum elatum	AY265124.1	AY265170.1	EF490272	AY596838	AY596882
Viburnum ellipticum	AY265125.1	AY265171.1	NA	AY596839	AY596883
Viburnum erosum	AY265126.1	AY265172.1	EF490273	AY596840	AY596884
Viburnum erubesens	AY265127.1	AY265173.1	NA	AY596874	AY596917
Viburnum farreri	AY265128.1	AY265174.1	EF490274	AY596841	AY596885
Viburnum foetidum	NA	EF490245	NA	EF490293	EF490304
Viburnum furcatum	AY265129.1	AY265175.1	EF490275	AY596842	AY596886
Viburnum hartwegii	AY265130.1	AY265176.1	NA	AY596868	AY596910
Viburnum japonicum	AY265131.1	AY265177.1	NA	AY596843	AY596887
Viburnum jucundum	AY265132.1	AY265178.1	NA	AY596869	AY596911
Viburnum kansuense	AY265133.1	AY265179.1	EF490276	AY596844	AY596888
Viburnum koreanum	EF462983	EF490246	EF490277	EF490294	EF490305
Viburnum lantana	AY265134.1	AY265180.1	EF490278	AY596845	AY596889
Viburnum lantanoides	AY265135.1	AY265181.1	EF490279	AY596846	AY596890
Viburnum lentago	AY265136.1	AY265182.1	EF490280	AY596847	AY596891
Viburnum lobophyllum	AY265137.1	AY265183.1	NA	AY596848	AY596892
Viburnum macrocephalum	EF462984	EF490247	NA	EF490295	EF490306
Viburnum melanocarpum	AY265138.1	AY265184.1	NA	AY596849	AY596893
Viburnum molle	AY265139.1	AY265185.1	EF490281	AY596850	AY596894
Viburnum mongolicum	EF462985	EF490248	NA	EF490296	EF490307

Table A1 (*Continued*)

Species	ITS	*matK*	*trnS-G*	*WAXY1*	*WAXY2*
Viburnum nudum	AY265140.1	AY265186.1	EF490282	AY596851	AY596895
Viburnum odoratissimum	AY265141.1	AY265187.1	NA	NA	AY596918
Viburnum opulus	AY265153.1	AY265199.1	EF490283	EF490297	EF490308
Viburnum orientale	EF462986	EF490249	EF490284	EF490298	EF490309
Viburnum plicatum	AY265143.1	AY265189.1	EF490285	AY596852	AY596896
Viburnum propinquum	EF462987	EF490250	NA	EF490299	NA
Viburnum prunifolium	DQ005993.1	AY265190.1	EF490286	AY596853	AY596897
Viburnum rafinesquianum	AY265145.1	AY265191.1	NA	AY596854	AY596898
Viburnum rufidulum	AY265147.1	AY265193.1	EF490287	AY596855	AY596899
Viburnum sargentii	AY265148.1	AY265194.1	EF490288	AY596856	AY596900
Viburnum setigerum	EF462988	EF490251	NA	EF490300	EF490310
Viburnum sieboldii	AY265149.1	AY265195.1	NA	AY596875	AY596919
Viburnum stenocalyx	AY265150.1	AY265196.1	NA	AY596870	AY596912
Viburnum suspensum	AY265151.1	AY265197.1	NA	AY596857	AY596901
Viburnum sympodiale	NA	EF490252	EF490289	EF490301	EF490311
Viburnum taiwanianum	EF462989	EF490253	NA	AY596858	NA
Viburnum tinus	AY265152.1	AY265198.1	NA	EF490302	NA
Viburnum trilobum	EF462990	EF490254	EF490290	AY596859	AY596902
Viburnum triphyllum	AY265154.1	AY265200.1	NA	AY596871	AY596913
Viburnum urceolatum	AY265155.1	AY265201.1	NA	AY596860	AY596903
Viburnum utile	AY265156.1	AY265202.1	EF490291	AY596861	AY596904

Note: NA = not available.

