

ABSTRACT

Title of dissertation: USING A COMBINATION OF PHYLOGENETIC
COMPARATIVE AND PALEOBOTANICAL METHODS
TO ELUCIDATE PATTERNS OF LINEAGE
SELECTION IN ROSALES (PLANTAE:
ANTHOPHYTA)

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An increasing focus in evolutionary biology is on the interplay between mesoscale ecological and evolutionary processes such as population demographics, habitat tolerance, and especially geographic distribution, as potential drivers responsible for patterns of diversification and extinction over geologic time. However, few studies to date connect organismal processes such as survival and reproduction through mesoscale patterns to long-term macroevolutionary trends. In my dissertation, I investigate how mechanism of seed dispersal, mediated through geographic range size, influences diversification rates in the Rosales (Plantae: Anthophyta).

In my first chapter, I validate the phylogenetic comparative methods that I use in my second and third chapters. Available state speciation and extinction (SSE) models assumptions about evolution known to be false through fossil data. I show, however, that as long as net diversification rates remain positive – a condition likely true for the Rosales – these violations of SSE’s assumptions do not cause significantly biased results.

With SSE methods validated, my second chapter reconstructs three associations that appear to increase diversification rate for Rosalean genera: (1) herbaceous habit; (2) a three-way interaction combining animal dispersal, high within-genus species richness, and geographic range on multiple continents; (3) a four-way interaction combining woody habit with the other three characteristics of (2). I suggest that the three- and four-way interactions represent colonization ability and resulting extinction resistance in the face of late Cenozoic climate change; however, there are other possibilities as well that I hope to investigate in future research. My third chapter reconstructs the phylogeographic history of the Rosales using both non-fossil-assisted SSE methods as well as fossil-informed traditional phylogeographic analysis. Ancestral state reconstructions indicate that the Rosaceae diversified in North America while the other Rosalean families diversified elsewhere, possibly in Eurasia. SSE is able to successfully identify groups of genera that were likely to have been ancestrally widespread, but has poorer taxonomic resolution than methods that use fossil data.

In conclusion, these chapters together suggest several potential causal links between organismal, mesoscale, and geologic scale processes, but further work will be needed to test the hypotheses that I raise here.

USING A COMBINATION OF PHYLOGENETIC COMPARATIVE AND
PALEOBOTANICAL METHODS TO ELUCIDATE PATTERNS OF LINEAGE
SELECTION IN ROSALES (PLANTAE: ANTHOPHYTA)

by

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Introduction

The relative diversity of different clades of organisms changes over geologic time in an uneven, yet nonrandom manner (Van Valen 1973, Sepkoski 1981; Raup & Sepkoski 1982, Niklas et al 1983, Sepkoski 1984, Niklas et al 1985, Van Valen 1985, Valentine et al 1991, Alroy 2004, Alroy et al 2008). Broad-brush studies of these patterns of biodiversity change have identified macroevolutionary characteristics that correlate with patterns of faunal or floral change, such as faunal turnover rates (Sepkoski 1984), exploitation of previously vacant adaptive space (Niklas et al 1983, 1985), heritable geographic range (Jablonski 1987, Jablonski & Raup 1995, Jablonski & Roy 2003, Jablonski & Hunt 2006), ecological traits such as metabolic rate (Bambach 1993, 1999, Boyce et al 2009), pollination syndrome (Stebbins 1970, Eriksson & Bremer 1992, Fenster et al 2004, Bremer & Eriksson 2008, Vamosi & Vamosi 2010, 2012) dispersal efficacy (Stebbins 1971, Eriksson & Bremer 1991, Tiffney & Mazer 1995, Bolmgren & Eriksson 2005), or developmental characteristics such as modularization (Hughes 2007). Work is being done on the actual causal links between characteristics of individuals (e.g. developmental or ecological traits), species and population properties (geographic range size, habitat breadth), and macroevolutionary trends (e.g. Larson-Johnson 2016). However, more work is needed in order to generalize the patterns being observed to understand the processes underlying the rise and fall of biological diversity over geologic time.

In my dissertation, I investigated the biogeographical and evolutionary history of the angiosperm order Rosales (Angiosperm Phylogeny Group IV, 2016), with an emphasis on how seed dispersal mechanism relates to geographic range size, and how

these in turn relate to diversification over the clade's history. In the first of my three chapters, I investigated the assumptions made by the phylogenetic comparative methods that I wanted to use in my subsequent chapters, building on previous criticisms of phylogenetic comparative methods (Rabosky 2010, Davis et al. 2013, Machac 2014, Rabosky & Goldberg 2015). In my second chapter, I investigated the four-way relationship between seed dispersal mechanism, woody versus herbaceous habit, geographic range size, and within-genus species richness, on genus-level diversification rates in the Rosales. My final chapter consists of reconstructing the phylogeographic origins of the Rosales using two different methods, one that takes advantage of fossil data (Matzke 2013) and the other which models the effect of range size on diversification rate (Fitzjohn 2012, Matzke 2014).

My three chapters are reproduced here, in manuscript form, as I intend to submit them to peer-reviewed journals. Together, they add to the body of work tying geographic distributions with diversification and extinction of evolutionary lineages (Rabinowitz 1984, Jablonski & Hunt 2006, Payne & Finnegan 2007, Vamosi & Vamosi 2012, Larson-Johnson 2016).

Chapter 1 - Binary-State Speciation and Extinction method is conditionally robust to realistic violations of its assumptions

CHAPTER ABSTRACT

Phylogenetic comparative methods allow us to test some evolutionary hypotheses that otherwise require an extensive *fossil record*. However, the fossil record illustrates some scenarios that may violate the assumptions of these methods, among them discontinuous rates of character evolution and long-term declines in taxonomic turnover rates. For example, it is well documented that many fossil groups decline in diversity over time, even resulting in extinction of the entire group, in violation of the assumptions of a comparative method to determine the causes of patterns of phenotypic diversity, namely the Binary State Speciation and Extinction (BiSSE). Here, we assess the model's performance when declining speciation rates lead to net extinction using a model of simulated clade evolution. We test both BiSSE's propensity to detect a difference in speciation or extinction rates as a function of character state when no such difference is present (i.e., type-I error), and also its failure to detect such a difference when it is present (type-II error). BiSSE performs well at avoiding type-I error even under substantial diversification rate slowdown, so long as the rate of net diversification always remains positive. However, it incorrectly favors higher diversification rates in the ancestral state if the simulation is run long enough for net diversification to become negative. BiSSE is remarkably robust to type-II error even in the face of these violations of its assumptions. BiSSE's ability to detect a real difference in diversification rates increased with

simulation time, even as the clade peaked in diversity and went into decline. Fortunately, many studies using BiSSE and similar models to infer past clade evolution focus on recent, rapid diversifications and are thus unlikely to run afoul of the circumstances whereby BiSSE provides spurious results, but caution should be taken in inferring past diversification patterns in the absence of fossil data.

INTRODUCTION

A recurring key question in evolutionary biology is what causes shifts in speciation and/or extinction rates. Historically, evolutionary scientists have turned to the fossil record to address this question, but more recently numerous methods of phylogenetic comparative analysis have been devised to account for the fact that many clades have severely incomplete or altogether lacking fossil data (Pagel 1994; Ng and Smith 2014). These models range from simple lineages through time methods (Nee et al. 1994) to complex likelihood-based models that attempt to infer both rates of diversification and evolution of character traits responsible for differential diversification (Maddison et al. 2007; Rabosky et al. 2007). These models have been directed at a number of different clades (e.g. evening primroses: Johnson et al. 2011; mammals: Price et al. 2012; birds: Hugall and Stuart-Fox 2012).

In the absence of fossil data, however, methods that reconstruct diversification rates from phylogenies must make assumptions about evolution that in many cases are shown to be untrue by paleontological data. In particular, most phylogenetic methods assume continuous rates of diversification that may be affected by the presence or absence of certain character states (Maddison et al. 2007), but which are otherwise

constant over time in the absence of state change. A model that assumes continuous and constant diversification rates can never allow for negative changes in richness of a lineage except over short durations and due purely to stochastic variation. The fossil record is rife, however, with clades that diversify rapidly following their initial appearance, reach peak richness, and then decline consistently over geologic time.

The extreme cases of complete extinction of major groups (e.g., trilobites, ammonites or non-avian dinosaurs) do not have obvious effects on what we infer from molecular trees. However, the fossil record also shows that many extant groups were once more diverse in the past. Sepkoski's (1981) "three faunas" provide many of the textbook examples for marine invertebrates: many members of the Paleozoic fauna (e.g., articulate brachiopods, bryozoans and crinoids) and even members of the Cambrian fauna (e.g., inarticulate brachiopods) still exist at reduced diversities today. Many examples exist among vertebrates (e.g., Benton 2005) and plants (Taylor et al. 2009). Sepkoski (1984) proposed that this is a general behavior of clades, with currently diversifying clades having not yet reached the declining phase of their history. Wagner and Estabrook (2014) corroborate this by showing that extinction of "primitive taxa" rather than diversification of "derived taxa" underlies trait-dependent diversity shifts among fossil taxa, even while the overall diversity of those clades is decreasing.

Several studies have examined the possible effects of inconsistent diversification rates on tree-based inferences of origination and/or extinction rates from both paleontological (Wagner 2000; FitzJohn 2010; Liow et al. 2010) and neontological perspectives (e.g., Freckleton et al. 2008; Rabosky 2009, 2010; Machac et al. 2013). Machac (2014) examined both constant rate estimator (CR) models and the much more

recent quantitative state speciation and extinction algorithm (QuaSSE; FitzJohn 2010) in the context of diversification rate “slowdown” driven by logistic diversification, finding that QuaSSE performs poorly under decreasing diversification rates, but that CR better reconstructs rates of paleodiversification in character space. However, his models consider only declining increases in diversity, rather than negative diversification (i.e., origination rates below extinction rates). Furthermore, methods of inferring past diversity using only living taxa consistently misrepresent true past diversity relative to the fossil record (Quental and Marshall 2010) and thus fail to identify diversification shifts induced by elevated extinction rather than elevated origination (Freckleton et al. 2008). Theoretical models of phylogenies representing different diversification histories can attempt to infer past patterns of diversification and extinction (see Morlon 2014 for review). Some models have been used to enable phylogenies to reconstruct paleodiversity albeit violating assumptions of BiSSE-like methods (e.g. Morlon et al. 2011 for successively-diversifying subclades, Etienne et al. 2012 for density-dependent diversity). However, these success stories remain disconcertingly few.

We set out to test the ability of a widely used tree-based method, binary state speciation and extinction (BiSSE; Maddison et al. 2007), in detecting differential diversification using simulated clades with declining and ultimately negative diversification rates. The clades range from those that maintain a positive though declining rate of diversification throughout the simulation (increasing richness), to those that have had a negative diversification rate for much of their history. We used BiSSE (Maddison et al. 2007) instead of QuaSSE because BiSSE is mathematically more tractable (since its character state is binary) but provides many of the same benefits as

QuaSSE, such as parsing whether a high proportion of extant species with a particular character state results from enhanced diversification or from high rates of transition to the common character state.

In this paper, we addressed the following questions: (1) how severely can BiSSE's constant evolutionary rate assumptions be violated and yet still provide accurate assessment of lineage diversification rates and character evolution? (2) Does punctuated equilibrium as applied to character state evolution (Eldredge & Gould 1972) affect whether BiSSE is able to recover evolutionary rates? (3) Does the sign of the derivative of extinction rate (i.e. positive, negative, zero) while speciation rate declines affect the severity of the biases that occur with dropping net diversification rate? Specifically, we set out to test the ability of BiSSE to recover the effect of character state on speciation and extinction rates in more paleontologically realistic scenarios featuring overall declines in evolutionary rates over geologic time. We first simulated clades in which there was no effect of the focal character on diversification rate. In these runs, we ascertained the frequency by which BiSSE incorrectly evaluated the character state as having an effect on diversification rates when it did not. Conceptually, this is not unlike Rabosky & Goldberg's (2015) study in which the character under study had no effect on diversification rate but in which a second, unrelated, character did – here, the “unrelated character” is the intrinsic, long-term, decline in speciation (and also, depending on our simulation) extinction rate. Second, we simulated clades in which the derived state of the simulated character enhanced speciation rates, but still featured the extrinsic long-term decline in speciation rate. In these, we examined BiSSE's ability to recover this difference between the two character states, even in the face of overall long-term decline.

METHODS

Simulating clade diversification

Here, we use a series of birth-death models of diversification in which both origination and extinction change over time. In our first model, both diversification and extinction decline with time, but where the origination rates decline more rapidly such that net diversification becomes negative after a certain amount of time (Fig. 1A; see also Gilinsky & Bambach 1987: Fig. 3E). In our second, diversification rate declines while extinction rate is constant (Fig. 1B; see also Gilinsky & Bambach 1987: Fig. 3C). Third, we simulated models where extinction rate actually increases even as diversification declines (Fig. 1C; see also Gilinsky & Bambach 1987: Fig. 3A). This results in a “bottom-heavy” clade richness patterns (Gould et al. 1987), which are common to animal and plant groups from the marine (e.g., trilobites; Sepkoski 1981) and terrestrial (e.g., perissodactyls and conifers; Uhen 1996; Farjon 1995). To simulate different clade ages, we run simulations for different lengths of time. The shortest simulations cease after approximately one quarter of the time needed to reach zero net diversification (time = 0.25 arbitrary units, Fig. 1); the longest simulations run twice as long as needed to reach zero net diversification (Fig. 1). Simulations begin with extinction rates half that of origination rates. By the end of the longest runs, origination rates are half of the extinction rates. These different run approaches yield a range of histories, from still increasing diversity to plateaued diversity to declining diversity. The first and even

second patterns can be reconstructed by lineage through time methods (see, e.g., Nee et al. 1994), but the latter cannot.

BiSSE is known to have low power with fewer than 50 terminal tips (Davis et al. 2013). For this reason, we discarded simulations with fewer than this number of species surviving at the end of the simulation (i.e. when the assessment was made). Our simulations of punctuated equilibrium had an even lower cutoff of 36 terminal tips. For each combination of parameters (Table 1), we continued simulating (and analyzing) clades until we had 100 runs that yielded useable data (i.e. sufficient species diversity, nonuniformity in character states). Simulations that failed to meet these criteria were repeated until the criteria were met. Thus, more than a third of all simulations are discarded for having too few taxa. Moreover, many simulated clades quickly go extinct; approximately one third of runs never generate a second species. In our case, low power due to low sample size would only affect our shortest (not enough time to speciate) and our longest (most of the simulated clade's diversity is extinct) trial runs; intermediate lengths typically had hundreds to thousands of species.

We use simulations in which all evolutionary rates (speciation, extinction, and character state change) are unaffected by character state to test for type-I error (falsely rejecting the null hypothesis that evolutionary rates are affected by character state; Table 1). We test for type-II error (falsely accepting the null hypothesis) in estimates of speciation rate by running two sets of simulations (Table 1). In the first set, the speciation rate of the derived state (state 1) is 1.33 times the speciation rate of the ancestral state (state 0). In the second set, the speciation rate of the derived state is only 1.05 times the speciation rate of the ancestral state. These rates are well within the ranges of both

modeled (e.g. Machac 2014) and observed (e.g. Sepkoski 1981) differences in speciation and extinction across characters or across clades. In both cases, speciation rate declines exponentially with time as it did in the type-I error tests, but the ratio of the speciation rates of the derived to ancestral states remains constant as both decline.

Davis et al. (2013) tested even more extreme differences in speciation rate of one state (up to five times greater) relative to the other. We did not simulate asymmetry in speciation rate of the derived state greater than 1.33 for the following reason: at time 0 in our simulation, speciation rates are twice extinction; at time 1, speciation and extinction rates become equal; at time 2, speciation rate is half that of extinction. The asymmetry in our speciation rate constitutes a multiplier to the speciation rate of the derived state. Thus, for instance, using an asymmetry of 2 (i.e. derived state has twice the speciation rate as the ancestral state), the speciation and extinction rates of species with the derived state would be equal to extinction rates at time 2; as a consequence, we would not be able to test the effect of net-negative diversification in which extinction outpaces speciation.

Simulating morphologic change

We used two different models to simulate morphological change. First was our punctuated equilibrium model, in which there is some probability of changing from state 0->1 or back from state 1->0 at each speciation event (see, e.g., Raup and Gould 1974). We used a rate of change of 0.09 per branch, which is a typical average rate reconstructed by minimum steps parsimony in phylogenetic studies of fossil taxa (Wagner 2000). In the shortest runs, this results in a median expectation of 4.7 changes and in the longest runs, this results in an expectation of 15.2 changes. Note that because of extinction, not all of

the changes happen along branches leading to “extant” taxa. Our second model was a continuous model of character evolution, in which a lineage will undergo an average of 1.2 changes over one time unit, irrespective of how many speciation events there were (or weren’t) in that time. These 1.2 changes per time unit include both transformations from state 0→1 as well as from state 1→0. In no model was state change in one direction more likely than state change in the other direction; character states were only “favored” or not based on their effect on speciation rate.

Assessment

We simulated trees until we had 100 runs, each with sufficient terminal taxa, for each combination of parameters (Table 1). For each tree, we then used BiSSE to assess the level of significance between shifts in speciation and/or extinction and the acquisition of derived state 1. Note that the choice of state is arbitrary; if state 1 is less diverse, then “significant” shifts would purport low net diversification for taxa with state 1 and thus relatively high net diversification for taxa with state 0. In addition to the complexities of the comparative character analysis itself, any comparative analysis on real data would also have to assume recovery of the correct phylogenetic history of the group under study. However, we used the “true” evolutionary history created by our simulation, in effect assuming that any phylogenetic analysis done prior to BiSSE had arrived at the correct phylogeny (The effect of erroneous tree reconstruction is a separate issue that cannot be addressed here.) We then assess the significance, calculated via likelihood-ratio test based on AIC scores implemented in Diversitree (FitzJohn 2012), of single-rate and two-rate origination and extinction models given the distribution of 0’s and 1’s across

that tree. Finally, we assess the “significance” of patterns based on the frequencies of simulations that show significant differences in estimated origination or extinction rates.

RESULTS

Type-I error assessment

BiSSE tests a null hypothesis that character states have no effect on diversification rates. False rejection rates (i.e., Type-I error) are generally low (indistinguishably close to null expectation of $\alpha = 0.05$) for simulations of length less than one, but become significant as simulation length exceeds one (Table 2, Figure 2). In our punctuated equilibrium simulations (Fig. 2A), high rates of type-I error are observed in very short (length 0.25) and in longer (length 1 and longer) runs, but departures from null expectations (type-I error rate equal to α) are not statistically significant at intermediate (length 0.5 and 0.75) length runs. Using a continuous model of character evolution (Fig. 2B-D), the high rate of type-I error in the very shortest simulations does not occur, but still rises at length 1 or greater. The rates at which type-I error increase are affected by whether extinction rate is decreasing (Fig. 2A-B), constant (Fig. 2C), or increasing (Fig. 2D), but type-I error remains statistically indistinguishable from null values as long as simulation length is less than 1 (Table 2).

We analyzed the sign of inferred differences in the three parameters between the different states to check for systematic bias in the direction of inferred evolutionary trends (Table 3). Different combinations of continuous versus punctuated character evolution model and change in extinction rate produce different apparent trends in inferred speciation rates relative to inferred extinction rates, but this relationships are not

(and cannot be) statistically significant with only six simulation lengths. Nonetheless, in our punctuated character evolution model, speciation rates estimated by BISSE were significantly more likely to favor state 1 in 0.25-length runs than in the longer simulations (binomial test, $P < 0.001$). Comparing length-2 runs with all shorter runs, BISSE appears to be likely to favor the ancestral state in two out of the four sets of analyses; however, the result is not significant ($P = 0.147$). Other parameters, especially state transition rates, also show apparent similar patterns of bias, but these trends are less striking (Table 3). Table 4 shows only the inferences of differential evolutionary rates that are significant at the 0.05 level. In general, the patterns are similar to those of Table 3: in our punctuated evolution model, and in our continuous evolution model with constant extinction, BiSSE favors the ancestral state as causing higher rates of speciation, extinction, and state transition at simulation length 2, but these do not carry over to the other two sets of models. In no model, however, does the opposite occur to an extent that is statistically significant.

BiSSE inferred extinction rates of zero for both character states in 81 out of 600 runs in our punctuated model and in 28 out of 1800 runs in our continuous models (Table 3). This is also an error because all of the simulated runs produced species that became extinct during the simulation (in no individual run did more than 56% of the species created survive to the end of the simulation). The great majority of these inferences of zero extinction in the punctuated model (72 out of 81) were for the length-2 series, which is the simulation length for which extinction was most prevalent (fewer than 10% of the total species generated survived to the end of the length-2 simulations). Furthermore, all 0.5- and 0.75-length runs in the punctuated model inferred positive extinction rates.

However, in our continuous character evolution simulations, the inferences of zero extinction are clustered toward the short-duration simulations. Even in these, however, this is an error, due to the fact that all runs simulated extinct species.

Type-I error in speciation rates was highly correlated with type-I error in extinction rates (Table 5). In our simulations of punctuated character evolution, there were 39 runs that incorrectly inferred unequal extinction rates, 26 of which also inferred unequal speciation rates, while only 13 inferred unequal extinction without unequal speciation. However, only 121 out of 600 total runs inferred unequal speciation rates. In simulations of continuous character evolution, 315 runs inferred unequal extinction rates, but only 71 of those did not also infer unequal speciation rates. Contrastingly, only 468 out of the total 1800 inferred unequal speciation rates. For both sets of runs, the association between different types of type-I error is significant far below the $P = 0.0001$ level using Fisher's Exact Test (Table 5).

Type-II error assessment

In simulations wherein the difference between speciation rates of the derived and ancestral states is large (derived is 1.33 x ancestral state), the rate of type-II error drops off with increasing length of the simulation, even though the assumption of net-positive diversification rate made in BiSSE is more and more severely violated as simulation length increases (Figure 3). This pattern is present, but less pronounced, if the difference in speciation rates of the derived and ancestral state is smaller (1.05 x), only showing up with 95% confidence from length 1.5 onward, after the peak diversity has been reached and the clade has begun to decline. There is no qualitatively obvious difference between

simulations run using a continuous model of character evolution versus a punctuated model of character evolution.