Table A2: GenBank accession numbers for Valerianaceae species

Species	ITS	*matK*	*psbA*	*trnL-trnF* IGS
Triplostegia glandulifera	AY236189.1	AY794323.1	AY794234.1	AF367424.1
Centranthus calcitrapae	DQ354163.1	DQ354181.1	DQ354215.1	DQ354197.1
Centranthus lecoqii	AY310447.1	DQ354184.1	DQ354216.1	DQ354198.1
Centranthus macrosiphon	AY792823.1	AY794312.1	AY794224.1	AY792885.1
Centranthus ruber	AY310448.1	AY794313.1	AY794225.1	AF446986.1
Centranthus sieberi	DQ354162.1	DQ354179.1	DQ354213.1	DQ354195.1
Fedia cornucopiae	AY236193.1	AY290037.1	AY794226.1	AF446983.1
Nardostachys jatamansii	AY236190.1	AY290038.1	AY794227.1	AF446980.1
Patrinia gibbosa	AY792824.1	AY794317.1	AY794229.1	AY792886.1
Patrinia scabiosifolia	AY792825.1	AY794318.1	AY794230.1	AY792887.1
Patrinia triloba	AY236191.1	AY290039.1	AY794228.1	AF446981.1
Patrinia villosa	AY310493.1	AY794319.1	NA	AY792888.1
Plectritis brachystemon	AY792828.1	AY794320.1	AY794231.1	AY792890.1
Plectritis congesta	AY792827.1	AY794321.1	AY794232.1	AY792889.1
Plectritis macrocera	AY236195.1	AY290036.1	AY794233.1	AF446985.1
Valeriana acutiloba	AY792829.1	AY794324.1	AY794235.1	AY792891.1
Valeriana adscendens	AY792830.1	AY794325.1	AY794236.1	AY792892.1
Valeriana albonervata	AY792831.1	AY794326.1	AY794237.1	AY792893.1
Valeriana apiifolia	AY792832.1	AY794327.1	AY794238.1	AY792894.1
Valeriana arborea	AY360096.1	AY794328.1	AY794239.1	AY360116.1
Valeriana aretioides	AY792833.1	AY794329.1	AY794240.1	AY792895.1
Valeriana arizonica	AY792834.1	AY794330.1	AY794241.1	AY792896.1
Valeriana asarifolia	DQ354167.1	NA	NA	DQ354200.1
Valeriana barbareifolia	AY792835.1	AY794331.1	AY794242.1	AY792897.1
Valeriana bracteata	AY792836.1	AY794332.1	AY794243.1	AY792898.1
Valeriana bryophila	AY792837.1	AY794333.1	AY794244.1	AY792899.1
Valeriana bulbosa	AY792838.1	AY794334.1	AY794245.1	AY792900.1
Valeriana californica	AY360098.1	AY794335.1	AY794246.1	AY360118.1

Table A2 (*Continued*)

Species	ITS	*matK*	*psbA*	*trnL-trnF* IGS
Valeriana candolleana	AY792839.1	AY794336.1	AY794247.1	AY792901.1
Valeriana celtica	AY310494.1	AY794337.1	AY794248.1	AY360121.1
Valeriana ceratophylla	AY792840.1	AY794338.1	AY794249.1	AY792902.1
Valeriana chaerophylloides	AY360103.1	AY794339.1	NA	AY360126.1
Valeriana clematitis	AY792841.1	AY794340.1	AY794251.1	AY792903.1
Valeriana coarctata	AY792884.1	AY794341.1	AY794252.1	AY792904.1
Valeriana connata	AY792842.1	AY794342.1	AY794253.1	AY792905.1
Valeriana densiflora	AY792843.1	AY794343.1	AY794254.1	AY792906.1
Valeriana dioica	AY360107.1	AY794344.1	AY794255.1	AY360119.1
Valeriana edulis	AY360104.1	AY794345.1	AY794256.1	AY360127.1
Valeriana fauriei	AY792844.1	AY794346.1	AY794257.1	AY792907.1
Valeriana flaccidissima	AY792845.1	AY794347.1	AY794258.1	AY792908.1
Valeriana gallinae	AY792846.1	AY794348.1	AY794259.1	AY792909.1
Valeriana henrici	AY360105.1	AY794349.1	AY794260.1	AY360128.1
Valeriana hirtella	AY360114.1	AY794350.1	AY794261.1	AY360134.1
Valeriana interrupta	AY792847.1	AY794351.1	AY794262.1	AY792910.1
Valeriana kawakamii	AY792848.1	AY794352.1	AY794263.1	AY792911.1
Valeriana laurifolia	AY360112.1	AY794353.1	AY794264.1	AY360133.1
Valeriana mexicana	AY792849.1	AY794354.1	AY794265.1	AY792912.1
Valeriana microphylla	AY360113.1	AY794355.1	AY794266.1	AY360122.1
Valeriana minutiflora	AY236192.1	AY794356.1	AY794267.1	AF446982.1
Valeriana montana	AY360100.1	AY794357.1	AY794268.1	AY360124.1
Valeriana naidae	AY792850.1	AY794358.1	AY794269.1	AY792913.1
Valeriana niphobia	AY360106.1	AY794359.1	AY794270.1	AY360129.1
Valeriana nivalis	AY792851.1	AY794360.1	AY794271.1	AY792914.1
Valeriana occidentalis	AY792852.1	AY794361.1	AY794272.1	AY792915.1
Valeriana officinalis	DQ180745.1	AY794362.1	AY794273.1	AF366917.1
Valeriana palmeri	AY792853.1	AY794363.1	AY794274.1	AY792916.1
Valeriana pauciflora	AY792878.1	AY794364.1	AY794275.1	AY792944.1
Valeriana pilosa	AY360109.1	AY794365.1	AY794276.1	AY360131.1
Valeriana pinnatifida	AY792854.1	AY794366.1	AY794277.1	AY792917.1
Valeriana plantaginea	AY792855.1	AY794367.1	AY794278.1	AY792918.1
Valeriana polemonioides	AY792856.1	AY794368.1	AY794279.1	AY792919.1
Valeriana prionophylla	AY792857.1	AY794369.1	AY794280.1	AY792920.1
Valeriana procera	AY792858.1	AY794370.1	AY794281.1	AY792921.1
Valeriana pyramidalis	AY792859.1	AY794371.1	AY794282.1	AY792922.1
Valeriana pyrenaica	AY310453.1	AY794372.1	AY794283.1	AY360132.1
Valeriana rigida	AY360108.1	AY794373.1	AY794284.1	AY360130.1
Valeriana robertianifolia	AY792860.1	AY794374.1	AY794285.1	AY792923.1
Valeriana rumicoides	AY792861.1	AY794375.1	AY794286.1	AY792924.1
Valeriana rzedowskiorum	AY792862.1	AY794376.1	AY794287.1	AY792925.1
Valeriana scandens	AY310454.1	AY794377.1	AY794288.1	AY792926.1
Valeriana scouleri	AY792864.1	AY794378.1	AY794289.1	AY792927.1
Valeriana secunda	AY792865.1	AY794379.1	AY794290.1	AY792928.1
Valeriana selerorum	AY792866.1	AY794380.1	AY794291.1	AY792929.1
Valeriana sitchensis	AY360097.1	AY794381.1	AY794292.1	AY360117.1
Valeriana sorbifolia	AY360102.1	AY794382.1	AY794293.1	AY360125.1
Valeriana stenoptera	AY792867.1	AY794383.1	AY794294.1	AY792930.1
Valeriana sterophylla	AY792868.1	AY794384.1	AY794295.1	AY792931.1
Valeriana supina	AY360099.1	AY794385.1	AY794296.1	AY360123.1
Valeriana tanacetifolia	NA	NA	AY794297.1	AY792932.1
Valeriana texana	AY792870.1	AY794387.1	AY794298.1	AY792933.1
Valeriana tomentosa	AY792871.1	AY794388.1	AY794299.1	AY792934.1
Valeriana trichostoma	AY792872.1	AY794389.1	AY794300.1	AY792935.1
Valeriana triphylla	AY792873.1	AY794390.1	AY794301.1	AY792936.1