The small-difference simulations, reveal a second type of error, one in which BiSSE rejects the null hypothesis but in the wrong direction; finding that the ancestral state has a higher speciation rate than the derived state, the opposite of the simulated condition. This effect is small at length-1 and below, but becomes significant above length-1. There are four (out of 600) cases of this error type in the large-difference simulations, three of them in the longest (length-2) category. This apparent pattern lies within the 95% confidence limit for the other lengths of simulation. The frequency of this type of error is much larger in the simulations in which the derived state induced only 1.05 times the speciation rate as the ancestral state, with 31 out of 100 of the length-2 runs exhibiting this type of error.

DISCUSSION

As predicted from first principles, BiSSE is biased towards rejecting the correct null hypotheses in favor of models indicating higher rates of speciation, extinction, and state transition for lineages retaining ancestral character states relative to those retaining derived states. However, BiSSE is also biased toward rejecting correct null hypotheses in the opposite direction as well. The tipping point where type-I error rates become noticeably elevated above normally expected rates (i.e., *statistically different from expected rates of 5%*) is roughly the point at which speciation rates drop below extinction rates and clades begin to decline in richness. Thus, BiSSE seldom finds significant differences in speciation, extinction and state transition where none exist, as long as net

diversification rates remain positive. Type I error increases dramatically, though, for clades that have peaked in diversity and are in decline before the end of the simulation. These results are similar to those found by Rabosky & Goldberg (2015), but where they found a misleading correlation between diversification and an unimportant character due to a time-associated acquisition of an unrelated, but important, character, the bias we observe is driven by an intrinsic property of clade evolution. As such, the problems we investigate in this paper will apply to all clades, instead of only those undergoing evolution of multiple characters simultaneously. The bias we here illustrate, however, can be avoided by only studying clades believed to be currently still diversifying, while that illustrated by Rabosky & Goldberg is more difficult to anticipate.

Simulations inducing Type-I error in extinction rate tests frequently induce Type-I error in speciation rate tests, too. This is not surprising: simulated clades that have particularly large pulses of diversification early in their history, or those that undergo fewer than average transitions to the derived character state early on, will accentuate BiSSE's systematic bias. As a consequence, these clades are far more likely to reject the null hypothesis incorrectly than clades that evolve differently.

Unexpectedly, simulations reveal high Type-I error rates for very young clades when using our punctuated equilibrium model of character evolution. However, simulations using a continuous model of character evolution do not result in this bias. It is possible that our cutoff of simulations that fail to reach a minimum number of species is partially responsible for this bias. Clades that reach our cutoff threshold under the null model are relatively "lucky": one or a few early species give rise to many more species than would be expected on average. BiSSE may be detecting this random early burst of

diversification and erroneously associating it with (usually) primitive states. It is puzzling, however, that this bias does not exist in simulations with continuous character evolution. We hypothesize that this early burst of speciation, which would necessarily also cause character evolution in a model based on punctuated equilibrium, exacerbates a bias that is not otherwise strong enough to yield statistical significance in a continuous evolution model. Nonetheless, when using BiSSE-type algorithms, one should be careful with young, rapidly diversifying groups that otherwise present good opportunities to study evolution (e.g., the Hawaiian silversword alliance; Carlquist et al. 2003). Punctuated equilibrium is a common pattern in the fossil record (Eldredge & Gould 1972; Gould & Eldredge 1977), so it would be dangerous to assume that clades without good fossil representation are free of its effects.

In other respects, our analyses did not detect an appreciable difference between analyses using a model of punctuated equilibrium versus continuous character evolution as BiSSE assumes. Exactly when relative to clade age BiSSE is liable to cause type-I error do differ between our analyses, with length-1 runs being safe in two of our four models and dangerous in the other two (Table 2, Figure 2), but in all cases length 0.75 is safe and length 1.5 is unsafe; the point at which BiSSE causes elevated rates of type-I error occur around the point where speciation rates drop below extinction rates, regardless of other circumstances.

It is also notable that the probability of Type II error under BiSSE declines as clades become older. It is unlikely that this pattern is due purely for a tendency for older clades to contain more species and thus more statistical power, as even our simulations of length 0.5 typically contained many hundreds to over a thousand species, thereby

providing adequate sample size (Davis et al. 2013). Furthermore, our length 1.5+ simulations had lower final diversity than our length-1 simulations, but still had lower rates of type-II error. The decline of type-II error with clade age is likely due instead to longer evolutionary branches that provide more statistical power to the model than due to larger numbers of species, because the trend continues after one time unit has elapsed, by which point total final richness has begun to decline. These results contrast with those of Machac (2014), who found that QuaSSE is very prone to type-II error if diversification is slow. However, in our simulation, BiSSE continues to improve even as net diversification rates become negative, a scenario that Machac's tests did not consider. BiSSE is computationally simpler and less intensive than QuaSSE, since the variable measured by BiSSE is binary instead of continuous, leading to much shorter computation times. The binary nature of the explanatory variable (character state) may afford BiSSE greater power to detect differences in the response (evolutionary rate parameters) than does QuaSSE in which the explanatory variable is continuous. Further examination of BiSSE-type algorithms is likely warranted.

As expected, under the range of parameters we tested, BiSSE performs fairly well at avoiding type-II error when the effects of character state on evolutionary rates are large. This is true regardless of whether character evolution only occurs with speciation (and thus is decreasing in rate as well) or whether character evolution rates are constant and independent of speciation. Not surprisingly, however, if the effect size is small, BiSSE is much less able to identify it. The necessary tendency for species early in a clade's history to have the ancestral character state instead of the derived state still creates a bias favoring higher diversification rates in the ancestral state. If the derived

state exhibits only slightly (1.05 times) higher speciation rates than the ancestral state, then the bias can overwhelm the true signal. As with type-I error, this phenomenon is only evident after the point when net diversification becomes negative. Type-II error rates in our smaller difference (1.05) simulations indicate that phylogenetic comparative methods such as BiSSE are nearly useless when the difference between the ancestral and derived state is this small. This was an expected result, however, in the light of the confidence limits calculated by Davis et al. (2013). Davis et al. (2015) further simulated clade evolution in which one character state had as much as five times higher speciation rates than the other character state. Constraints of the question we address in this paper preclude us from simulating differences between state 0 and state 1 this large because it would result in net positive diversification rates even in the longest simulation runs (for explanation see methods). Because we were able to discern that BiSSE increasingly recovers correct differences in speciation rates between the derived and ancestral states using our 1.33-fold difference, we can conclude that it will continue to do so with even larger asymmetries in speciation rates as a function of character state.

All of our simulations generated a substantial proportion of total species that became extinct during the run, from about 45% in the length-0.25 runs to more than 90% in the length-2 runs. In certain circumstances, BiSSE infers extinction rates for both character states as being zero; in the punctuated equilibrium model, this is true especially for depauperate clades that have lost most of their lineages to extinction (which occurred in all of our length-1.5 and 2 runs). In our simulations with continuous evolution, this misinterpretation of zero extinction still occurs (although less often), but in the shorter simulations with younger clades. Although this is more understandable than inferred

extinction rates might be lower, in none of our simulations did more than 57% of the species generated survive to the end of the simulation, and in most runs the proportion of survivors was much lower than this. Thus, BiSSE should not be trusted to successfully parse out rates of speciation from extinction, even when it is capable of distinguishing differences in net diversification rate. This problem, in which phylogenies of extant species and birth-death models of speciation and extinction imply zero or very low extinction rates, is not unique to BiSSE (e.g. Quental and Marshall 2010).

In summary, BiSSE performs well under certain circumstances, in particular for clades of intermediate age, after the initial pulse of rapid diversification, but prior to a long period of decline. In comparison to constant rate estimators, BiSSE is robust to type-I error for clades of intermediate age (Machac 2014). Probability of detection of true effects of character states on diversification depends on the age of the clade, with type-II error being less common in analyses of older clades. Predictably, larger differences in speciation rates between character states also increase their probability of being detected. BiSSE is more resistant to type-II error than Machac's (2014) analysis indicated QuaSSE to be when analyzing clades with declining diversification. However, BiSSE performs poorly when analyzing clades that have negative rates of diversification, or (in the event of punctuated character evolution) in clades that are extremely young.

There are ways to gauge whether a clade is currently diversifying or declining and thereby estimate whether BiSSE would be subject to the biases we illustrate in this paper when analyzing such a clade. Many groups (e.g. many insect orders, non-arborescent angiosperm families) have sufficient fossil records to propose a "diversity curve" (e.g. Sepkoski 1981) of richness over time, but insufficient fossil data to know exactly which

evolutionary novelties are responsible for their diversification. Such groups are potentially good targets for analysis using BiSSE, albeit with the caveats raised by Rabosky & Goldberg (2015). Other groups (e.g. scleractinian corals, many bivalve and gastropod clades) may have excellent fossil records recording diversity, but ambiguous morphological characteristics that obscure relatedness of extinct groups. For lineages with no appreciable fossil record (e.g. many herbaceous angiosperm groups, many protists), there are ways to estimate whether clades are diversifying or declining based on their phylogenies (see Morlon 2014 for review), but these too use some simplifying assumptions. Groups with well-resolved fossil histories that inform both phylogeny and paleodiversity (most fossil vertebrate groups) are best analyzed with paleontologically-driven models and not with BiSSE, especially if these groups are declining as many such lineages are (e.g. brachiopods, many gymnosperm families).

Excluding paleontologists interested in understanding paleodiversity patterns, evolutionary biologists naturally have a tendency to study young, species-rich lineages in attempt to explain how they became as diverse (e.g. Goldberg et al. 2010, nightshades; Hugal & Stuart-Fox 2012, color-varying birds). Lineages known from fossil data to have been more diverse in the past than they are now should not be examined with BiSSE; instead, the fossil record itself may more accurately represent historical changes in their diversity. Of most concern, then, is the prevalence of type-I error that BiSSE, and probably other methods, exhibit for young adaptive radiations undergoing speciation-driven (and thus punctuated) character evolution, which are otherwise tempting targets for phylogenetic comparative analyses.

At present, BiSSE and its cousins MuSSE, QuaSSE, etc. are the only methods capable of addressing both character evolution and the effects of these evolving characters on diversification or extinction rates. However, apart from the use of fossils to build the phylogenies that these methods use (e.g. to calibrate dates), none of these algorithms are capable of incorporating fossil data, which will be needed in order to eliminate problems such as those investigated in this paper. One possible way to do this would be to enable time-variant rates of speciation and extinction using paleodiversity curves such as those constructed by Sepkoski (e.g. 1981). Also possible would be the ability to include extinct taxa on the phylogeny such as that used by BioGeoBEARS (Matzke 2013). Future development of comparative phylogenetic methods might focus on the ability to incorporate such data. Nonetheless, phylogenetic comparative methods including BiSSE remain a useful tool in an evolutionary biologist's arsenal, but reliance on them to the exclusion of other sources of data, especially fossil data, can lead to systematic inaccuracy when assessing evolutionary history. There are an increasing number of scenarios for which phylogenetic methods successfully recreate past patterns of diversification, but still many (e.g. Machac 2014, Rabosky & Goldberg 2015) where they fail.

CONCLUSIONS

Current phylogenetic comparative methods infer past diversification and extinction trends in clades from phylogenies of extant species. These methods assume positive net diversification throughout the clade's history, which the fossil record shows is incorrect for many clades. In comparison to other current phylogenetic methods (e.g.

QuaSSE, Machac 2014), BiSSE is moderately robust producing correct results even in clades that have undergone long-term declines in speciation and extinction rate, so long as net diversification (speciation minus extinction) remains positive, and so long as other, independently-evolving traits, do not incidentally coevolve with traits of interest (Rabosky & Goldberg 2015). However, in clades that have reached peak diversity and are now in decline, BiSSE is biased toward inferring higher speciation and extinction rates for the ancestral character state, even when no such association exists. If the derived state conveys substantially higher speciation rates than the ancestral state, BiSSE is robust to its assumptions being violated, even as net diversification for the entire clade becomes negative.

CHAPTER ACKNOWLEDGEMENTS

We acknowledge Brian O'Meara, Stacey DeWitt Smith, and Charles Delwiche for discussions in the formative stages of this project. Erik Simpson taught the first author how to write the software that was used to conduct the analysis. Members of the Dudash-Fenster lab group for comments on this manuscript at the University of Maryland, especially Michele Dudash, provided useful comments on this manuscript. Funding support came from the program in Behavior, Ecology, Evolution, and Systematics at the University of Maryland.

TABLES

Table 1 – Schematic of the data analyses. Error type assessment refers to whether the simulation was testing for type-I error (false rejection of the null hypothesis) or type-II error (false acceptance of the null hypothesis). Morphological evolution model refers to whether character state changes were assumed to happen only during speciation events (“Punctuated”) or whether character states could evolve at any point in a species’ history, being independent of speciation events (“Continuous”). λ ratio signifies the ratio of the speciation rate of the derived character state (state 1) relative to the ancestral character state (state 0). A λ ratio of unity indicates that the speciation rates of the two character states are exactly equal. The extinction rate change model represents what simulated long term trends existed in extinction rate (in all runs, speciation rate was decreasing, and more rapidly than extinction). All combinations of models were run with six different simulation lengths of 0.25, 0.5, 0.75, 1.0, 1.5, and 2.0, where length 1 is the time required for speciation rate to decay to the point where speciation and extinction rates are equal. Each combination of parameters (including length of simulation) was run 100 times.

Error type assessment	Morphologic evolution model	λ ratio	Extinction rate change model
Type-I	False rejection of the null hypothesis that there is no effect of character state on speciation rate (i.e. BiSSE detects an effect of character state when there is none).		
Type-I	Punctuated	1.0	Decreasing
Type-I	Continuous	1.0	Decreasing
Type-I	Continuous	1.0	Constant

Type-I	Continuous	1.0	Increasing
Type-II	False acceptance of the null hypothesis that there is no effect of character state on speciation rate (i.e. BiSSE fails to detect an affect of character state when one exists).		
Type-II	Punctuated	1.33	Decreasing
Type-II	Punctuated	1.05	Decreasing
Type-II	Continuous	1.33	Decreasing

Table 2 – Proportions of runs in which BiSSE caused type-I error when analyzing simulated data for six different simulation lengths. The simulation model specifies the model parameters we used to simulate the clade. The first set used a punctuated equilibrium model of character evolution wherein character state transition rates occur only during speciation events. The rest used a model of character evolution wherein state changes are independent of speciation events. Our first two sets have both speciation and extinction rates declining with time as in Fig. 1A. The third has extinction rate constant and only speciation declining as in Fig. 1B. The final set has extinction rate increasing as in Fig. 1C. The significance threshold for all type-I error assessments is 0.05. Simulation length refers to the amount of simulated time that the program was run for; one unit represents approximately the time needed for extinction to outpace origination (see Fig. 1). Speciation rate, extinction rate, and transition rate represent the type-I error rates (out of 100 runs) for BiSSE inferring a statistically significant difference between the evolutionary rate associated with state 0 versus that for state 1 with a significance threshold of α . The number of asterisks indicates whether the type-I error rates are themselves statistically greater than the expected error rates of α following a sequential Bonferroni correction (+ $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Assessment of statistical significance is conducted using a likelihood-ratio test.

Simulation model	Simulation length	Type I error	Type I error	Type I error
		Speciation rate	Extinction rate	Transition rate
Punctuated	0.25	0.19***	0.04	0.22***
character	0.5	0.05	0.02	0.08
evolution,	0.75	0.02	0.07	0.08
extinction	1	0.03	0.05	0.13*

decreasing	1.5	0.21***	0.03	0.09
	2	0.71***	0.18***	0.51***
Continuous	0.25	0.06	0	0.06
character	0.5	0	0	0.03
evolution,	0.75	0.04	0	0.02
extinction	1	0.1	0.01	0.03
decreasing	1.5	0.55	0.04	0.14**
extinction	2	0.93***	0.26***	0.36***
	0.25	0.03	0	0.04
Continuous	0.5	0.03	0.04	0.05
character	0.75	0	0.02	0.05
evolution, constant	1	0.14**	0.17***	0.2***
extinction	1.5	0.25***	0.23***	0.25***
	2	0.99***	0.63***	0.43***
Continuous	0.25	0.02	0	0.06
character	0.5	0.04	0.02	0.04
evolution,	0.75	0.07	0.03	0.04
increasing	1	0.08	0.06	0.07
extinction	1.5	0.36***	0.69***	0.77***
	2	0.99***	0.95***	0.45***

Table 3 – Estimates of systematic bias in directionality of inferred differences in evolutionary rates by BiSSE when no real differences exist. The simulation model specifies the model parameters we used to simulate the clade. The first set used a punctuated equilibrium model of character evolution wherein character state transition rates occur only during speciation events. The rest used a model of character evolution wherein state changes are independent of speciation events. Our first two sets have both speciation and extinction rates declining with time as in Fig. 1A. The third has extinction rate constant and only speciation declining as in Fig. 1B. The final set has extinction rate increasing as in Fig. 1C. Length refers to the simulated time in the run: one unit is approximately the amount of time needed for speciation rate to decay below extinction rate (see Fig. 1). Speciation, extinction, and transition refer to the parameters being estimated (transition to the rate of change from state 0 to state 1 or vice versa). “0 high” signifies the number of runs (out of 100 for a given simulation length) that BiSSE inferred higher rates of the parameter in question for the ancestral state (state 0) than for state 1. “1 high” signifies the converse. Extinction has a third category of “none” for runs in which BiSSE inferred that the extinction rates of both state 0 and state 1 were zero (i.e. no extinction occurred, which was not the case in any simulation). These data do not reflect whether BiSSE found the difference between parameters was significantly different from null expectations, but only the sign of the difference between the estimated values.

Model	Length	Speciation		Extinction			Transition	
		0	1	0	1	None	0-1	1-0
		high	high	high	high		high	high
Punc. Eq.,	0.25	32	68	50	48	2	36	64

extinction	0.5	45	55	52	48	0	42	58
decreasing	0.75	49	51	56	44	0	42	58
	1	54	46	47	52	1	51	49
	1.5	56	44	48	46	6	50	50
	2	60	40	15	13	72	63	37
Continuous, extinction decreasing	0.25	54	46	34	56	10	59	41
	0.5	56	44	44	46	10	49	51
	0.75	48	52	52	48	0	50	50
	1	49	51	52	48	0	49	51
	1.5	49	51	46	54	0	48	52
	2	49	51	56	44	0	46	54
Continuous, extinction constant	0.25	45	55	38	59	3	55	45
	0.5	49	51	43	56	1	57	43
	0.75	49	51	46	54	0	48	52
	1	47	53	50	50	0	46	54
	1.5	48	52	51	49	0	50	50
	2	60	40	60	40	0	62	38
Continuous, extinction increasing	0.25	47	53	40	57	3	48	52
	0.5	40	60	43	56	1	47	53
	0.75	47	53	47	53	0	56	44
	1	51	49	51	49	0	49	51
	1.5	58	42	48	52	0	49	51
	2	46	54	46	54	0	55	45

Table 4 – Estimates of systematic bias in directionality of type-I error in evolutionary rates by BiSSE, but counting only those inferred differences that were significant at the 0.05 level. The simulation model specifies the model parameters we used to simulate the clade. The first set used a punctuated equilibrium model of character evolution wherein character state transition rates occur only during speciation events. The rest used a model of character evolution wherein state changes are independent of speciation events. Our first two sets have both speciation and extinction rates declining with time as in Fig. 1A. The third has extinction rate constant and only speciation declining as in Fig. 1B. The final set has extinction rate increasing as in Fig. 1C. Length simulated time in the run: one unit is approximately the amount of time needed for speciation rate to decay below extinction rate (see Fig. 1). Speciation, extinction, and transition refer to the parameters being estimated (transition to the rate of change from state 0 to state 1 or vice versa). “0 high” signifies the number of runs (out of 100 for a given simulation length) that BiSSE inferred higher rates of the parameter in question for the ancestral state (state 0) than for state 1. “1 high” signifies the converse. Assessment of statistical significance is conducted using a likelihood-ratio test.

Model	Length	Speciation		Extinction		Transition	
		0 high	1 high	0 high	1 high	1 high	0 high
Punc. Eq., extinction decreasing	0.25	7	12	2	7	12	2
	0.5	1	4	0	1	4	0
	0.75	1	1	5	1	1	5
	1	3	0	5	3	0	5
	1.5	10	11	2	10	11	2
	2	46	25	7	46	25	7

Continuous, extinction decreasing	0.25	3	3	0	0	2	4
	0.5	0	0	0	0	1	2
	0.75	2	2	0	0	1	1
	1	4	6	0	1	1	2
	1.5	24	31	2	2	7	7
	2	43	50	17	9	12	24
Continuous, extinction constant	0.25	1	2	0	0	0	4
	0.5	0	3	0	4	2	3
	0.75	0	0	2	0	0	5
	1	6	8	8	9	9	11
	1.5	16	9	15	8	10	15
	2	59	40	41	22	30	13
Continuous, extinction increasing	0.25	1	1	0	0	3	3
	0.5	1	3	0	2	3	1
	0.75	3	4	1	2	2	2
	1	7	1	4	2	5	2
	1.5	21	15	35	34	38	39
	2	46	53	45	50	23	22

Table 5 – Association between type-I error inferred in speciation rates and in extinction rates for our BiSSE simulations. (A) refers to results of our punctuated equilibrium model of character evolution, and (B) refers to our continuous model of character evolution. The numerator in the ratio is the number of runs in which there is (or isn't) error as described for both the focal parameter and the covariate parameter. The denominator in the ratio represents the total number of runs for which there is or is not error as indicated in the focal parameter only. For instance, in the second row of (A), there were 13 runs in which BiSSE committed type-I error in inferring differences in extinction rate but not speciation rate, and 479 total runs in which BiSSE did not infer type-I error in speciation rate. The proportions, calculated from the ratios, indicate that for type-I error in both parameters (speciation rate or extinction rate), if BiSSE commits type-I error inferring one parameter, it is more likely to do so with the other parameter than if BiSSE did not commit type-I error in the first parameter. Type-I error in speciation and extinction rates are significantly more likely to occur together in the same run than expected by chance in both of our models (Fisher's Exact Test $P < 0.0001$).

A.

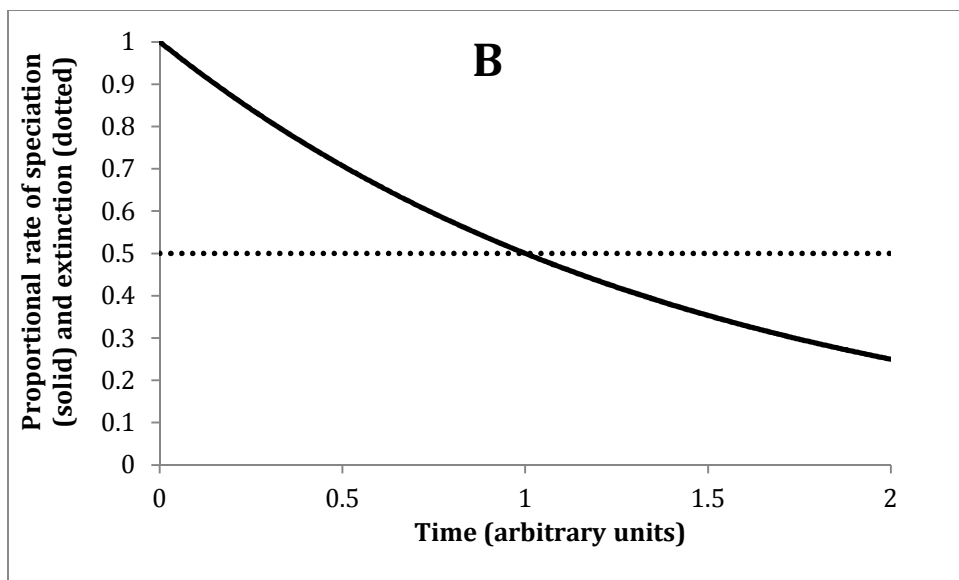
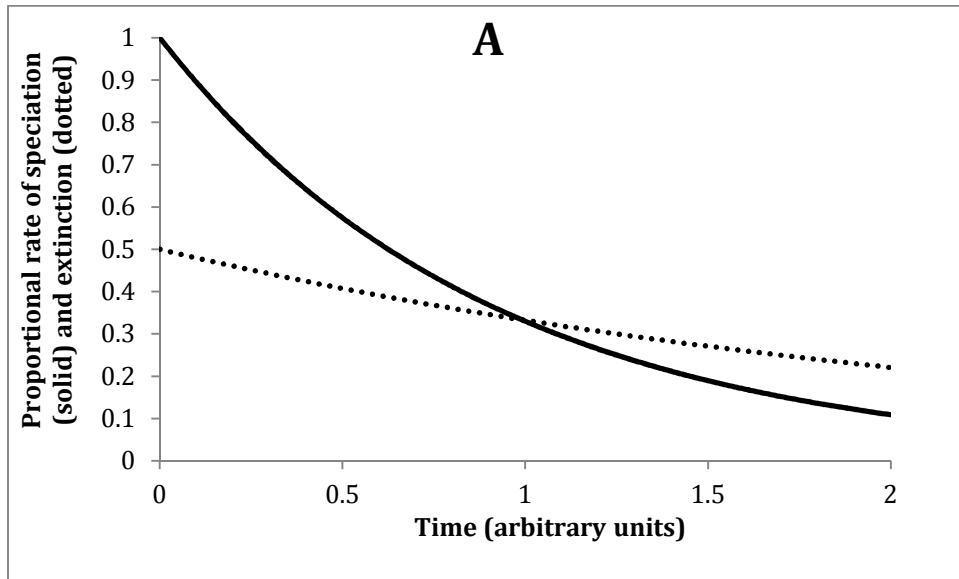
Focal parameter	Covariate parameter	Ratio	Proportion
Error in Speciation	Error in Extinction	26/121	0.21
No Error in Speciation	Error in Extinction	13/479	0.03
Error in Extinction	Error in Speciation	26/39	0.67
No Error in Extinction	Error in Speciation	95/561	0.17

B.

Focal parameter	Covariate parameter	Ratio	Proportion
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Error in Speciation	Error in Extinction	244/468	0.52
No Error in Speciation	Error in Extinction	71/1332	0.05
Error in Extinction	Error in Speciation	244/315	0.77
No Error in Extinction	Error in Speciation	224/1485	0.15

FIGURES



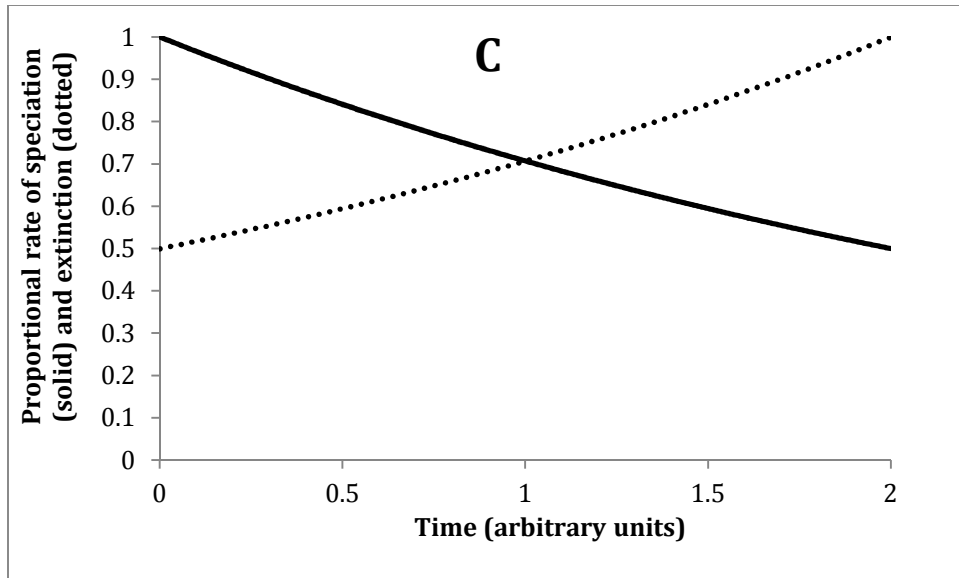
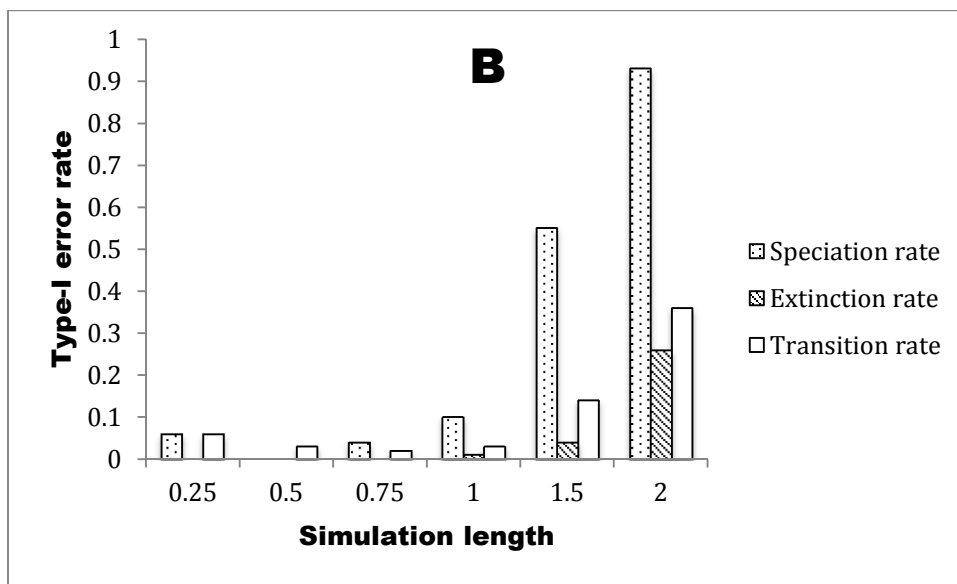
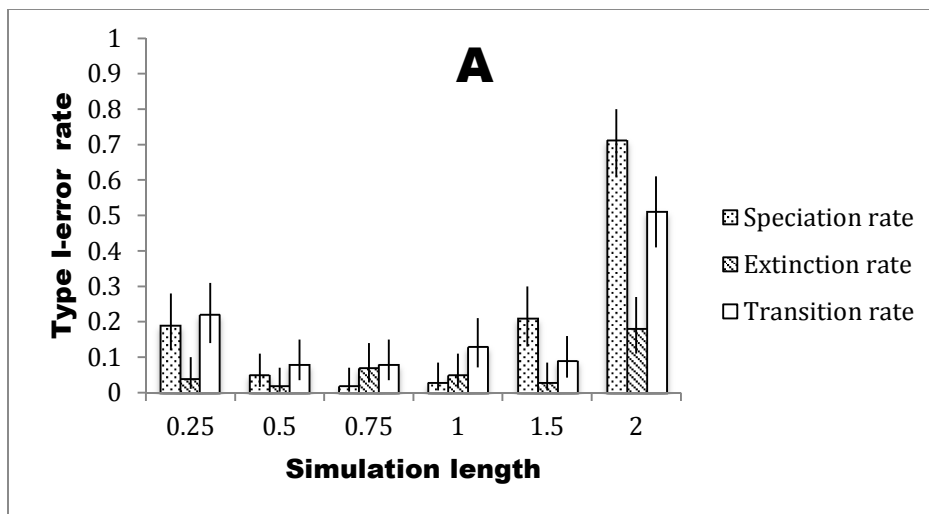


Figure 1. Graphical depiction of speciation and extinction model. The solid line represents the relative speciation rate, and the dotted line represents the relative extinction rate. (A) Speciation and extinction rates begin high, then decay exponentially through time, with the slower rate of decay in extinction rate eventually leading to extinction outpacing speciation. (B) Speciation rate begins high and decays exponentially, while extinction remains constant. (C) Speciation begins high and decays, while extinction begins low and increases. Speciation is scaled to 1 and extinction to 0.5, representing that our simulations had an initial extinction rate half that of speciation. For trials in which the derived state had higher speciation rates than the ancestral state, the multiplier for the derived state was in addition to that shown here; thus, speciation rate began at 1.05 or 1.33 for the derived state in these simulations, rather than 1. Time is scaled such that one unit represents approximately the amount of time necessary for the two rates to reach equal levels; before one time unit has passed, a clade is still diversifying, but afterwards, it is declining. For each set of state parameters, we ran 100 trials with each that ending at time $t = 0.25, 0.5, 0.75, 1, 1.5,$ and 2. In real-world taxa, the

exact length of time that one unit corresponds to, as well as the relative decay constants, varies among groups (Sepkoski 1981, 1984; Valentine et al. 1991).



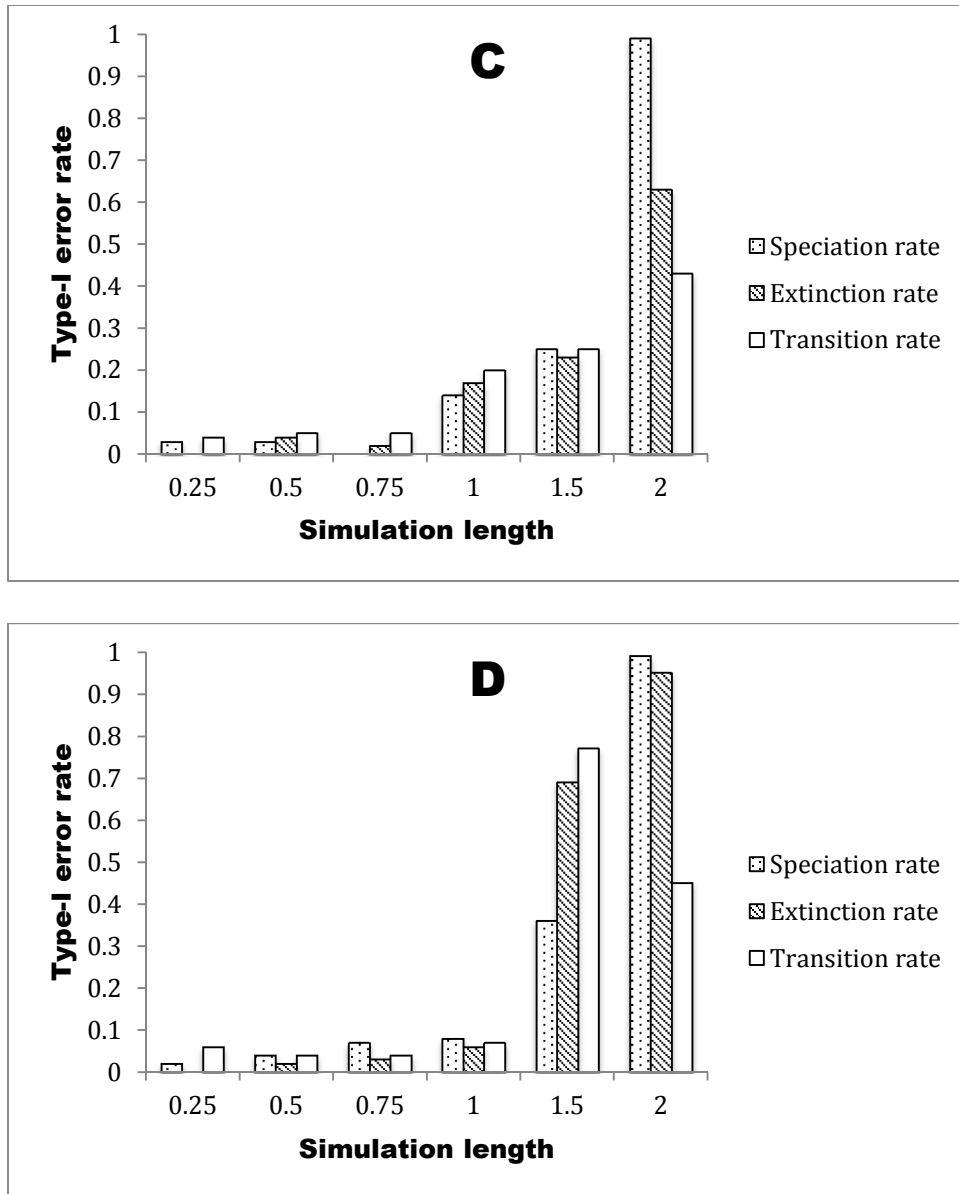
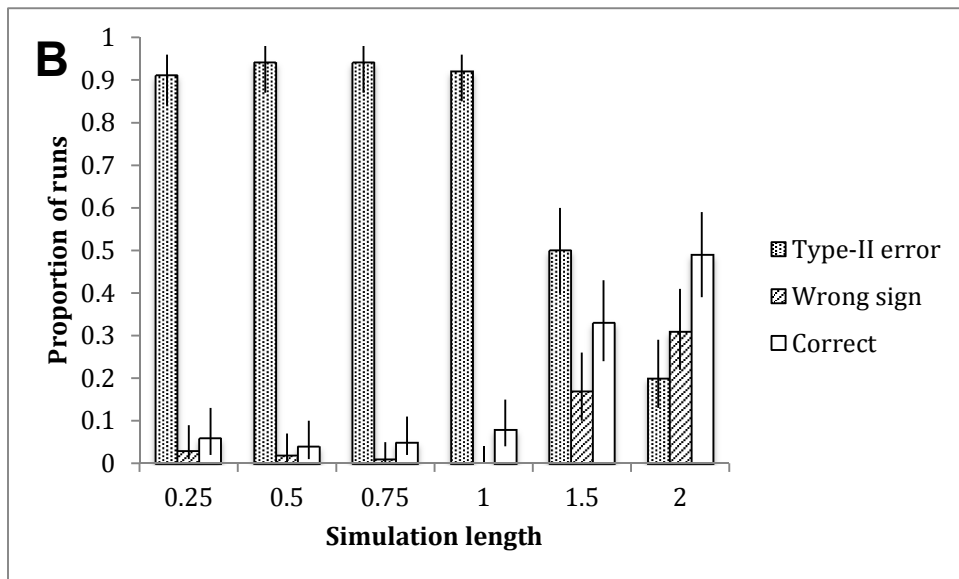
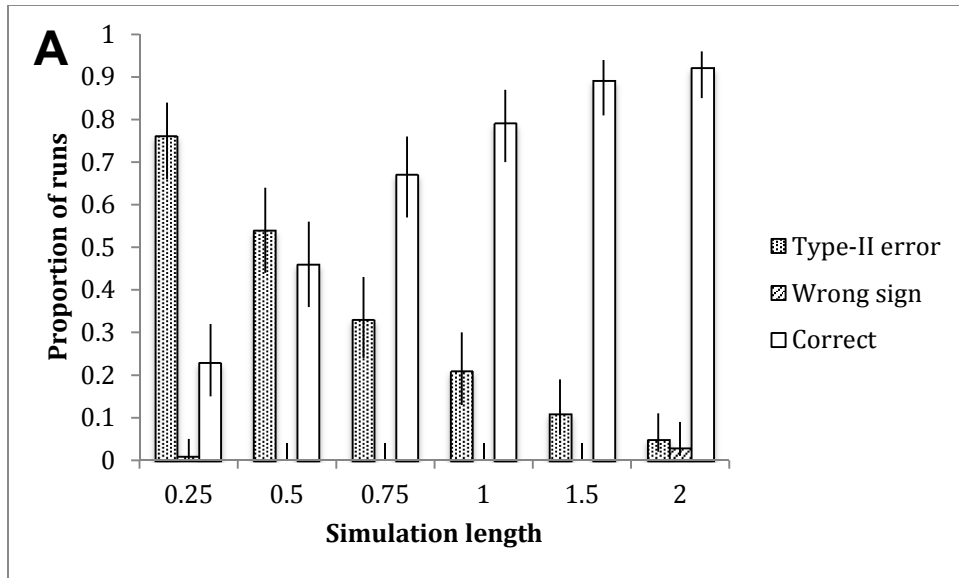


Figure 2— Proportions of runs exhibiting type-I error by BiSSE on simulated clade data. Simulation length is the amount of time the simulation ran to generate the simulated clade, with one unit being roughly the time necessary for the speciation rate to drop below the extinction rate (see Fig. 1). (A, B) Speciation and extinction rates both decline, but at different rates such that extinction eventually overtakes speciation, as in Fig. 1A. (C) Speciation rates decline while extinction rate is constant, so that eventually extinction dominates, as in Fig. 1B. (D) Speciation rate decreases while extinction rate increases, as

in Fig. 1C. The relative rates of speciation and extinction are the same as those described in the corresponding graph in Fig. 1. (A) Character evolution follows a punctuated equilibrium model, whereby character evolution only occurs during speciation events. (B, C, D) Character evolution is continuous and proceeds irrespective of speciation. Type-I error signifies the proportion of 100 runs for which BiSSE incorrectly determined parameters of the derived state (state 1) to be statistically different from those of the ancestral state (state 0). The speckled bars represent differences in speciation rates, the striped bars extinction rates, and the unfilled bars character state transition rates. Error bars represent the 95% confidence limits on the actual rate of type-I error based on the size of the sample. In these simulations, the true evolutionary rates associated with ancestral and derived states are equal, and thus BiSSE's finding them to be unequal constitutes type-I error. Assessment of statistical significance is conducted using a likelihood-ratio test.



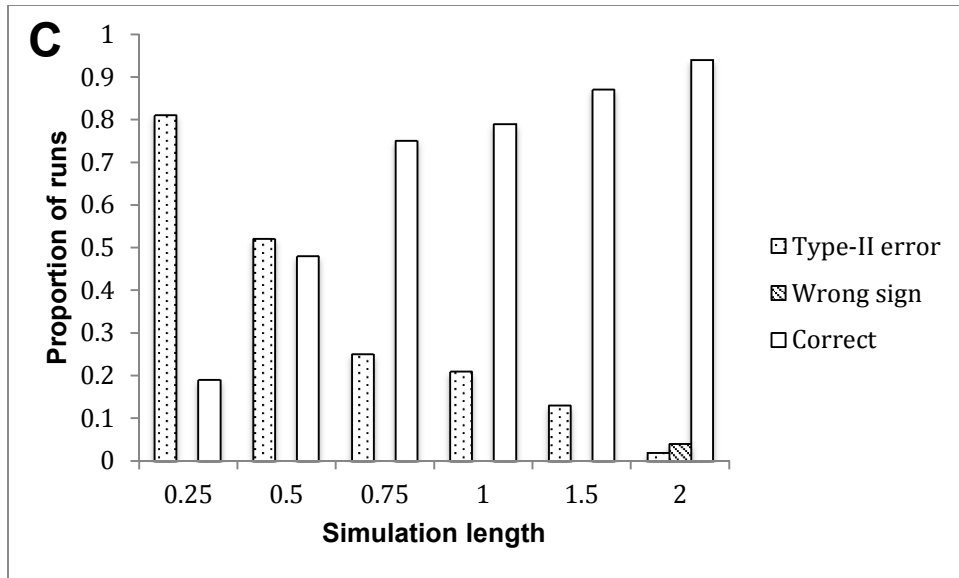


Figure 3 – Error and success rates of BiSSE in type-II error simulations at estimating speciation rates of respective character states (not extinction or state transition rates, unlike Fig. 2). In (A), the speciation rate of the derived state (state 1) is 1.33 times the speciation rate for the ancestral state (state 0) at any given point in time, but both decline exponentially with time as in Fig. 1A. Moreover, character states only change during speciation events, as predicted by punctuated equilibrium. In (B), the speciation rate of state 1 is only 1.05 times that of the ancestral state, and character state changes only at speciation events. In (C), the speciation rate of state 1 is 1.33 times that of the ancestral state, but character evolution occurs independently of speciation. The speckled bar represents the proportion of runs in which type-II error occurred (i.e. BiSSE failed to correctly reject the null hypothesis that the speciation rates were the same). The striped bar signifies that BiSSE rejected the null hypothesis but in the wrong direction, estimating state 0 to have a higher speciation rate. The clear bar indicates that BiSSE successfully rejected the null hypothesis and found a difference of the correct sign. All three bars refer to (non-)error in speciation rates. Proportion of runs represents the

proportion (out of 100 runs) that each result for simulation length. Length of simulation is scaled such that one unit is approximately the time required for speciation rate to drop below extinction rate (see Fig. 1A). Error bars represent the 95% confidence limits on the actual frequency of the particular type of (non-)error being represented. Assessment of statistical significance is conducted using a likelihood-ratio test.