Table A2 (*Continued*)

Species	ITS	*matK*	*psbA*	*trnL-trnF* IGS
Valeriana tripteris	AY792874.1	AY794391.1	AY794302.1	AY792937.1
Valeriana tuberosa	DQ354166.1	DQ354185.1	DQ354212.1	DQ354199.1
Valeriana urticifolia	AY792875.1	AY290035.1	AY794304.1	AY792938.1
Valeriana wallrothii	AY792877.1	NA	AY794305.1	AY792940.1
Valerianella amarella	DQ354177.1	DQ354192.1	DQ354217.1	DQ354210.1
Valerianella carinata	DQ354169.1	DQ354180.1	DQ354218.1	DQ354202.1
Valerianella coronata	AY792879.1	AY794395.1	AY794306.1	AY792941.1
Valerianella dentata	AY792880.1	AY794396.1	AY794307.1	AY792942.1
Valerianella discoidea	DQ354171.1	DQ354187.1	DQ354219.1	DQ354204.1
Valerianella eriocarpa	AY792881.1	AY794397.1	AY794308.1	AY792943.1
Valerianella florifera	DQ354178.1	DQ354190.1	DQ354220.1	DQ354211.1
Valerianella locusta	AY310456.1	AY794398.1	AY794309.1	AF446984.1
Valerianella microcarpa	DQ354170.1	DQ354183.1	DQ354221.1	DQ354203.1
Valerianella muricata	DQ354172.1	DQ354188.1	DQ354222.1	DQ354205.1
Valerianella pumila	AY792882.1	AY794399.1	AY794310.1	AY792945.1
Valerianella radiata	DQ354176.1	DQ354189.1	DQ354226.1	DQ354209.1
Valerianella stenocarpa	DQ354175.1	DQ354191.1	DQ354225.1	DQ354208.1
Valerianella texana	DQ354173.1	DQ354193.1	DQ354223.1	DQ354206.1
Valerianella umbilicata	DQ354174.1	DQ354194.1	DQ354224.1	DQ354207.1
Valerianella vesicaria	AY792883.1	AY794400.1	AY794311.1	AY792946.1

Note: NA = not available.

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