Chapter 2 - Evidence for clade selection in the Rosales influenced by dispersal, geographic range size, and species richness

CHAPTER ABSTRACT

Increasingly, scientists are linking ecology to evolutionary biology by finding evidence for macroecological explanations for patterns of evolutionary diversification and extinction, with particular attention given to geographic range size and related factors. Here we explore the relationships between plant habit, mechanism of seed dispersal, geographic range size, within-genus species richness, and net diversification rate in the angiosperm order Rosales using comparative approaches. About half of the variation in net diversification rate is largely explained by habit; this is large enough that herbaceous genera have net positive diversification rates regardless of other character states. The rest of the variation in rate among Rosalean genera is explained by a three-way interaction between multi-continent geographic range, animal-mediated dispersal, and possession of 20+ species per genus, whereby genera possessing all three traits have high diversification rates while genera lacking even one have much lower rates. Without the interaction woody genera are more likely to become extinct before giving rise to more genera. This interaction may reflect the importance of colonization ability in surviving late Cenozoic (especially Pleistocene) climate volatility.

Keywords: Geographic range size, dispersal, clade selection, Rosales, MuSSE

INTRODUCTION

The diversification and extinction of lineages is nonuniform across taxa and has been proposed to correlate to macroevolutionary (Van Valen 1973, Sepkoski 1981, Raup & Sepkoski 1982), morphological (Hughes 2007), and ecological (Simpson 1944, 1953; Stebbins 1970, 1971; Bambach 1993, Tiffney & Mazer 1995) features. Explaining trends in the diversity and ecological prominence of clades over geologic time in terms of ecological interactions is complicated because of the contrasts between ecological and geological time scales. Predator-prey dynamics, competitive exclusion, selective sweeps, etc. have measurable effects on generational time scales, but long-term patterns in diversification and extinction are visible only over geologic time. This disparity in time scale between pattern and process raises questions about how one could be responsible for the other. One way of potentially establishing this link is through investigating intermediate-scale emergent properties, such as geographic range size, in a phylogenetic context. Does long-term diversification correlate as predicted with traits believed to be important at ecological scales?

Geographic range size is frequently believed to be important in studies of lineage diversification and survivorship (IUCN 2012; see also Payne & Finnegan 2007; Vamosi & Vamosi 2012). Because a larger geographic range size buffers a taxon against extinction by disturbance or environmental change, many have predicted that lineages possessing larger ranges would exhibit higher probabilities of survivorship over geologic time (e.g. Rabinowitz 1981, 1986; Jablonski & Raup 1995, Yu and Dobson 1999). Tests using fossil data generally confirm this prediction and also that geographic range is at least partially heritable (Jablonski & Hunt 2006), but with the caveat that factors

unrelated to range size are also important (Jablonski & Raup 1995, Foote & Miller 2013) and also that extinction selectivity on range size differs between background and mass extinctions (Payne & Finnegan 2007). Additionally, one might predict that larger range size would influence a taxon's propensity to give rise to new lineages, but here the predictions are less clear: small ranges potentially allow for greater niche partitioning and greater species richness while larger ranges may allow for colonization of distant habitat and founding new populations that through allopatric or parapatric speciation process ultimately become new species or larger taxonomic groups (Ricklefs & Latham 1992 and references therein). Although there are mechanisms by which geographic range could directly influence the number of species or larger taxonomic units, relatively little work has been on how ecological traits might influence geographic range, which would in turn affect geologic-term survival and diversification of evolutionary lineages.

Here we focus on how the mechanism of seed dispersal in plants is associated with geographic range dynamics, and how they together affect diversification and survival. Seed dispersal has been related to angiosperm diversity in past studies (Stebbins 1971, Herrera 1989, Tiffney & Mazer 1995, Bremer & Eriksson 2008), although rarely in a phylogenetic context (but see Vamosi & Vamosi 2012; Larson-Johnson 2016).

Numerous other characters have also been implicated in influencing diversification patterns in angiosperms, including pollination syndrome (Fenster et al. 2004), leaf vein density (Boyce et al. 2009), and growth rate and adaptation to fire (Bond & Scott 2010). Tiffney (2004) has addressed this somewhat in other plant groups in the fossil record, suggesting that climate-driven coevolution between seed plants and vertebrate dispersal agents leads to differential diversification of different traits in different time periods.

Rather than identifying individual dispersal characters as important for diversification, Stebbins (1970, 1971) pointed to combinations of interacting characters that create functional dispersal syndromes and also aid in establishment (see also Tiffney & Mazer 1995; Vamosi & Vamosi 2010, 2012; Larson-Johnson 2016). Vamosi & Vamosi (2010) correlated range size with dispersal type in fossil angiosperms, and subsequently (2012) found a correlation of range size with proportion of threatened species listed by the IUCN. Numerous studies on the latitudinal seed size gradient (e.g. Moles et al. 2007, Wright et al. 2007) have demonstrated possible associations between seed dispersal type and other factors, notably habit. Although Vamosi & Vamosi (2012) reviewed character state evolution in functional and life history traits as well as geographic range, they did not quantify the interactions between all three sets of characteristics: range size, morphological character states, and lineage survivorship, simultaneously (but see Jablonski & Hunt 2006).

To our knowledge, ours is the one of few studies (but see Larson-Johnson 2016) that investigates a causal mechanism connecting everyday ecology (dispersal), macroecological processes (geographic range size), and lineage survivorship over geologic time in a single analysis. To examine the three-way relationship between animal dispersal, geographic range size, and diversity, we chose to focus on the angiosperm order Rosales as our study group. The Rosales includes roughly 250 genera, accounting for approximately 2.5% of extant eudicot species (Magallón et al. 1999). The Rosales disperse their seeds with a variety of different methods. Those dispersed by animals can have fleshy fruit that animals eat and later defecate the seeds (*Fragaria*, *Ficus*), cacheable seeds (*Rhamnidium*, *Humulus*), both (most *Prunus*), or even burrs that adhere

to fur or feathers (*Acaena*). Additionally there are clades with winged samaras (*Ulmus*) and feathered stylochia (*Cercocarpus*) that catch the wind, and even capsules that dehisce violently, ballistically ejecting seeds (*Ceanothus*, *Dorstenia*). These different mechanisms are not mutually exclusive; for example, *Paliurus* has both a samara and a cacheable seed. Additionally, most of the aforementioned seed dispersal mechanisms are represented in multiple families in the order. The parallel appearance of similar dispersal modes in many monophyletic families in the Rosales (Zhang et al. 2011), indicates that phylogenetic comparative analysis is possible within the group. Finally, the Rosales, especially the Rosaceae, have an excellent fossil record (Devore & Pigg 2007), allowing us to trace their divergence history, and ultimately (in future studies) to compare inferred trends in Rosalean diversity, evolution, and morphology against known details about the past.

In addition to analyzing the effect of character states on diversification rates, phylogenetic comparative methods can also elucidate patterns of differential transition between character states as part of the same analysis. We predicted that long-distance animal dispersal, especially by birds, would enhance geographic range size, which would in turn increase lineage survival over geologic time. We predict this because the Rosales, like all other plant groups living in temperate latitudes, had to withstand cooling and drying Cenozoic climate (Graham 1999, Zachos et al. 2001, Bredenkamp et al. 2002, Strömberg 2011). The amplitude of orbital-scale climate cycles intensified with the overall cooling trend (Zachos et al. 2001, Alley et al. 2003), which we expect to have caused population-level extirpations. Lineages possessing good long-distance dispersal could recolonize areas where they had been locally extirpated, and therefore maintain

larger geographic range sizes, be buffered against extinction, and ultimately have positive net diversification rates. We further predicted that this effect would be stronger in woody lineages than herbaceous lineages (see Sanderson & Donoghue 1994) because herbs typically have shorter generation times than trees, thus enabling them to make climate-induced range shifts in a larger number of short-distance dispersal events, instead of requiring the long-distance dispersal that trees with decades-long generation times would. Finally, we predicted that within-genus species richness would have an independent positive association with genus-level diversification because any new genus must begin as a new species and the propensity to speciate would thus allow for more genus origination as well.

METHODS

Ascertaining character state information

We conducted our study of diversification in the Rosales at the genus level. As such, the units of diversification are genera per million years, and the units of extinction are the probability of genus-level extinction per million years. We did this for the following reasons: Rosales contains many thousands of species, too many for current phylogenetic methods to process, but only about 250 genera. We wish to be able to apply our results to fossil data on the Rosales, and fossil taxa more than a 5-10 million years old very rarely belong to modern species but often are identifiable to modern genera. We sought to address hypotheses about evolution above the species level, i.e., are there evolutionary/ecological units above the species level that exhibit emergent behavior that

cannot be extrapolated from knowledge of species alone? Finally, a number of diverse genera in the Rosales, among them *Crataegus*, *Amelanchier*, and *Ficus*, exhibit a high degree of apomixis (e.g. Campbell & Dickinson 1990), rendering biological species concepts only marginally less arbitrary than genera.

Our four characters and their respective states are outlined in Table 6. Because of the abundant literature implying animal dispersal to be important in lineage diversification in angiosperms (e.g. Tiffney & Mazer 1995 and many others), we scored dispersal type as either being with or without animal-assisted dispersal, recognizing that biotic and abiotic dispersal mechanisms are not always mutually exclusive and genera with both types them as animal-dispersed. Geographic range size we scored as whether a genus was present on a single continent, or more than one; our reasons for doing this are discussed in the section on geographic range data below. We scored habit as whether a genus was woody or herbaceous, on the assumption that woody taxa necessarily have multi-year generation times while herbaceous taxa often include annuals. We coded species richness as whether a genus contains at least 20 species. This includes roughly 20% of the Rosalean genera.

We measured fruits of one species per genus of all genera in the Rosales using herbarium collections of the United States National Museum of Natural History. For genera that NMNH did not have, we supplemented our data by measuring collections at the Missouri Botanical Garden. We used Kubitzki (1990) to quantify genera unavailable at either institution, and to verify observations from herbarium specimens. Generic names were standardized using the Angiosperm Phylogeny Working Group online database hosted by the Missouri Botanical Garden

(<http://www.mobot.org/MOBOT/research/APweb/>). Characters measured include fruit type, fruit dimensions and volume, seed dimensions and volume, number of seeds per fruit, presence of wings on the fruit and/or seeds, presence of hooks on the fruit, and overall habit of the plant with emphasis on length of the plant's life cycle. Fruit type included both the developmental origin and consistency of the fruit itself as well as of organs connected to the fruit that play roles in dispersal, such as the fleshy receptacle of *Fragaria* (strawberry).

Although quantitative variation in fruit and seed characteristics is widespread withinin genera of the Rosales, only very rarely do qualitative fruit characteristics vary significantly below the genus or even the tribe level (see Kubitzki 1990 for details; see also Potter et al. 2007). Much of the intrageneric variation in fruit type is the result of genera that have both drupes and nuts (e.g. *Prunus*), of which both fruit types share one mechanism of dispersal, caching. This is not a concern for our analysis, because both are still animal dispersed and such genera were coded as animal-dispersed. Quantitative morphological variation, correspondingly, rarely exceeds a factor of two in dimensions (see Kubitzki 1990), which is likely sufficient to affect which animals are responsible for dispersal, but less likely to affect underlying dispersal types, given the size ranges of major animal seed-dispersing groups (mammals, birds, insects).

By reducing our characters, especially geographic range size, to binary states, we discarded much of the information available on the Rosales. For instance, it is possible that extreme long-distance wind dispersal might substitute for animal dispersal in some (especially short-generation) taxa. While no Rosalean taxon has seeds as small and long-ranging as those of many Orchidaceae (Kubitzki 1990), discounting the possibility of

such long-distance wind dispersal may add some imprecision in our dataset regarding the ecological consequences of the traits that we investigated, thereby reducing our statistical power in identifying the true effects of the characters we here study.

Geographic range data

Assessing geographic ranges for Rosalean genera was a two-step process. Geographic range maps were acquired from the Global Biodiversity Informatics database (GBIF, www.gbif.org). However, because GBIF maps provide information on the collecting locations of specimens in herbaria, ranges include individuals from gardens and other introduced populations, and other locations that can distort the pre-human range of a taxon. For this reason, maps examined with GBIF were then compared against the literature (Kubitzki 1990) in order to identify which collection localities should be included in our estimates of natural geographic range.

Because our initial hypotheses focused on the effectiveness of long-distance dispersal to cross geographic barriers, we defined geographic range size by the number of continents upon which a genus is found. Thus, if a genus is present on multiple continents, we here classified it as widespread, but if it is found on only one continent, we coded it as restricted. We did this in an attempt to estimate a taxon's ability to disperse/colonize across geographical barriers such as ocean basins, we counted the number of continents upon which a genus was present. Large oceanic islands separated by other landmasses by ocean basins such as Madagascar and New Zealand were treated as continents for this reason. These land masses split during the Late Cretaceous (Scotese 2001), after the divergence of the Rosalean families from the last common ancestor of the

order, but before the lineages within the families themselves began to appreciably diverge (see Appendix I and clade age discussion below). For this reason, vicariant biogeography resulting from continental drift should not be relevant to determining geographic ranges of living Rosalean genera. We similarly considered Wallacea (Mayr 1944) to be a continent, because it was not connected to either Asia or Australia during Pleistocene ice age driven sea-level drops (Lambeck et al. 2002), unlike New Guinea or the rest of Indonesia. Treating large or separated oceanic islands as continents affects the coding of only one genus (*Dallachya*), and three genera are coded as widespread because they cross Wallace's Line (*Parartocarpus*, *Nothocnide*, and *Leucosyke*).

Phylogenetic analysis

In order to conduct a phylogenetic comparative analysis of character-associated diversification across the Rosales, we needed a phylogeny with branch lengths scaled to time, which was not available from the literature. To address this, we used the multiple sequence alignment of Potter et al. (2007) for the Rosaceae, and appended it with the other Rosalean families using NCBI BLAST (Madden 2002), choosing GenBank accessions possessing the most sequence data available covering the same genes used by Potter et al. (2007). Sequences were then aligned using MUSCLE (Edgar 2004).

We used BEAST (Drummond et al. 2012) to construct the phylogeny. Nodes and subclades within the Rosales were constrained using Potter et al.'s (2007) tree, and the Angiosperm Phylogeny Group III phylogeny (Angiosperm Phylogeny Group 2009). We calibrated our tree using one fossil date for each major Rosalean group (Appendix I). Priors were uniform in the absence of reason to assign nonuniform priors.

Character-associated diversification analysis

We used the Multiple-State Speciation and Extinction (MuSSE) method implemented in Diversitree (Fitzjohn, 2012) to reconstruct associations between diversification and character state in the Rosales. MuSSE infers origination and extinction rates from the shape and topology of the phylogenetic tree without fossil data, making some simplifying assumptions about evolution. In chapter 1, I investigated these assumptions in the context of declining diversification rates. The Rosales are presently still diversifying (e.g. see DeVore & Pigg 2007), and therefore do not violate MuSSE's assumptions severely enough to invalidate our results (Simpson et al. submitted). We considered four variables, the maximum number that was computationally feasible with the size of our dataset. As described above, each quantitative or multi-category variable was converted to a binary one: (1) presence or absence of animal dispersal; (2) single-year life cycle or multi-year life cycle; (3) genus occupies one continent or multiple continents; (4) genus has 20+ species or 19- species.

MuSSE-type models excel by accounting for both the effect of character state on parameters relevant to diversification rates (speciation, extinction), as well as rates relating to differential character state change, analyzing and predicting these two factors simultaneously (Fitzjohn 2012). The most complex model we could (and did) use has 96 evolutionary parameters: 16 parameters associated with origination as a function of “character” state (the analysis treating species richness and geographic range size as characters), 16 parameters associated with extinction as a function of character state, and 64 characters representing state transition rates (16 for each of the four characters, as

influenced by the other characters). By constraining or not constraining each of these parameters, there are 2^{96} (approximately 10^{28}) different possible models of evolution; thus, we were forced to choose only a subset of these possible models. It is computationally unfeasible to test all of these possible models. Therefore our comparison and test for statistical significance used only a small subset of these models. We are aware of two different strategies for doing this with a MuSSE dataset with this many (four) character variables: either by subsetting models based on pairs of characters (O'Meara et al. in press), or by subsetting models based on the processes that they effect such as origination, extinction, and state transitions (Price et al. 2012). We expected that different characters were likely to interact in complex ways and wishing to parse out the most substantive effects on diversification. For this reason, we elected to use a system more similar to that of Price et al. (2012) that allows us to compare the relationship between diversification rate and all four characters and their interactions simultaneously. For this reason, our “base” model was a complete model, using all 96 parameters, instead of a null model where all evolutionary rates were uniform and unaffected by character state. From this complete model, we then excised sets of the terms in order to see if individual sets were unnecessary in fitting the data, and then compared them to the complete model using AIC scores in a fashion similar to Price et al. (2012)’s MuSSE analysis of mammal diversity. In total, we ran eight MuSSE models (Table 7). First of these was a full model with all 96 parameters free to vary. The other seven had subsets of our parameters constrained to be unaffected by character state. In order to test if there was an effect of character state on diversification rates, we ran one model in which character state did not affect origination rates, and another in which it did not affect

extinction rates. We ran five models to test for asymmetrical rates of change between the different character states: one in which no state transition rate was affected by any character, one in which dispersal mechanism evolution was unaffected by character state, one in which evolution of woody versus herbaceous habit was unaffected by character state, one in which geographic range size was unaffected by character state, and one in which species richness was unaffected by character state. In all of these, we compared our constrained model to the full model to assess whether diversification rates or state change rates were affected by character state. That we are using only these eight models limits our statistical power: the sets of parameters that we are using represent 32 AIC points each, with the result that if some of the parameters in a set are statistically significant but others are not, AIC may still give the model that uses the block in question a worse AIC score than a model that does not use the block.

In order to elucidate exactly which characters within a set were responsible for changes in diversification and extinction rates as opposed to merely whether characters affected diversification at all, we ran BiSSE analyses on all four characters and all eleven possible interactions between these variables, as well as a sixteenth, null model. For simple effects, each genus was coded as having a 1 for animal dispersal, woody habit, multiple-continent geographic range, or 20+ species within the genus. For interactions, a genus was scored as having 1 if it had all of the states that are part of the interaction and 0 if it did not. We then compared AIC scores in order to select characters and their interactions.

RESULTS

Our constrained, time-calibrated phylogenetic tree of the Rosales with 250 terminal tips is presented in Figure 4 (see Appendix II). The Rosaceae are sister to the rest of the Rosales, with the Rhamnaceae, Elaeagnaceae, and Barbeyaceae forming one clade, the Moraceae and Urticaceae form a clade, the Cannabaceae sister to Moraceae + Urticaceae, and the Ulmaceae sister to the Cannabaceae-Urticaceae-Moraceae clade. All of these relationships were required by the constraints we placed on our phylogeny. Several Rosalean genera had no sequence available from NCBI, and so were assumed to be of equal branch lengths to their sister genera based on Kubitzki's (1990) classification system.

The complete model has lower (i.e. better) AIC scores for predicting the effect of character state on genus-level origination rate than a simpler model in which diversification rate is unaffected by any of the character states (Table 8). The complete model is also better at predicting evolution of dispersal type. However, for habit, geographic range size, and species richness, AIC scores are better for models in which these character states do not influence rates of state change.

Effects of different character states on net genus-level diversification rates are shown in figure 5. There are three dominant factors correlated with net-diversification: (1) herbaceous genera have higher diversification rates than woody genera, (2) genera with the combination of animal dispersal, large geographic range size, and high species richness have higher diversification rates than those that lack any of the three, and (3) among woody genera, the effect of (2) is more pronounced than in herbaceous genera.

Noticeably, tree genera without animal dispersal have net negative diversification rates (i.e. preferentially become extinct), even if they are species-rich and widespread.

Estimated state transition rates are presented in Table 9. The patterns in state transition rates between the four variables are complex due to the number of variables under scrutiny, but some patterns emerged. Higher species-richness within a genus is correlated with the evolution of animal dispersal. Our MuSSE analysis, treating geographic range size as a character, finds a weaker effect suggesting that genera with large ranges are more likely to evolve abiotic dispersal. The rates of evolution, however, are extremely slow, with a maximum rate of one state change in twenty million years, which is in keeping with the fact that dispersal type in the Rosales is conserved at a fairly high taxonomic level (Kubitzki 1990). Several other patterns emerge from our MuSSE output but are not statistically significant (Table 8). Despite their non-statistical significance, it is possible that these are real results due to the limited choice of models that computation times forced us to work with. Among the largest combined effects are: (1) Among herbaceous genera, high diversity is associated with larger range, regardless of dispersal type; (2) Among woody plants speciose genera with animal dispersal are associated with larger ranges; (3) Animal dispersal is associated with lower species richness except when genera are also woody and wide-ranging; (4) Animal dispersal and large range size, together, may precede (re-)evolution of woody habit. Apart from changes in dispersal type, however, the AIC scores of a model in which character state transition rates are not affected by existing character states are better than those of a model in which transition rates are so affected (Table 8). As such, the values presented in

Table 9b-d should be taken with a lower degree of confidence than the results of Table 9a and Fig. 5.

The results from using BiSSE to identify which character(s) have the most statistically robust impact indicate the best model to be the four-way interaction (Table 10). Although this model is better by a 5:1 likelihood ratio than any other model, two other models stand out as explaining a large portion of the data: an independent effect of habit, and a three-way interaction between animal dispersal, large geographic range size, and high within-genus species richness.

DISCUSSION

Several patterns stand out from the results of our analysis. There are three effects influencing net diversification in the Rosales: (1) a positive three-way interaction between animal dispersal, large geographic range size, and high within-genus species richness, (2) a negative effect of woody habit, and (3) a positive four-way interaction between woody habit, high within-genus species richness, animal dispersal, and large geographic range size (Table 10, Fig. 5). Of these, the best supported is the four-way interaction; however, because our BiSSE-based analysis of each individual interaction or independent effect could only analyze one such effect at a time, it is likely that the biological reality consists of multiple effects acting together or against one-another. Next, while there are factors that appear to influence or correlate with evolution of dispersal mechanism in Rosalean genera, the rate of evolution of dispersal type in the Rosales is relatively slow (Table 9). At the same time, we did not detect strong effects of character

states on rates of evolution of either habit, or of geographic range size or within-genus species richness (Table 8), even though the apparent effect sizes (Table 9) were larger than for evolution of dispersal type.

Geographic range size and its interaction with species richness and dispersal mode

Our best model did not include an effect of character state on genus-level extinction rate, implying that all effects of dispersal type, range size, and species richness on diversification rate are driven instead by origination. This finding is consistent with the view presented by Ricklefs & Latham (1992) that better dispersal and larger range size covering more habitats leads to superior colonization ability, more opportunities for specialization, and ultimately higher diversification rates. Ricklefs & Latham's hypotheses focus on diversity at the species level rather than the genus level, and we did not find a simple association between species richness and diversification rate, implying that processes responsible for genus-level origination rates are likely to be more complex than those that Ricklefs & Latham identify. However our result that extinction is unaffected by character state should be taken with caution, as methods using phylogenetic trees constructed from genetic data of exclusively living taxa are known to cause problems when used to estimate extinction rates (Freckleton et al. 2008; Liao et al. 2010; Rabosky 2010). For this reason, we feel safe in concluding that animal dispersal and range size, together, lead to higher net diversification, but cannot discount the possibility that much of this effect is due to extinction and not origination.

Because of the possibility that our failure to detect differential extinction may be a limitation of our molecularly-derived phylogeny, we consider the studies of numerous

other authors suggesting that large range size enhances lineage survivorship instead of (or as well as) origination rates. Larson-Johnson (2016) found that animal dispersal in the Fagales leads to larger geographic range size, which in turn leads to higher diversification rate, but did not find the interactions that we did. Our results concerning seed dispersal mechanism influencing geographic range size are similar, if not statistically significant, but also more complex in that we find a correlation between dispersal and range size only among woody taxa in the Rosales (notably the Fagales have no herbaceous lineages). Like ours, Larson-Johnson's analysis focused on net diversification rather than specifically on extinction, but numerous other papers do connect geographic range size or dispersal to extinction. Many of these studies also suggest that processes responsible for long-term extinction patterns involve other lineage characteristics in addition to geographic range size (e.g. Yu & Dobson 1997; Jablonski & Hunt 2006; Vamosi & Vamosi 2012) or that the relationship between range size and extinction is context-dependent (e.g. Payne & Finnegan 2007). Considering these other analyses and our own, it is clear that geographic range size plays an important role in lineage survivorship and diversification across many groups, although it is also clear that other factors are frequently involved and the details likely vary between major taxonomic groups.

Our results do not appear to be the result of purely species-based processes. If they were, then we would have predicted an independent effect of species richness on genus-level diversification. The reasons for this are (1) having multiple species within a genus would require more species extinctions to wipe out a genus, and (2) more species in a genus represents more opportunity for those existing species to give rise to new species. However, we only observed species-richness to have an effect on genus-level

diversification rate when interacting with geographic range size, dispersal mechanism, and potentially habit. Likewise, the results of our analysis do not reflect metapopulation-level processes either, because larger geographic range size would correspond to more populations. As a result, we would predict an independent effect of geographic range size, which, like species richness, only significantly affects genus-level diversification when interacting with other factors. Therefore we must seek a more complex mechanism underlying the association between the aforementioned variables and diversification rate than is initially apparent. We propose that this interaction represents a measure of the colonization or invasion ability, including not only the ability to disperse to a novel habitat, but also to establish and proliferate having once arrived. Extreme long-distance animal dispersal is prerequisite to acquiring this ability, but alone is not sufficient. Colonization ability would also be important in maintaining species richness via founder propagules, explaining why within-genus species richness is also part of the interaction.

If the interactions that correlate with increased diversification rate in our study do represent colonization ability, then this has several implications that could potentially be tested. First, there exist numerous woody plant genera, especially but not exclusively among gymnosperms, that were once far more diverse than they are at present (Graham, 1999). Anecdotally, many of these genera do not possess the combination of animal dispersal, high species richness, and large range size, and never did, having never been animal-dispersed. How is it that these genera became numerous, widespread, and prevalent in the first place? We propose that colonization ability might have been less important in a world that had weaker latitudinal climatic gradients and smaller amplitude climatic fluctuation on orbital time scales. Over the Cenozoic Era, the flora of the

Northern Hemisphere has become considerably more spatially heterogeneous (Graham 1999; Strömberg 2011), with increasing global mean temperature volatility (Zachos et al. 2001) resulting in increasing temporal variability in many places as well (Graham 1999). Could late Cenozoic climate variability be responsible for a decline (presumably through extinction, although decreased origination could play a role as well) in woody plant genera that lack animal dispersal? This would also explain why the interaction between dispersal, range size, and richness is stronger in woody genera: woody genera with longer generation times must respond to changing climate in a smaller number of dispersal and colonization steps than herbaceous genera do. If so, then there are several predictions that we can make. First, woody plant lineages that became extinct or suffered major range collapse during the second half of the Cenozoic should lack animal dispersal and/or other traits associated with colonization ability. This pattern would be complicated by the cooling and drying trend also characteristic of the late Cenozoic (Zachos et al. 2001) and its effects on terrestrial vegetation (Graham 1999; Strömberg 2011), so care would be needed to identify genera that had become extinct due to variability instead of desertification.

There are several other predictions that the hypothesis that our interaction terms represent colonization ability make that can potentially be tested with modern, as opposed to fossil, data. One is that while lineage survivorship should be influenced by geographic range size, this relationship should not be between survivorship and simple area of geographic range but rather between survivorship and range in habitat tolerances that a genus possesses. Taxa that merely have large ranges could become restricted if their range shifts to a smaller area due to climate fluctuations. Successful (i.e. likely to

survive) lineages would have both effective long-distance dispersal ability and wide climate tolerances, enabling them to both arrive and successfully invade new ecosystems.

Herbaceous habit and its role in angiosperm diversification

Another prominent pattern in the analysis is the strong association of woody habit with lower net diversification rate. This has been observed before and is consistent with higher rates of molecular evolution that have been observed in herbaceous campanulids relative to woody campanulids (Smith & Donoghue 2008, Beaulieu et al. 2013). We suggest two possible explanations in the context of our analyses. First, higher rates of evolution in herbaceous Rosales could lead to more rapid adaptation and speciation, which would explain why herbaceous genera have a higher net genus-level diversification rate as well. Second, herbs have shorter life cycles than woody plants, perhaps leading to higher colonization ability (via reduced time to reach reproductive maturity), which could decrease extinction rate during periods of rapid climate changes such as those that characterized the Pleistocene (Zachos et al. 2001, Alley et al. 2003). If rapid evolution in short-generation herbs leads to rapid adaptation and speciation, then long-generation perennial herbs living at high elevation or latitude might have lower diversification rates than herbs at low elevation and latitude. Additionally, if the short life cycles enhance colonization potential, then the spread of herbs across landscape should be measurably faster than that of large-ranging animal-dispersed trees. This could potentially be investigated using pollen data, or with *Neotoma* middens (e.g. Jackson et al. 2005).

Character evolution: dispersal type evolves slowly

Our analysis identified a weak correlation in which genera with the combination of large range size, high species richness, and woody habit, have an increased chance of acquiring animal dispersal. Genera possessing large range size without either woody habit or high species richness, however, are more likely to lose animal dispersal. With this interaction and all linear effects, MuSSE predicts that the net transition rate toward animal dispersal will be 0.054 occurrences per million years (Table 9). Species richness and geographic range size are not characteristics of individual organisms, so it is implausible that they would directly select for individual traits like dispersal mechanism (but see Van Valen 1971). It is likely therefore that the correlation detected by MuSSE instead reflects coevolution between dispersal and other variables related to colonization such as environmental tolerance, which we did not include in our analysis.

We do not have statistical support for character state in the Rosales having effects on state change rates expect for state changes in dispersal type (Table 8); however, the apparent trends visible in Table 9 are in agreement with those found more robustly by Larson-Johnson (2016). One possible explanation for this is that the radiation, geographic spread, and expansion of Rosalean lineages into their various habitats occurred so quickly that we lack the phylogenetic resolution to be confident in all of our results. The rate trends seen for non-dispersal characters in Table 9 may be real, but we lack the statistical power to identify them as better than equal rates of change. However, we cannot be certain that we are seeing such an effect, given the poorer AIC score of the full model.

Further potential implications

If colonization ability is important in the long-term survival of woody plant lineages, then our results have some implications for conservation, but these implications must be taken with numerous caveats. Some Pleistocene climate changes (e.g. the Younger Dryas; see Carlson 2013 and refs therein) were of both comparable magnitude and rapidity to projected anthropogenic warming (e.g. Held et al. 2010, Donohoe et al. 2014). However, the majority of Pleistocene climate shifts did not have the rapidity of projected anthropogenic change (e.g. Zhang et al. 2014), and those that did also correlate temporally with some (but not all) significant Pleistocene extinction events (Barnosky et al. 2004). For these reasons, extinction risk from anthropogenic climate change may be significantly more severe even for groups that successfully withstood past climate shifts. Nonetheless, identifying lineages with poor colonization ability, being unable either to disperse or to establish, and aiding their migration may reduce the risk of their extinction. This must be undertaken with care, however, since assisting colonization would mean deliberately creating what are effectively invasive species where new populations are to be founded.

Surprisingly, Vamosi & Vamosi (2012) found different results with respect to fruit type from what we found for dispersal, with them failing to recover an association between fruit type and either richness or range size. It is possible that the difference is because Vamosi & Vamosi divided different types of animal and non-animal-dispersed fruit types into separate categories instead of treated them as animal-dispersed or not animal-dispersed as we did. Using only fruit type would detect animal dispersal by means of frugivores, but animals that cache seeds are often effective and important dispersal

agents even in the absence of fleshy, edible fruit, as demonstrated by the effects of chipmunks on the winged-seeded *Pinus jeffreyi* (Briggs et al. 2009). Also of note is that their scoring of characters was done at the family level, while their identification of extinction risk was by counting endangered species. By contrast we did everything at the genus level. Nonetheless Vamosi & Vamosi argue that geographically-restricted, species-poor families become priority targets for apriori conservation efforts, even those species not on the IUCN Red List. Because of the timescale over which the processes we study in this paper occur, typical conservation implications (i.e. conserving taxa from human-induced extinction) are difficult to glean from our study. However, those interested in longer-term conservation, we would add woody genera lacking effective extreme long-distance dispersal as potential targets as well.

It is similarly interesting to compare our results to those of Larson-Johnson (2016). Her results suggest less complicated mechanisms underlying diversification rates than ours do. It is possible that the processes she observed of animal dispersal leading to large range size and then higher diversification in the Fagales are the same as those underlying the interaction we observed in the Rosales, but that the nature of our phylogeny and character states interpreted as an interaction instead of a simple effect. However, it is also possible that she detected a different mechanism by which animal dispersal and geographic range size influence lineage diversification and survivorship than we did.

Concluding remarks

Our study illustrates three important factors influencing net diversification in the Rosales: (1) an independent effect of habit in which herbaceous genera are favored; (2) a positive three-way interaction between animal dispersal, large geographic range size, and high within-genus species richness, which, together, may reflect colonization potential; (3) a four-way interaction by which the effect of the three-way interaction is accentuated in woody genera. Any of these three factors is sufficient to enable a genus to have net-positive diversification rates, but lacking all of them (i.e. woody genera without at least one of the three parts of the three-way interaction) will preferentially lead to a genus' extinction. A possible explanation for these results is a macroecological hypothesis by which late Cenozoic climate volatility results in extirpation of local populations, thus colonization ability is an important factor in preventing an entire lineage from becoming extinct. If so, then there are several predictions that can be tested, some using fossil data and others with data from the present day. Further research will be needed to test this and other hypotheses relating to the mechanisms by which geographic range, dispersal, and other traits affect survival of lineages over geologic time.

CHAPTER ACKNOWLEDGEMENTS

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TABLES

Table 6 – Schematic of the four different characters measured in this study. Our geographic range criterion was that widespread genera had to be present on multiple continents, while restricted genera were found on only a single continent, where a continent was any land mass separated from other land masses by an ocean basin that was not exposed during the last glacial maximum at 20 Ka. The four binary characters together create $2^4 = 16$ possible character state combinations.

Character	State A	State B
Seed dispersal by animals	Absent	Present
Geographic range size	Restricted	Widespread
Genus size	<20 species	20+ species
Habit/Generation time	Herbaceous/short	Woody/long

Table 7 – Description of the eight models of evolution used in our phylogenetic comparative analysis of the Rosales, identifying the evolutionary parameters we used for each model. “Yes” indicates that the set of parameters was free to vary and was incorporated in the model; “No” signifies that the parameters for that set were constrained to be equal. For detailed description of the characters being analyzed, see Table 6.

Model	Origination	Extinction	Evolution of dispersal	Evolution of habit	Evolution of richness	Evolution of range size
Full	Yes	Yes	Yes	Yes	Yes	Yes
No effect on origination	No	Yes	Yes	Yes	Yes	Yes
No effect on extinction	Yes	No	Yes	Yes	Yes	Yes
No effect on dispersal	Yes	Yes	No	Yes	Yes	Yes
No effect on habit	Yes	Yes	Yes	No	Yes	Yes
No effect on richness	Yes	Yes	Yes	Yes	No	Yes
No effect on range	Yes	Yes	Yes	Yes	Yes	No
No effect on characters	Yes	Yes	No	No	No	No

Table 8 – AIC scores for different MuSSE models of character evolution and diversification in the Rosales. All models are listed with their AIC relative to the full model that includes all 96 parameters. Models that refer to specific characters refer to the state transition rates of that character (i.e. “no effect on dispersal” signifies that there is no preferred direction in evolution of dispersal modes). A lower AIC score signifies a better model. Models significantly better than the full model are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), while models significantly worse than the full model are marked with daggers († $p < 0.05$, †† $p < 0.01$, ††† $p < 0.001$). Rank lists the models by the best (lowest) AIC score.

Model	AIC	AIC difference	Significance	Rank
Full	3178.8	0	-	5
No effect on origination	3192.9	14.1	†††	6
No effect on extinction	3062.2	-116.6	***	1
No effect on dispersal	3201.8	23	†††	7
No effect on habit	3160.6	-18.2	***	4
No effect on range	3155.7	-23.1	***	3
No effect on richness	3154.4	-24.4	***	2
No effect on all characters	3192.9	14.1	†††	6

Table 9 – Relative rates of “character” state transition influenced by state combinations in the Rosales in our four-way analysis of dispersal type (animal or abiotic), geographic range size (single or multi-continent), within-genus species richness (≤ 20 species), and habit (woody or herbaceous). Each number represents the average net change per lineage per million years. Positive numbers indicate an imbalance of state transitions favoring the direction indicated; negative numbers represent the inverse. AIC comparisons analysis (Table 3) indicates that the parameters for evolution rates of dispersal type (a) are statistically significant, but that the other variables (b, c, d) are not.

a) change in dispersal type (positive favors gain of animal dispersal; negative favors loss)

	Low richness		High richness	
	Narrow range	Broad range	Narrow range	Broad range
Herbaceous habit	-0.0079	-0.026	0.033	-0.0078
Woody habit	-0.013	-0.024	0.012	0.054

b) change in range size (positive favors evolving larger range)

	Abiotic dispersal		Animal dispersal	
	Low richness	High richness	Low richness	High richness
Herbaceous habit	-0.054	0.014	0.52	-1.07
Woody habit	-0.098	-0.004	0.33	0.81

c) change in species richness (positive favors within-genus richness increase)

	Abiotic dispersal		Animal dispersal	
	Narrow range	Broad range	Narrow range	Broad range

Herbaceous habit	-0.091	-0.74	-0.018	-0.49
Woody habit	-0.086	-0.89	0.032	0.11

d) change in habit type (positive favors acquisition of woody habit; negative favors acquisition of herbaceous habit)

	Abiotic dispersal		Animal dispersal	
	Narrow range	Broad range	Narrow range	Broad range
Low richness	0.039	0.23	0.014	0.74
High richness	0.029	0.22	0.011	9.3×10^{-5}

Table 10 – AIC scores of binary state speciation and extinction (BiSSE) analyses of different characters and interactions in our diversification analysis of the Rosales. All models are scaled relative to the best model (animal dispersal x woody habit x large geographic range x high species richness); thus, Δ AIC is relative to this value. A difference in AIC scores of 3.22 is sufficient to distinguish between the quality of models (Burnham & Anderson 2010). However, because these are BiSSE models that can account for only one variable or interaction at a time and real diversification rates are likely influenced by several factors (e.g. see Fig. 5), rejecting models with high AIC/low likelihood should be done with caution. A positive direction indicates that the traits (or combination of traits) consisting of animal dispersal, woody habit, large geographic range size, or high within-genus species richness contributes to greater net diversification rates; negative direction indicates the opposite.

Model	Δ AIC score	Penalized Likelihood	Direction
Dispersal x habit x range x richness	0	1	positive
Habit	4.29022	0.11705516	negative
Dispersal x range x richness	4.62079	0.099222051	positive
Dispersal x habit x richness	13.57571	0.001127384	positive
Dispersal x richness	25.63141	2.71775×10^{-6}	positive
Habit x range x richness	32.73503	7.79253×10^{-8}	positive
null	49.05054	2.2326×10^{-11}	NA
Habit x richness	56.44862	5.52507×10^{-13}	positive
Dispersal x habit	57.31759	3.57803×10^{-13}	positive
Range x richness	70.49482	4.92316×10^{-16}	positive
Dispersal	76.35543	2.62802×10^{-17}	negative

Dispersal x habit x species richness	89.82115	3.13029×10^{-20}	negative
Species richness	93.62897	4.66367×10^{-21}	negative
Dispersal x range	96.76219	9.73548×10^{-22}	negative
Habit x range	133.03935	1.29084×10^{-29}	negative
Range	158.7474	3.37629×10^{-35}	negative

FIGURES

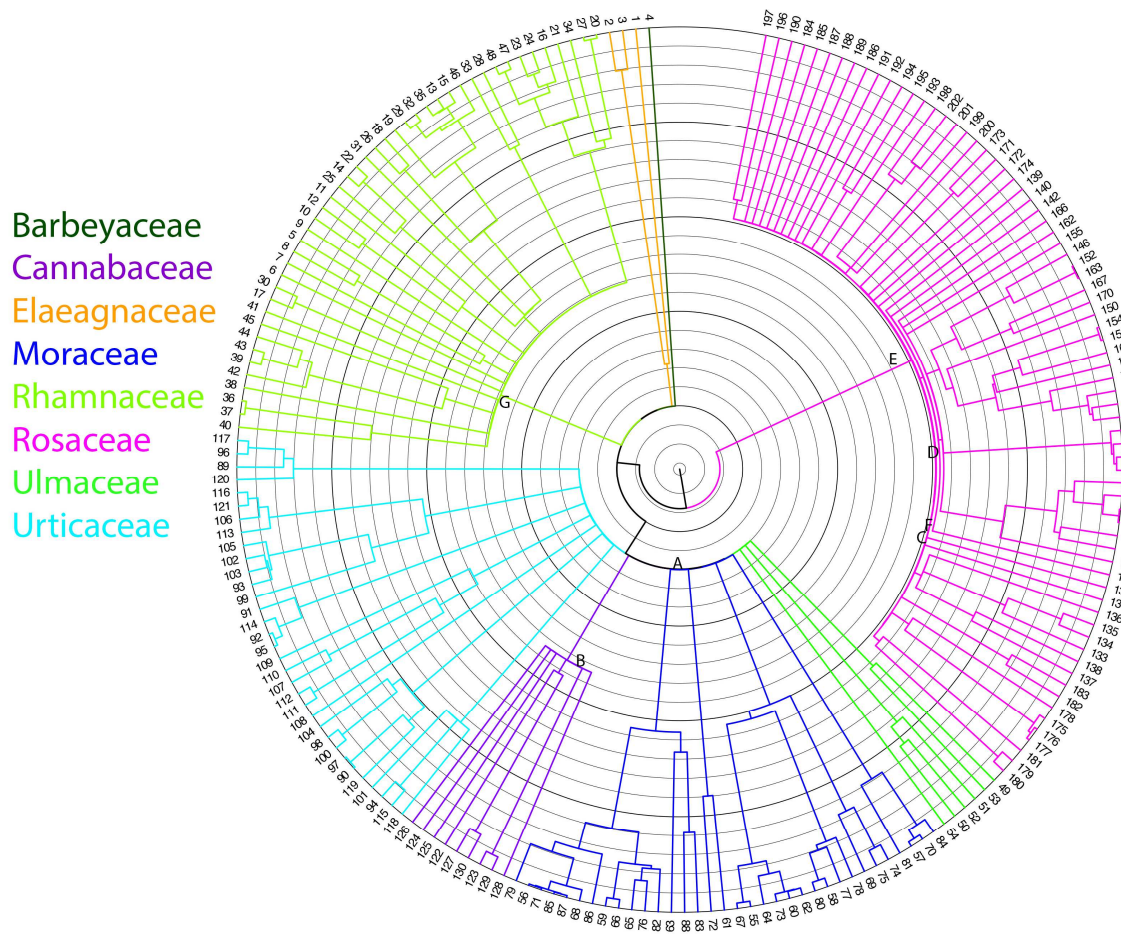


Figure 4 – Phylogenetic tree of the genera of Rosales, with families color-coded as shown. This tree was constructed using BEAST, using sequences downloaded from NCBI, phylogenetically constrained using APGIII, and calibrated to time using fossils representing each major clade. Only genera for which we were able to obtain sequence data are plotted on this phylogeny. Major gridlines (dark gray) represent increments of 25 million years; minor gridlines (light gray) represent increments of 5 million years. Letters A through G on the phylogeny identify the (approximate) positions of nodes used for time calibration. The taxa and ages for these nodes are given in Appendix I. Numbers on tips identify individual genera, which are listed in appendix II.

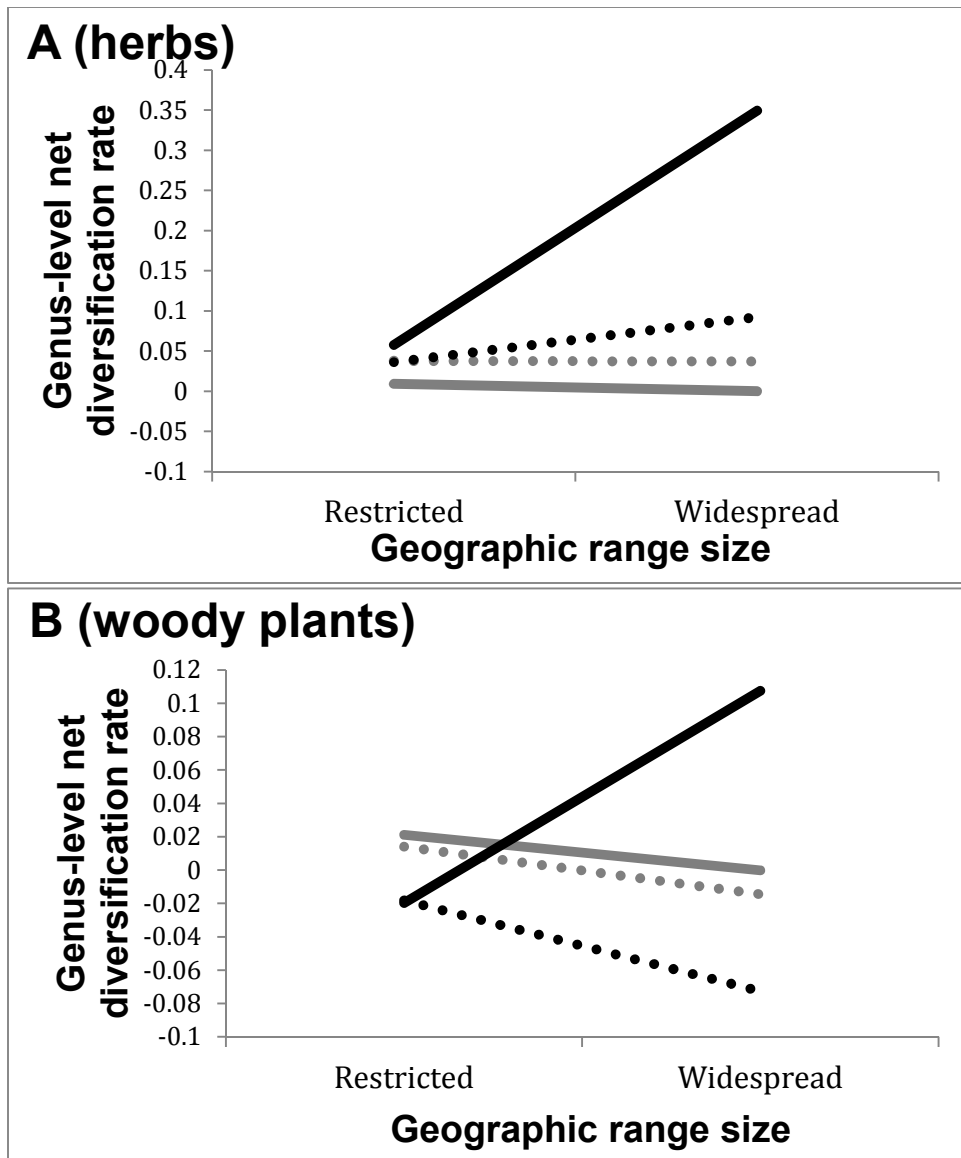


Figure 5 – Genus-level net diversification rates as a function of different “characters” in the Rosales, using a conservative (one versus multiple continents) geographic range

evaluation. (A) displays net diversification rates for herbaceous plants, (B) for woody plants. Gray lines represent genera with low species richness (<20 species per genus; see legend); black lines represent genera with high species richness. Dotted lines indicate genera lacking animal dispersal; solid lines indicate genera possessing some form of animal dispersal (not mutually exclusive with wind dispersal). Units of net diversification are genus originations minus genus extinctions per million years.

Chapter 3 - A phylogeographic history of the Rosales (Plantae: Anthophyta) using traditional phylogeographic, fossil, and phylogenetic comparative methods

CHAPTER ABSTRACT

Phylogeography has become a well-recognized field within historical biology, using a combination of modern and fossil data to elucidate the distribution of ancestral organisms. However, while geographic distribution, particularly range size, is widely believed to be important in determining lineage survivorship and diversification rates, few phylogeographic studies to date account for the effect that paleodistribution has on ancestral lineages' tendencies to survive and diversify. We apply two different methods to understand the phylogeographic history of the Rosales (Plantae: Anthophyta) and how it relates to contemporary patterns of diversity. We use a traditional phylogeographic method, contained in the R package BioGeoBEARS, which makes use of the fossil distribution of the Rosales in its reconstruction. Second, we apply a phylogenetic comparative method of ancestral state reconstruction, *asr.bisse* in the *diversitree* package in R, which accounts for the effect of range size on diversification rate but cannot make use of fossil data. *Asr.bisse* identifies two diverse clades in the Rosaceae to have been widespread, and one more in the Urticaceae, as well as several smaller groups. Fossil-assisted reconstructions using BioGeoBEARS indicates that some of these ancestors likely were widespread, but that many were not. However, only one genus, *Celtis* in the Cannabaceae, is inferred to have been widespread by BioGeoBEARS but not by *asr.bisse*. These results suggest that the modern data-only algorithm of *asr.bisse* may be making accurate assessments but lacking in taxonomic precision. Additionally,

BioGeoBEARS infers that within the Rosales, the Rosaceae diversified in North America and then spread to other continents, while other families in the Rosales more likely diversified in Eurasia. While part of this geographic analysis is likely biased by the distribution of fossil occurrences, it is likely that the northern hemisphere biogeography of the Rosales is reconstructed correctly.

Keywords: ancestral state reconstruction, geographic range, Rosales, BiSSE, BioGeoBEARS

INTRODUCTION

Geographic range is ecologically and evolutionarily significant as it limits the number and identity of species and ecosystems that a taxon can interact with, determines where allopatric versus sympatric speciation can happen, and is an important driver in determining extinction risk of lineages of varying taxonomic levels on both theoretical (Rabinowitz 1984) and empirical bases (Jablonski & Raup 1995; Payne & Finnegan 2007; Larson-Johnson 2016; Simpson 2016 chapter 2). Thus, while geographic ranges are often correlated with various morphological and ecological variables, they are an emergent property of species and higher taxa that merits attention. Phylogeography, or ancestral state reconstruction (ASR) on geographic distributions, uses methods similar to those used in reconstructing morphological character states, and these methods pose many similar challenges as well. Geographic ranges have been shown to be heritable at the level of the species (Jablonski 1986; Jablonski & Hunt 2006), indicating that they are suitable for ASR. For these reasons, software packages exist to conduct ASR on geographic ranges (e.g. BioGeoBEARS: Matzke 2013; RASP: Yu et al. 2015, and there is continued development of phylogenetic comparative methods to infer diversification and extinction patterns based on geographic distribution (GeoSSE: Goldberg et al. 2011).

There are, however, some limitations in the set of ASR methods that are currently available. We are unaware of any current method of ASR of paleogeographic ranges that explicitly accounts for the effect that large lineage range sizes have on long-term survivorship, even though some (e.g. Matzke 2013; Yu et al. 2015) do allow for population-level extinction. For this reason, methods of ASR that do take differential lineage survivorship into account (e.g. Goldberg et al. 2011) would be expected to make

better predictions of paleogeographic ranges than models such as BioGeoBEARS that do not account for differential diversification in situations where no fossil data are available. Most phylogenetic comparative methods however, suffer from the requirement that input phylogenetic trees must be ultrametric, thus precluding the use of fossil data to inform paleo-range reconstructions. Many non-comparative ASR methods, by contrast, can incorporate fossils. Thus, there is currently a trade-off between having more comprehensive evolutionary models versus more complete datasets.

In this paper, we set out to address several questions. Biologically, we ask which lineages in the angiosperm order Rosales (Angiosperm Phylogeny Group 2009) are likely to have been widespread in the past or descended from widespread ancestors. Can patterns of modern biodiversity help inform biogeographers about how widespread ancestral lineages were? How well do these estimates match up to what we know from the fossil record? These biological questions also raise methodological concerns as well: how well can a phylogenetic comparative method, specifically *asr.bisse* in *diversitree* (Fitzjohn 2012) reconstruct the past, given its known problematic assumptions (e.g. Rabosky & Goldberg 2015, Simpson 2016 chapter 1)? What of more traditional phylogeographic methods such as BioGeoBEARS (Matzke 2013) that account for fossil data but not diversification rates? If these methods are both effective at reconstructing the past, their answers should agree.

METHODS

Modern geographic range data

We conducted our study of geographic range in the Rosales at the genus level because of the difficulty in identifying fossil specimens either to living species or their direct ancestors. Because our analysis was undertaken at the genus level instead of at the species level, using comparative methods in this context results in inferences of geographic range evolution and associated origination and extinction at the genus rather than species level. Because phylogeographic analyses of populations within species involve colonization and extinction dynamics, and because geographic location is not itself a genetically heritable trait, we did not anticipate that ‘scaling up’ in taxonomic level from species to genus would cause any difference in the nature of our analysis apart from the scale itself.

Assessing geographic ranges for living Rosalean genera was a two-step process. Geographic range maps were acquired from the Global Biodiversity Informatics database (GBIF, www.gbif.org). However, because GBIF maps provide information on the collecting localities of specimens in herbaria, ranges include individuals from gardens and other introduced populations, which can distort the pre-human range of a taxon. For this reason, maps examined with GBIF were then compared against the literature (Kubitzki 1990) in order to identify which collection localities represented the natural geographic range.

In order for modern geographic ranges to be comparable with spatially heterogeneous and often sparse fossil data, we categorized genera as widespread if found on multiple continents but restricted if found only on a single continent. The ability to

disperse/colonize across geographical barriers such as ocean basins has been linked to genus-level lineage survivorship in this group (e.g. see Larson-Johnson 2016). Large oceanic islands such as Madagascar and New Zealand that are separated from other landmasses by ocean basins were treated as continents for this reason. These land masses split during the Late Cretaceous (Scotese 2001), after the divergence of the Rosalean families from the last common ancestor of the order, but before the lineages within the families themselves began to appreciably diverge (see Appendix III for fossil occurrences). For this reason, vicariant biogeography as a result of continental drift should not be an important factor in determining geographic ranges of living Rosalean genera. We similarly considered Wallacea (Meyr 1944) to be a continent, because it was not connected to either Asia or Australia during Pleistocene ice age driven sea-level drops (Lambeck et al. 2002), unlike New Guinea or the rest of Indonesia.

Paleogeographic range data

Data on the geographic distribution of Rosalean fossils (extant and extinct genera) was taken from the literature (Appendix III). We assessed fossil identifications using recent publications on fossil Rosales (e.g. DeVore & Pigg 2007). Many paleobotanical workers prior to 2000 attempted to place all plant fossils into living genera (see many papers by Axelrod, e.g. Axelrod 1987; Raven & Axelrod 1998), despite rampant convergence in leaf morphology leading to false identification (see Leaf Architecture Working Group 1999). Much of this taxonomy has been or is being revised (e.g. Wolfe & Schorn 1990, Erwin & Schorn 2000, Manchester et al. 2002, DeVore et al. 2005, Peppe et al. 2007). In order to minimize the effect of misidentified fossil taxa affecting our

results, we adopted a conservative approach, rejecting equivocal records. We considered publications more recent than 2000 to be trustworthy, and also papers by authors that Devore & Pigg (2007) cite without reservation. The geological age and continent of the first occurrence for each genus was noted, and genera were coded as becoming widespread when they were first recorded on a different continent.

By excluding much of the older literature we reduce both the age and paleogeographical extent of many fossil genera, as well as exclude other genera from the analysis entirely. Because it is possible that some of these old identifications are in fact correct (e.g. Peppe et al. 2007), we may be exacerbating the incompleteness of the fossil record by excluding the older literature. This reduces increases the risk that genera that were widespread in the past will not be detected as such by the fossil record. At the same time, we reduce the risk created by inaccurate taxonomic identifications that could also bias the fossil record in multiple, difficult to anticipate, ways.

Phylogenetic analysis

In order to conduct a phylogenetic comparative analysis of character-associated diversification across the Rosales, we needed a phylogeny with branch lengths equal to time, which was not available from the literature. To address this, we used the multiple sequence alignment of Potter et al. (2007) for the Rosaceae, and appended it with the other Rosalean families using NCBI BLAST (Madden 2002), choosing GenBank accessions possessing the most sequence data available covering the same genes used by Potter et al. (2007). Sequences were then aligned using MUSCLE (Edgar 2004).

We used BEAST (Drummond et al. 2012) to construct the phylogeny. Nodes and subclades within the Rosales were constrained using Potter et al.'s (2007) tree, and the Angiosperm Phylogeny Group III phylogeny (Angiosperm Phylogeny Group 2009). We calibrated our tree using our database of the Rosalean fossil record, which contains at least one fossil date for each major Rosalean group. Priors were uniform in the absence of reason to assign nonuniform priors.

The fossil record of the Rosales is heavily biased toward the Eocene and Oligocene of North America, and to the Miocene of Europe, with a few records in Africa and South America, as well as some Paleogene European records and a number of Neogene North American records (Appendix III). Many modern genera in the order are presently found on continents where they do not occur as fossils. Taxonomically, the fossil record of the Rosales also heavily favors the Rosaceae over the other Rosalean families. For these reasons our comparison of the fossil distribution of Rosalean taxa to ASR results was most reliable for genera that are distributed in temperate regions of the northern hemisphere. There are numerous tropical lineages, especially in the Moraceae and Urticaceae, for which we have no paleontological data, and these were excluded from the analysis.

We used the same time-calibrated phylogenetic tree of the Rosales as depicted by Simpson chapter 2 Fig. 6 (2016). About 50 Rosalean genera (~20% of the order) had no sequence available from NCBI, and so were assumed to be of equal branch lengths to their sister genera based on Kubitzki's (1990) classification system. Extinct Rosalean genera represented in Appendix III are placed as sister to the ancestral group to which they are referred in the paleobotanical literature describing them (figure 6).

BiSSE-Ancestral State Reconstruction

Ancestral state reconstruction of geographic range sizes was conducted using the `asr.bisse` set of functions implemented in the `diversitree` package in R (Fitzjohn 2011). We used BiSSE (binary state speciation and extinction) as the basis of ancestral state reconstruction because the version of `diversitree` available does not allow ancestral state reconstruction using a more appropriate state speciation and extinction model (i.e. GeoSSE). In order to do ancestral state reconstruction, `asr.bisse` requires that characters be coded as binary; as described above, we divided genera into categories based on whether they occupied one or multiple continents.

The `asr.bisse` function, like all state-speciation and extinction algorithms akin to BiSSE, requires that all phylogenetic trees be ultrametric. This prevents the inclusion of fossil data in estimating paleoranges of genera, since any fossil genus (especially any genus that is extinct) must necessarily represent a branch on a phylogeny that does not reach the present. Therefore, `asr.bisse` provides an estimate of paleogeographic range using modern data only, which we can then compare to paleogeographic range inferences informed by the fossil record.

BioGeoBEARS-Ancestral State Reconstruction

In addition to scoring the paleogeographic ranges of Rosalean genera using the fossil database alone, we conducted a phylogeny-based ancestral state reconstruction of paleoranges using the R package `BioGeoBEARS` (Matzke 2013). Unlike `asr.bisse` in

diversitree, BioGeoBEARS does not use a BiSSE-type model that accounts for character-associated diversification; however, BioGeoBEARS can incorporate fossil data, along with the distributions of living taxa, into its estimates of past geographic distributions of organisms being studied.

Using fossil dates in BioGeoBEARS requires adding fossils to the phylogenetic tree as stem taxa. Where possible, we attached fossil members of living genera to the tree at the dates of their occurrence (Fig. 6). Extinct genera we placed as stem lineages to their presumed closest living relative as described in the literature. If fossils, even of extant genera, were older than the last common ancestor with another genus inferred from the phylogeny, but the identifying characters of the genus could be ancestral, we placed the fossils before this common ancestor.

Comparison between BiSSE-ASR and BioGeoBEARS-ASR

Asr.bisse yields inferred probabilities of a lineage's last common ancestor being distributed on multiple continents versus a single continent. BioGeoBEARS produces estimates of what continents the ancestors of extant genera occupied at each phylogenetic node. We compared the inferred probabilities made by asr.bisse against both raw observations of the continents on which fossils were found (appendix III) in two ways: first, we conducted a Kolmogorov-Smirnov test of the probabilities inferred by asr.bisse against whether or not a genus is widespread in the fossil record. Second, we bootstrapped the result by randomly sorting genera with fossil records and checking whether asr.bisse's inference was better or worse than this random bootstrap sampling. We conducted one million of these bootstrap replicates.

The `asr.bisse` function identifies monophyletic groups of genera that are inferred to have had ancestors present on multiple continents. We then compared range reconstructions from BioGeoBEARS against `asr.bisse`'s ancestral reconstructions, identifying whether they match up using a contingency table Fisher's Exact Test.

RESULTS

The molecular phylogeny of the Rosales, modified from chapter, with inferences of range size mapped onto the tips, is shown in Figure 7. `Asr.bisse` identified groups of genera with a high probability ($> \sim 0.5$) of having widespread ancestors. Notably these include the Maleae, Roseae excluding *Agrimonia* and its immediate relatives, a large clade of tropical trees in the Urticaceae including *Oreocnide* and its relatives, as well as a number of smaller groups.

Comparing results of `asr.bisse` to the fossil record directly, the reconstruction on average assigned higher probability of large paleo range to genera with widespread fossil records than in genera with restricted fossil records (Fig. 8). While this difference is visually striking, it is statistically weak (Kolmogorov-Smirnov test $D = 0.2859$, $p = 0.2582$; one million R bootstrap replicates yields 81% confidence that ASR-BiSSE is better than random).

BioGeoBEARS infers a high probability that the last common ancestor of the Rosaceae was located in North America, and that most of the major groups within the Rosaceae also have a high probability of a North American origin (figures 9 & 10). BioGeoBEARS has lower confidence on the geographic location of the ancestors of the

other families in the Rosales, although likely places of origin include Eurasia or simultaneous distribution in North America and Eurasia.

Notably, genera identified by BioGeoBEARS as having been widespread are in almost all cases inferred by asr.bisse as belonging to clades with widespread ancestors (Fig. 7; Table 11). While asr.bisse infers roughly twice as many genera as likely to have had widespread ancestors than BioGeoBEARS, the only genus inferred by BioGeoBEARS to have been widespread but which asr.bisse does not infer to be widespread is *Celtis*. The clades of genera that asr.bisse infers to have had large ranges are much more likely to contain genera with a widespread fossil record than would be expected by selecting clades of genera at random (Table 12; Fisher's Exact Test $p < 0.0001$).

DISCUSSION

Possible biogeographic origins of the Rosales

Based on our BioGeoBEARS inference, the Rosaceae originated and did most of their early diversification (late Cretaceous through Eocene) in North America, while the analysis is less decided on whether the rest of the Rosales, sister to the Rosaceae, diversified in Eurasia alone or in Eurasia and North America simultaneously. Much of the diversification of the former Urticales (Urticaceae, Ulmaceae, Cannabaceae, Moraceae), sister to the Rhamnaceae, does appear to have taken place in Eurasia. Nonetheless several Rosaceous genera show up in Eurasia as well as North America remarkably early, among them *Rosa*, *Pyracantha*, *Sorbus*, and *Prunus*. BioGeoBEARS recovers this well, but infers them to have had recent North American ancestors; the European Eocene

representatives of these genera were (geologically) recent immigrants from North America. All of the Rosalean families subsequently expanded to other continents later in the Cenozoic, with the Cannabaceae on multiple continents by the Eocene, Rosaceae and Ulmaceae during the Oligocene, and Moraceae during the early Miocene.

It is very probable that these results are affected by biases in paleobotanical sampling, especially in the Southern Hemisphere; for instance, our literature database contains 20 publications detailing fossils in North America, eight from Europe, six from Asia, two from South America, and one from Africa. This pattern is accentuated by the fact that the Rosaceae, a largely temperate family today, have a much better fossil record than the comparably diverse Rhamnaceae, Moraceae, and Urticaceae, which have more subtropical and tropical distributions today and likely did in the past as well. The fossil record of the Rosales heavily represents these continents, especially the Eocene Okanogan Highlands floras of Washington and adjacent British Columbia, and Miocene sites in Germany (DeVore & Pigg 2007). Nonetheless, the early appearances of a number of Rosaceous genera in the Eocene of Europe (notably *Rosa*, *Prunus*, *Sorbus*, and *Pyracantha*) suggests that the absence of other Rosaceous taxa in Eurasia during the early Cenozoic is real. Thus, while we cannot say with confidence that the Rosaceae do have a North American origin as BioGeoBEARS infers, it is certainly plausible, and the Rosaceae were in North America before expanding to Eurasia. Likewise, some of the other families' early appearance in Eurasia suggests that their modern representatives in North America represent reflect immigration from elsewhere.

ASR on modern data alone only marginally agrees with fossil data

ASR is commonly used to infer character states of ancestral taxa from the distribution of character states of living taxa within a phylogenetic tree (Pagel 1999). Despite numerous criticisms (e.g. Omland 1999; Finarelli & Flynn 2006; Litsios & Salamin 2012), ASR remains widely applied to infer character evolution in groups as disparate as passerine birds (Kondo & Omland 2007), assassin bugs (Hwang & Weirauch 2012), and seed plants (Forbis et al. 2002). Our reconstruction using *asr.bisse*, based entirely on modern data, appears at first glance to usefully estimate the paleogeographic ranges of Rosalean genera (Fig. 8). However, we did not recover a p-value of less than 0.05 in any of the statistical assessments of *asr.bisse*'s output. It is possible that our inability to detect a statistical difference between *asr.bisse*'s inference and a random distribution owes to a lack of power due to a relatively small number of genera with fossil records to compare (59 taxa). It is unlikely that our limitations stem from limited taxa in *asr.bisse*'s analysis (see Davis et al. 2013) because 250 genera were included: we only compared the results to those genera with fossil records. It is also possible that an ASR model using a GeoSSE-type algorithm (Goldberg et al. 2011) instead of a BiSSE-type algorithm would have been more effective, but the existing GeoSSE only attempts to reconstruct speciation, extinction, and state-transition rates rather than do ASR. Lastly, the fossil record itself is incomplete and many of the genera that we record as having been restricted may have been in actuality widespread; however, *asr.bisse*'s analysis is nonetheless only marginally capable of reconstructing what fossil data we do have. Thus, while our reconstruction of paleogeographic range using *asr.bisse* is suggestive of what

we know from fossil data, its power is too weak to confidently reconstruct the past without additional assistance.

Comparison of asr.bisse to BioGeoBEARS

Although within our sample asr.bisse is not statistically better than random at reconstructing paleogeographic range size in general, some additional patterns reveal asr.bisse to be far more useful than appearances might suggest. Using asr.bisse we identify clades of genera that have a high probability of having widespread ancestors (Table 11). These clades vary in taxonomic scale from individual genera to entire tribes. Many of these clades have no verifiable fossil record, but when compared with BioGeoBEARS results, we find that nearly all of the genera identified by BioGeoBEARS as having been widespread fall into one of these clades that asr.bisse identifies as being ancestrally widespread. There are, however, many other genera that are in these clades but which BioGeoBEARS does not infer as having had large paleoranges. Still, unlike the result of our direct comparison of asr.bisse to the fossil record, genera inferred by BioGeoBEARS as having large paleoranges are far more likely to fall into asr.bisse's ancestrally widespread clades than we would expect by chance (Table 12).

This result is significant because it means that asr.bisse can identify “taxa of interest” that have a strong possibility of having been widespread even if it cannot definitively determine if this was the case. Effectively, asr.bisse's reconstruction is accurate, but imprecise. By contrast, genera inferred by asr.bisse to have had geographically restricted ancestors most likely were indeed restricted.

Implications and conclusions

We identify several clades that are inferred to have been ancestrally widespread. Many of these groups have high species or generic richness today, presumably because geographic range size correlates positively with diversification rate (Larson-Johnson 2016, Simpson 2016 chapter 2). Some of the member genera of these clades almost certainly were widespread, but our fossil-assisted analysis agrees imperfectly with our analysis that accounted for the effect of range size on diversification rate. Because of collection biases in the fossil record, it is likely that a higher proportion of Rosalean genera were widespread in the past than our fossil dataset would indicate. Groups such as the Maleae, with good fossil records and temperate distributions, still show a disparity in the results of the two methods, however (Table 11, Fig. 7), so we conclude that our phylogenetic comparative analysis has poorer taxonomic resolution than our fossil-assisted phylogeographic analysis. Some of the genera that were resolved as ancestrally widespread were probably more restricted than *asr.bisse*'s results would indicate.

Within the limits of the fossil record, it appears that the Rosaceae diversified in North America, while the other Rosalean families diversified in other continents, particularly Eurasia. This conclusion, especially for the non-Rosaceous Rosales, should be taken with some caution, however, since the fossil record of tropical continents is undersampled.

It can be difficult to infer ancestral ranges from either fossils or phylogenetic methods. The fossil record is incomplete and regionally biased, but phylogenetic methods require simplifying assumptions about evolution that are known to be incorrect (e.g. Rabosky 2010; Wagner & Estabrook 2014; Rabosky & Goldberg 2015; Simpson et

al. submitted). Methods of ASR that can incorporate paleontological as well as modern data (such as BioGeoBEARS) partially bridge this divide, but there remain problems that these composite algorithms do not yet provide the tools to solve, among them associations between character state or geographic location and diversification or extinction risk.

We conclude that phylogenetic comparative algorithms like *asr.bisse* are complimentary to fossil-using ASR methods such as BioGeoBEARS. We find that *asr.bisse* performs poorly at inferring geographic range size of genera in the past, but it does identify clades of taxa that deserve additional attention: *asr.bisse*'s inferences of ancestral geographic ranges are often accurate, but imprecise. We propose therefore that methods like *asr.bisse* that use only modern data are best used in concert with other methods such as BioGeoBEARS to identify taxonomic groups of interest. Ideally, future algorithms will be able to conduct phylogenetic comparative analysis as well as make use of fossil data.

CHAPTER ACKNOWLEDGEMENTS

We thank Daniel Potter for providing us with initial sequence data which we expanded to build our phylogenetic dataset. We thank the first author's dissertation committee members, Kate Lyons, Peter Wagner, Michele Dudash, and Charles Delwiche, who contributed useful ideas in the development of this work. Funding for this project was provided by the Behavior, Ecology, Evolution, and Systematics graduate program at the University of Maryland College Park.

TABLES

Table 11. Rosalean clades identified by asr.bisse as having a high probability of having been widespread versus BioGeoBEARS' assessment of the same clades. Clades identified by asr.bisse as having a high probability of being ancestrally widespread but which lack fossil records are not presented here as there is no basis to compare them to our BioGeoBEARS analysis that depend on fossil data. The only genus BioGeoBEARS infers to have been widespread in the past but which does not belong to one of the clades that of asr.bisse assigns a high-probability of large paleorange is *Celtis* (Cannabaceae).

Clade	Asr.bisse vs. BioGeoBEARS	Details
Ulmaceae	Agreement	<i>Ulmus</i> and <i>Zelkova</i> paleo-widespread
Moreae	Partial agreement	<i>Morus</i> widespread, <i>Artocarpus</i> restricted
<i>Humulus-Cannabis</i> clade	Agreement	<i>Humulus</i> widespread
<i>Prunus</i>	Agreement	<i>Prunus</i> widespread
<i>Holodiscus-Luetkea-Aruncus</i> group	Disagreement	<i>Holodiscus</i> restricted
Maleae	Partial agreement	<i>Crataegus</i> , <i>Pyracantha</i> , <i>Sorbus</i> widespread; many others not
Rosoideae	Partial agreement	<i>Potentilla</i> , <i>Rosa</i> widespread; <i>Rubus</i> restricted
<i>Sanguisorba-Bencomia-Margyricarpus</i> clade	Partial agreement	<i>Sanguisorba</i> widespread; <i>Polylepis</i> , <i>Cliffortia</i> restricted

Table 12. Contingency table of Rosalean genera comparing whether or not asr.bisse places them in clades with wide ancestral distribution versus whether or not BioGeoBEARS infers them to have wide paleodistributions. Genera belonging to clades identified as having a high probability of being widespread by asr.bisse are much more likely than random to have actually been widespread under BioGeoBEARS' inference (Fisher's Exact Test $p < 0.0001$).

		BioGeoBEARS inference	
		Widespread	Restricted
Asr.bisse inference	Widespread clades	11	11
	Not in widespread clades	1	36

FIGURES

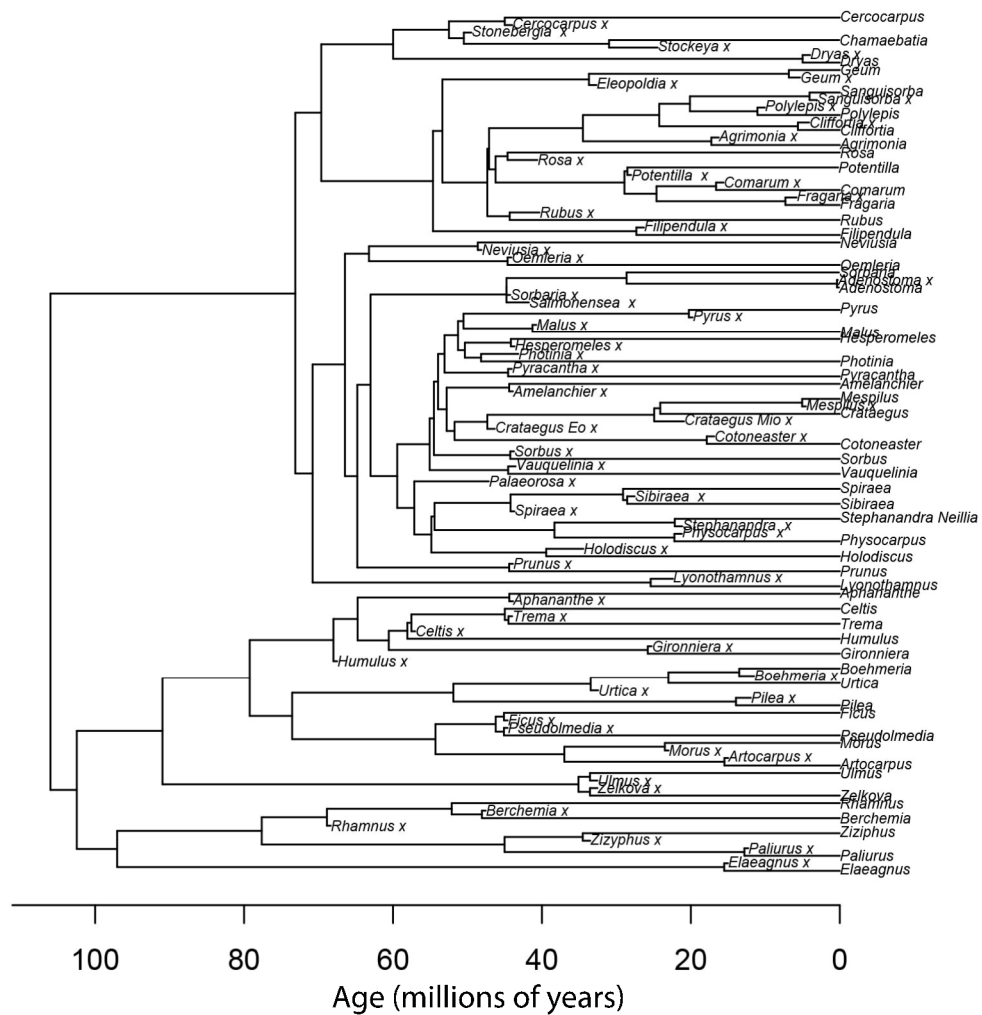


Figure 6. Phylogeny of fossil genera in the Rosales together with their living and sister-group relatives. The phylogeny is based on data from Potter et al. (2007) and sequences from GenBank, with fossil genera attached at their fossil ages. Genera with the label “x” indicate extinct genera or fossil representatives of living genera. The Rosaceous genera *Stephanandra* and *Neillia* are treated here as a single lineage because of missing phylogenetic data.

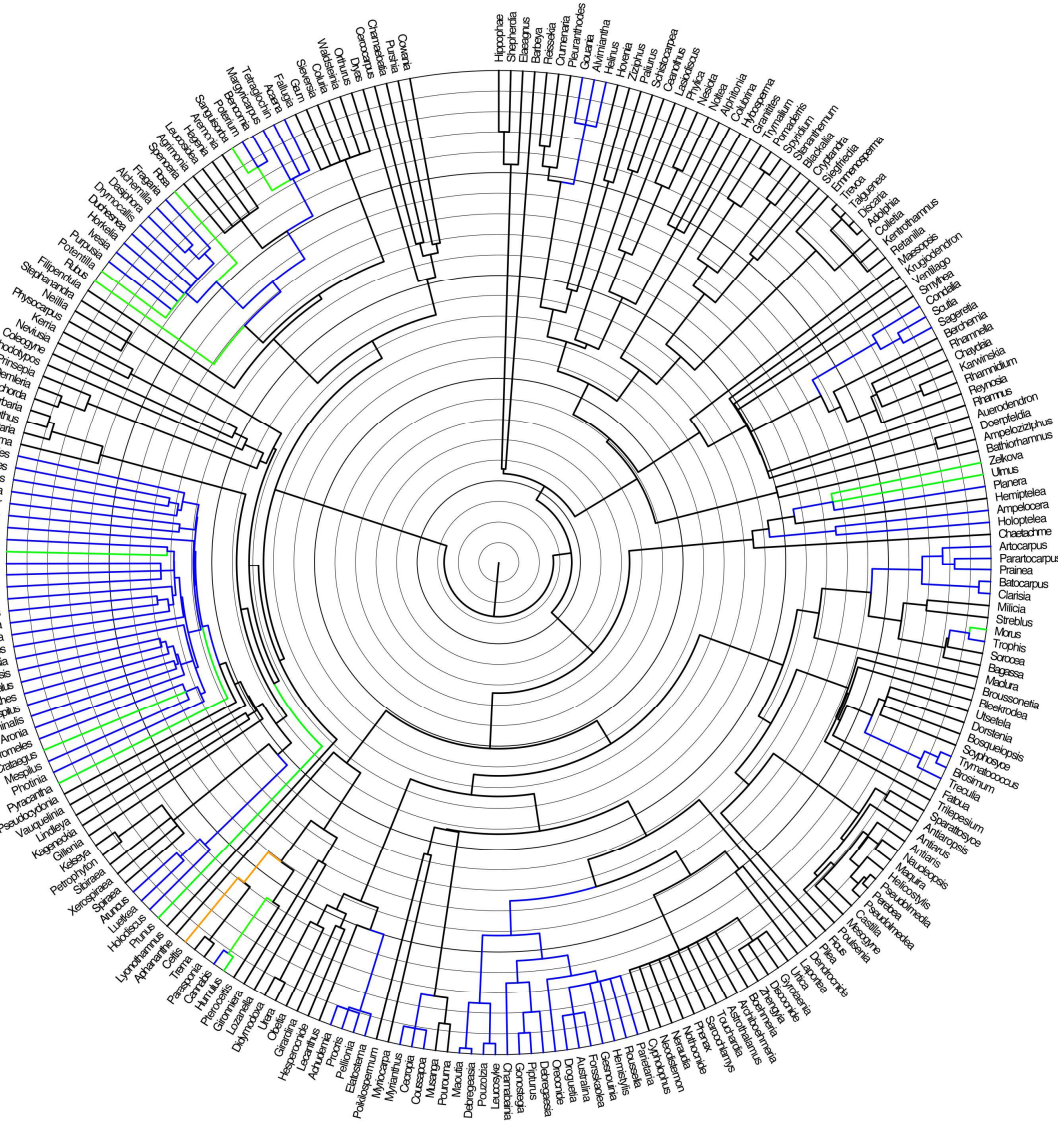


Figure 7. Phylogeny of the Rosales, with branches color-coded based on inference of paleorange size. Black indicates ancestors without a widespread fossil record and inferred to have been restricted by asr.bisse. Blue indicates ancestors without a widespread fossil record but which asr.bisse does infer to have been widespread. Green indicates genera with both a widespread fossil record and inferred to have been widespread by asr.bisse. Orange indicates genus (*Celtis*) that is widespread in the fossil record, but which asr.bisse infers to have been restricted. This tree was adapted from Simpson (2016, chapter 2).

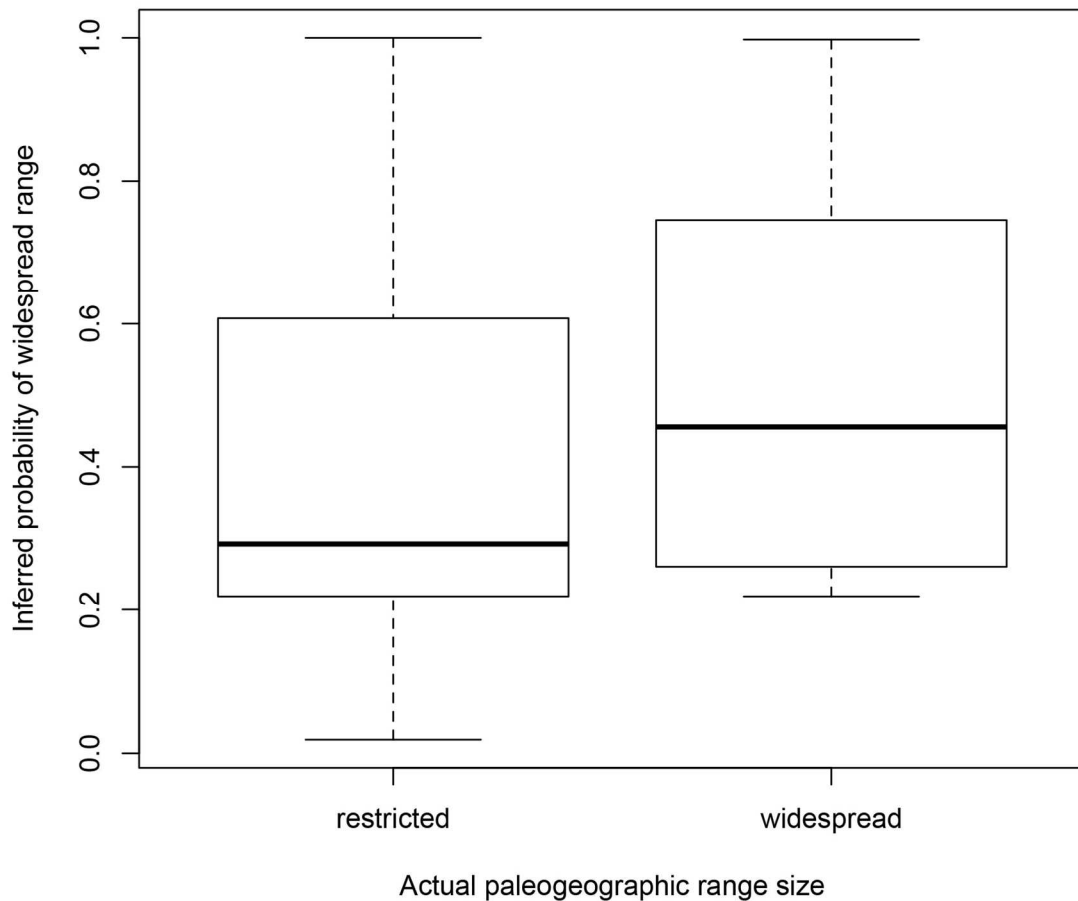


Figure 8. Boxplot of the distribution of inferred paleoranges of last common ancestors (LCA) of Rosalean genera with their sister groups using ASR-BiSSE. Genera present in the fossil record on multiple continents are classified as widespread, while those present on only a single continent are classified as restricted. The inferred probability of widespread range is calculated using the maximum likelihood model implemented in the `asr.bisse` function in `diversitree`. Although genera that are widespread in the fossil record are more likely to have been inferred as having been widespread (i.e. they have higher probabilities), this difference is not statistically significant (K-S test, $D = 0.2859$, $p = 0.2582$; 1,000,000 bootstraps yield 81% support).

■ _	■ SE	■ NIE	■ IEU	■ SIEF
■ N	■ SF	■ NIF	■ IFU	■ SIEU
■ S	■ SU	■ NIU	■ EFU	■ SIFU
■ I	■ IE	■ NEF	■ NSIE	■ SEFU
■ E	■ IF	■ NEU	■ NSIF	■ IEFU
■ F	■ IU	■ NFU	■ NSIU	■ NSIEF
■ U	■ EF	■ SIE	■ NSEF	■ NSIEU
■ NS	■ EU	■ SIF	■ NSEU	■ NSIFU
■ NI	■ FU	■ SIU	■ NSFU	■ NSEFU
■ NE	■ NSI	■ SEF	■ NIEF	■ NIEFU
■ NF	■ NSE	■ SEU	■ NIEU	■ SIEFU
■ NU	■ NSF	■ SFU	■ NIFU	□ NSIEFU
■ SI	■ NSU	■ IEF	■ NEFU	

Figure 9. Legend for Figure 10, containing continent codes. _ signifies that a genus has no range (i.e. it is extinct). N signifies North America; S, South America; I, Iceland; E, Eurasia; F, Africa; U, Australia. Combinations of multiple letters signifies that a genus is present on multiple continents. Regions of the Earth not represented by this list of continents are not represented in the known fossil record of the Rosales.

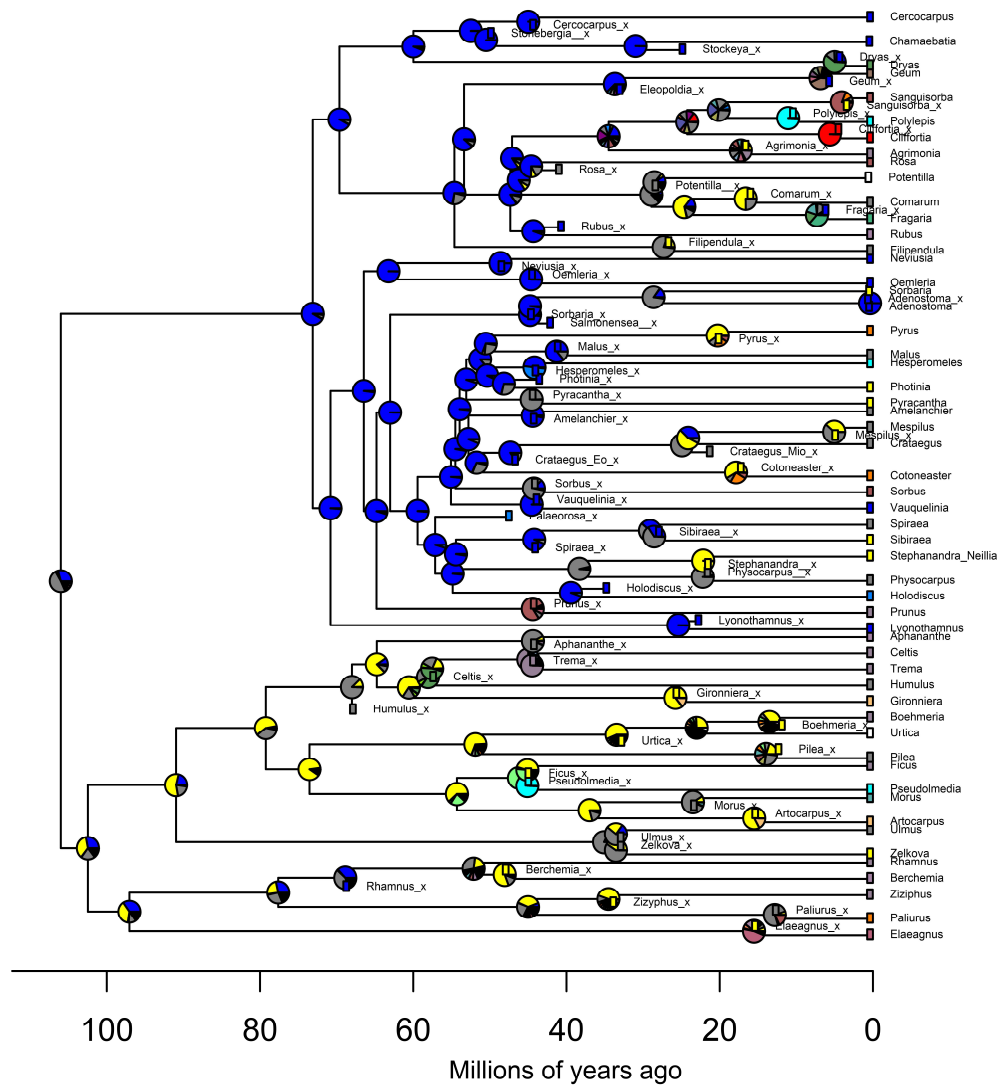


Figure 10. Phylogeny of the Rosales (e.g. Fig. 6) with probabilities of past generic continental distribution mapped onto ancestor nodes. Genera with “_x” added to their names indicate fossil genera. Each small pie chart represents the probability of a genus’ ancestor being distributed on one or more continents, color-coded according to Fig. 9. Tip (“leaf”) states are also represented with colored boxes color-coded according to Fig. 9.

Conclusion

In chapter one, I investigated the difficulties that phylogenetic comparative methods (in particular BiSSE) have in reconstructing speciation and extinction rates given violation of their assumptions. I discovered that as long as lineages are still diversifying, phylogenetic comparative methods work reasonably well despite these violations of their assumptions. The increasing number of modern genera through time in the Rosaceae over the Cenozoic (Devore & Pigg 2007) suggest that the Rosaceae at least are diversifying. Because of the comparatively sparse fossil record of the other Rosalean families, it is more difficult to ascertain whether or not they are also still diversifying. The high diversity of contemporary tropical genera in the Moraceae and Urticaceae as well as the radiation of temperate Urticaceous herbs is consistent with the possibility that they are still diversifying, however. Because of this, I feel that there is reason to put some credence into the use of phylogenetic comparative methods on the Rosales.

Genus-level diversification rates in the Rosales are influenced by three visible factors that I identified in my second chapter. These include (1) an independent effect of habit by which herbaceous genera diversify more rapidly than woody genera; (2) a three-way interaction by which species-rich, wide-ranging, and animal-dispersed genera diversify more rapidly than genera without one of the three of these; (3) a four-way interaction, where genera that are woody in addition to being animal dispersed, wide-ranging, and species-rich benefit even more from the aforementioned three-way interaction than do genera that are herbaceous. Genera benefitting from one of these three factors have negative net-diversification rates, i.e. lineages composed of such genera will preferentially become extinct. Because of known difficulties of phylogenetic methods to

recover extinction rates (Rabosky 2010), I cannot be confident that these differences in net diversification rates are due to processes related to increased rates of origination (e.g. Ricklefs & Latham 1992, O'Meara et al. in press), reduced rates of extinction (e.g. Jablonski & Hunt 2006, Payne & Finnegan 2007), or both. Testing hypotheses related to differential origination versus extinction rates represent an area of ongoing and future research.

Finally, in my third chapter, I was able to identify that the ability of state speciation and extinction (SSE) models to reconstruct ancestral character states, in particular geographic range size, has lower taxonomic precision than the fossil record, but is nonetheless useful in identifying clades of prospective genera. This identifies a number of groups in the Moraceae and Urticaceae that do not have fossil records as prospective hotspots of large paleo-range size and, potentially, paleodiversification (although in this chapter I used inferred paleodiversification to recover paleorange, so to do the same in reverse would fall victim to circular reasoning). Among temperate latitude taxa, the Rosaceae seem to have originated and then diversified in North America before spreading to Eurasia, while the rest of the Rosales either diversified in Eurasia or other continents. These findings are subject to collection biases in the fossil record, especially for the non-Rosaceous families, since tropical floras are comparatively poorly studied. As a result, the fossil-assisted phylogeographic origin of the Rosaceae, a largely temperate family, is more confident than that of the other families.

As mentioned above, a major direction of future research that I intend to pursue is lies in elucidating causes, rather than correlations, between ecology and diversification rates. Animal dispersal has been found to correlate with increasing geographic range size

in the Fagales (Larson-Johnson 2016), and I have an additional dataset that I intend to publish shortly that implies the same to be true among gymnosperms. These results together suggest that animal dispersal, leading to or interacting with geographic range size, may be an important driver in the patterns of diversification in seed plants as a whole, at least in the comparatively recent geologic past. This raises a number of interesting questions for future scientific endeavor. Do large range sizes enhance diversification rates by enabling opportunities for allopatry and thus speciation (Ricklefs & Latham 1992), buffer wide-ranging taxa against extinction (Payne & Finnegan 2007), or both? If paleoendemic relict genera became restricted due to a lack of geographic range size or colonization ability, then what enabled them to become more widespread in the past? Have range size and animal dispersal always been beneficial to diversification in woody plants, or are the patterns that Larson-Johnson (2016) and I observe a consequence of climatic or other conditions of the recent geologic past? How does the ecological representation of dispersal mechanism change over geologic time (e.g. Tiffney 2004), and does this correlate with the gain or loss of taxonomic distribution or diversity in communities? What other ecological traits, for instance dioecy (Sabath et al. 2016), might also interact with geographic range size to influence diversification rates? If range size and dispersal mechanism are so tightly related, can this information be used to inform conservation efforts designed to mediate the effects of ongoing and future climate change? While this dissertation itself does not answer these questions, it does suggest many possible avenues for future work that I wish to participate in.

APPENDICES

Appendix I – Paleontological references used to calibrate the time-phylogenetic analysis presented in Figure 1. Taxon reference cites the paper in which the fossil is identified, and age reference indicates the article giving the age of the fossil. Node labels are keyed to Figure 1.

Taxon	Taxon Reference	Age	Age Reference	Node Label
Cannabaceae + Urticaceae	Manchester 1989	90 Ma	Manchester 1989	A
<i>Celtis</i> (Cannabac.)	Manchester et al. 2002	64 Ma	Manchester 1989	B
Amygdaleae (Rosac.)	DeVore & Pigg 2007	47 Ma	Pearson & Obradovich 1977	C
Maloideae (Rosac.)	DeVore & Pigg 2007	48.7 Ma	Stockey 2001	D
Roseae (Rosac.)	DeVore & Pigg 2007	47 Ma	Pearson & Obradovich 1977	E
Spireae (Rosac.)	DeVore & Pigg 2007	47 Ma	Pearson & Obradovich 1977	F
Rhamnaceae	Calvillo-Canadell & Cevallos-Ferriz 2007	72.5 Ma	Eberth et al. 2004	G

Appendix II – List of genera used in our phylogenetic comparative analysis and represented in Figure 1. The index refers to the identification number given in figure 1.

Genus	Family	Index
<i>Hippophae</i>	Elaeagnaceae	1
<i>Shepherdia</i>	Elaeagnaceae	2
<i>Elaeagnus</i>	Elaeagnaceae	3
<i>Barbeya</i>	Barbeyaceae	4
<i>Reissekia</i>	Rhamnaceae	5
<i>Crumenaria</i>	Rhamnaceae	6
<i>Pleuranthodes</i>	Rhamnaceae	7
<i>Gouania</i>	Rhamnaceae	8
<i>Helinus</i>	Rhamnaceae	9
<i>Hovenia</i>	Rhamnaceae	10
<i>Ziziphus</i>	Rhamnaceae	11
<i>Paliurus</i>	Rhamnaceae	12
<i>Schistocarpea</i>	Rhamnaceae	13
<i>Ceanothus</i>	Rhamnaceae	14
<i>Lasiodiscus</i>	Rhamnaceae	15
<i>Phyllica</i>	Rhamnaceae	16
<i>Nesiota</i>	Rhamnaceae	17
<i>Noltea</i>	Rhamnaceae	18
<i>Alphitonia</i>	Rhamnaceae	19

<i>Colubrina</i>	Rhamnaceae	20
<i>Granitites</i>	Rhamnaceae	21
<i>Trymalium</i>	Rhamnaceae	22
<i>Pomaderris</i>	Rhamnaceae	23
<i>Spyridium</i>	Rhamnaceae	24
<i>Stenanthemum</i>	Rhamnaceae	25
<i>Blackallia</i>	Rhamnaceae	26
<i>Cryptandra</i>	Rhamnaceae	27
<i>Siegfriedia</i>	Rhamnaceae	28
<i>Emmenosperma</i>	Rhamnaceae	29
<i>Trevoa</i>	Rhamnaceae	30
<i>Discaria</i>	Rhamnaceae	31
<i>Adolphia</i>	Rhamnaceae	32
<i>Colletia</i>	Rhamnaceae	33
<i>Maesopsis</i>	Rhamnaceae	34
<i>Krugiodendron</i>	Rhamnaceae	35
<i>Ventilago</i>	Rhamnaceae	36
<i>Condalia</i>	Rhamnaceae	37
<i>Scutia</i>	Rhamnaceae	38
<i>Sageretia</i>	Rhamnaceae	39
<i>Berchemia</i>	Rhamnaceae	40
<i>Rhamnella</i>	Rhamnaceae	41

<i>Karwinskia</i>	Rhamnaceae	42
<i>Rhamnidium</i>	Rhamnaceae	43
<i>Reynosia</i>	Rhamnaceae	44
<i>Rhamnus</i>	Rhamnaceae	45
<i>Doerpfeldia</i>	Rhamnaceae	46
<i>Ampeloziziphus</i>	Rhamnaceae	47
<i>Bathiorhamnus</i>	Rhamnaceae	48
<hr/>		
<i>Zelkova</i>	Ulmaceae	49
<i>Ulmus</i>	Ulmaceae	50
<i>Hemiptelea</i>	Ulmaceae	51
<i>Ampelocera</i>	Ulmaceae	52
<i>Holoptelea</i>	Ulmaceae	53
<i>Chaetachme</i>	Ulmaceae	54
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<i>Artocarpus</i>	Moraceae	55
<i>Parartocarpus</i>	Moraceae	56
<i>Prainea</i>	Moraceae	57
<i>Batocarpus</i>	Moraceae	58
<i>Clarisia</i>	Moraceae	59
<i>Milicia</i>	Moraceae	60
<i>Streblus</i>	Moraceae	61
<i>Morus</i>	Moraceae	62
<i>Trophis</i>	Moraceae	63

<i>Sorocea</i>	Moraceae	64
<i>Bagassa</i>	Moraceae	65
<i>Maclura</i>	Moraceae	66
<i>Broussonetia</i>	Moraceae	67
<i>Bleekrodea</i>	Moraceae	68
<i>Utsetela</i>	Moraceae	69
<i>Dorstenia</i>	Moraceae	70
<i>Trymatococcus</i>	Moraceae	71
<i>Brosimum</i>	Moraceae	72
<i>Treculia</i>	Moraceae	73
<i>Fatoua</i>	Moraceae	74
<i>Trilepesium</i>	Moraceae	75
<i>Sparattosyce</i>	Moraceae	76
<i>Antiaropsis</i>	Moraceae	77
<i>Antiarus</i>	Moraceae	78
<i>Antiaris</i>	Moraceae	79
<i>Naucleopsis</i>	Moraceae	80
<i>Maquira</i>	Moraceae	81
<i>Helicostylis</i>	Moraceae	82
<i>Pseudolmedia</i>	Moraceae	83
<i>Perebea</i>	Moraceae	84
<i>Pseudolmedea</i>	Moraceae	85

<i>Castilla</i>	Moraceae	86
<i>Poulsenia</i>	Moraceae	87
<i>Ficus</i>	Moraceae	88
<i>Pilea</i>	Urticaceae	89
<i>Dendrocnide</i>	Urticaceae	90
<i>Laportea</i>	Urticaceae	91
<i>Urtica</i>	Urticaceae	92
<i>Zhengyia</i>	Urticaceae	93
<i>Boehmeria</i>	Urticaceae	94
<i>Parietaria</i>	Urticaceae	95
<i>Forsskaolea</i>	Urticaceae	96
<i>Droguetia</i>	Urticaceae	97
<i>Oreocnide</i>	Urticaceae	98
<i>Debregaesia</i>	Urticaceae	99
<i>Pipturus</i>	Urticaceae	100
<i>Gonostegia</i>	Urticaceae	101
<i>Chamabainia</i>	Urticaceae	102
<i>Leucosyke</i>	Urticaceae	103
<i>Pouzolzia</i>	Urticaceae	104
<i>Debregeasia</i>	Urticaceae	105
<i>Maoutia</i>	Urticaceae	106
<i>Pourouma</i>	Urticaceae	107

<i>Musanga</i>	Urticaceae	108
<i>Coussapoa</i>	Urticaceae	109
<i>Cecropia</i>	Urticaceae	110
<i>Myriocarpa</i>	Urticaceae	111
<i>Poikilospermum</i>	Urticaceae	112
<i>Elatostema</i>	Urticaceae	113
<i>Pellionia</i>	Urticaceae	114
<i>Procris</i>	Urticaceae	115
<i>Lecanthus</i>	Urticaceae	116
<i>Hesperocnide</i>	Urticaceae	117
<i>Girardina</i>	Urticaceae	118
<i>Obetia</i>	Urticaceae	119
<i>Urera</i>	Urticaceae	120
<i>Didymodoxa</i>	Urticaceae	121
<i>Lozanella</i>	Urticaceae	122
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<i>Gironniera</i>	Cannabaceae	123
<i>Pteroceltis</i>	Cannabaceae	124
<i>Humulus</i>	Cannabaceae	125
<i>Cannabis</i>	Cannabaceae	126
<i>Parasponia</i>	Cannabaceae	127
<i>Trema</i>	Cannabaceae	128
<i>Celtis</i>	Cannabaceae	129

<i>Aphananthe</i>	Cannabaceae	130
<i>Lyonothamnus</i>	Rosaceae	131
<i>Prunus</i>	Rosaceae	132
<i>Holodiscus</i>	Rosaceae	133
<i>Luetkea</i>	Rosaceae	134
<i>Aruncus</i>	Rosaceae	135
<i>Spiraea</i>	Rosaceae	136
<i>Petrophyton</i>	Rosaceae	137
<i>Kelseya</i>	Rosaceae	138
<i>Gillenia</i>	Rosaceae	139
<i>Kageneckia</i>	Rosaceae	140
<i>Lindleya</i>	Rosaceae	141
<i>Vauquelinia</i>	Rosaceae	142
<i>Pseudoccydonia</i>	Rosaceae	143
<i>Pyracantha</i>	Rosaceae	144
<i>Photinia</i>	Rosaceae	145
<i>Mespilus</i>	Rosaceae	146
<i>Crataegus</i>	Rosaceae	147
<i>Aronia</i>	Rosaceae	148
<i>Torminalis</i>	Rosaceae	149
<i>Chamaemespilus</i>	Rosaceae	150
<i>Dichotomanthes</i>	Rosaceae	151

<i>Malus</i>	Rosaceae	152
<i>Docyniopsis</i>	Rosaceae	153
<i>Stranvaesia</i>	Rosaceae	154
<i>Chamaemeles</i>	Rosaceae	155
<i>Aria</i>	Rosaceae	156
<i>Eriobotrya</i>	Rosaceae	157
<i>Rhaphiolepis</i>	Rosaceae	158
<i>Heteromeles</i>	Rosaceae	159
<i>Pyrus</i>	Rosaceae	160
<i>Cotoneaster</i>	Rosaceae	161
<i>Sorbus</i>	Rosaceae	162
<i>Cormus</i>	Rosaceae	163
<i>Eriolobus</i>	Rosaceae	164
<i>Peraphyllum</i>	Rosaceae	165
<i>Amelanchier</i>	Rosaceae	166
<i>Cydonia</i>	Rosaceae	167
<i>Osteomeles</i>	Rosaceae	168
<i>Chaenomeles</i>	Rosaceae	169
<i>Malacomeles</i>	Rosaceae	170
<i>Adenostoma</i>	Rosaceae	171
<i>Chamaebatiaria</i>	Rosaceae	172
<i>Spiraeanthus</i>	Rosaceae	173

<i>Sorbaria</i>	Rosaceae	174
<i>Exochorda</i>	Rosaceae	175
<i>Oemleria</i>	Rosaceae	176
<i>Prinsepia</i>	Rosaceae	177
<i>Rhodotypos</i>	Rosaceae	178
<i>Coleogyne</i>	Rosaceae	179
<i>Neviusia</i>	Rosaceae	180
<i>Kerria</i>	Rosaceae	181
<i>Physocarpus</i>	Rosaceae	182
<i>Neillia</i>	Rosaceae	183
<i>Filipendula</i>	Rosaceae	184
<i>Rubus</i>	Rosaceae	185
<i>Potentilla</i>	Rosaceae	186
<i>Dasiphora</i>	Rosaceae	187
<i>Alchemilla</i>	Rosaceae	188
<i>Fragaria</i>	Rosaceae	189
<i>Rosa</i>	Rosaceae	190
<i>Spenceria</i>	Rosaceae	191
<i>Agrimonia</i>	Rosaceae	192
<i>Sanguisorba</i>	Rosaceae	193
<i>Poterium</i>	Rosaceae	194
<i>Margyricarpus</i>	Rosaceae	195

<i>Fallugia</i>	Rosaceae	196
<i>Geum</i>	Rosaceae	197
<i>Dryas</i>	Rosaceae	198
<i>Cercocarpus</i>	Rosaceae	199
<i>Chamaebatia</i>	Rosaceae	200
<i>Purshia</i>	Rosaceae	201
<i>Cowania</i>	Rosaceae	202
<hr/>		
<i>Alvimiantha</i>	Rhamnaceae	no sequence
<i>Hybosperma</i>	Rhamnaceae	no sequence
<i>Talguenea</i>	Rhamnaceae	no sequence
<i>Kentrothamnus</i>	Rhamnaceae	no sequence
<i>Retanilla</i>	Rhamnaceae	no sequence
<i>Smythea</i>	Rhamnaceae	no sequence
<i>Chaydaia</i>	Rhamnaceae	no sequence
<i>Auerodendron</i>	Rhamnaceae	no sequence
<i>Planera</i>	Ulmaceae	no sequence
<i>Bosqueiopsis</i>	Moraceae	no sequence
<i>Scyphosyce</i>	Moraceae	no sequence
<i>Mesogyne</i>	Moraceae	no sequence
<i>Gyrotaenia</i>	Urticaceae	no sequence
<i>Discocnide</i>	Urticaceae	no sequence
<i>Archiboehmeria</i>	Urticaceae	no sequence

<i>Astrothalamus</i>	Urticaceae	no sequence
<i>Touchardia</i>	Urticaceae	no sequence
<i>Sarcochlamys</i>	Urticaceae	no sequence
<i>Phenax</i>	Urticaceae	no sequence
<i>Nothocnide</i>	Urticaceae	no sequence
<i>Neraudia</i>	Urticaceae	no sequence
<i>Neodistemon</i>	Urticaceae	no sequence
<i>Cypholophus</i>	Urticaceae	no sequence
<i>Rousselia</i>	Urticaceae	no sequence
<i>Hemistylis</i>	Urticaceae	no sequence
<i>Gesnouinia</i>	Urticaceae	no sequence
<i>Australina</i>	Urticaceae	no sequence
<i>Myrianthus</i>	Urticaceae	no sequence
<i>Achudemia</i>	Urticaceae	no sequence
<i>Xerospiraea</i>	Rosaceae	no sequence
<i>Sibiraea</i>	Rosaceae	no sequence
<i>Hesperomeles</i>	Rosaceae	no sequence
<i>Docynia</i>	Rosaceae	no sequence
<i>Stephanandra</i>	Rosaceae	no sequence
<i>Purpusia</i>	Rosaceae	no sequence
<i>Ivesia</i>	Rosaceae	no sequence
<i>Horkelia</i>	Rosaceae	no sequence

<i>Duchesnea</i>	Rosaceae	no sequence
<i>Drymocallis</i>	Rosaceae	no sequence
<i>Leucosidea</i>	Rosaceae	no sequence
<i>Hagenia</i>	Rosaceae	no sequence
<i>Aremonia</i>	Rosaceae	no sequence
<i>Bencomia</i>	Rosaceae	no sequence
<i>Tetraglochin</i>	Rosaceae	no sequence
<i>Acaena</i>	Rosaceae	no sequence
<i>Sieversia</i>	Rosaceae	no sequence
<i>Coluria</i>	Rosaceae	no sequence
<i>Waldsteinia</i>	Rosaceae	no sequence
<i>Orthurus</i>	Rosaceae	no sequence

Appendix III. The fossil records of Rosalean genera used in this study, their current geographic distributions, and references. Genera are sorted in alphabetical order by family and then by genus; family names are shown at the top of each respective subsection. Current distributions are shown by letter codes: N, North America; S, South America; I, Iceland; E, Eurasia; F, Africa; U, Australia. Genera with present-day distributions outside of these areas are denoted with a plus-sign (“+”), but these regions were not included in the analysis because there are no Rosalean fossils from these regions in our dataset. Records taken from the Fossilworks section of the Paleobiology Database (<http://www.fossilworks.org>) are labeled “PBDB”.

Genus name	First occurrence	Current distribution	References
Family Cannabaceae			
<i>Aphananthe</i>	Middle Eocene (Clarno)	N,E,U+	Dorofeev 1963; Manchester 1994
<i>Celtis</i>	Paleocene (Ft. Union)	N,S,E,F,U+	Wilf 2000; Manchester et al. 2002
<i>Gironniera</i>	Late Oligocene (25 Ma, Sachsen)	E,U+	Mai 1997, 2001
<i>Humulus</i>	Maastrichtian (Hell Creek)	N,E	Dorofeev 1963; Johnson 2002
<i>Trema</i>	Middle Eocene (Clarno)	N,S,E,F,U+	Manchester 1994
Family Elaeagnaceae			
<i>Elaeagnus</i>	Middle Miocene (Silesia)	N,E,F,U+	Szafer 1961
Family Moraceae			
<i>Artocarpus</i>	Middle Miocene (Siwalik)	E,U+	Bera et al. 2006
<i>Ficus</i>	Early Miocene of Europe	N,S,E,F,U+	Mai 1991, 2001

<i>Morus</i>	Miocene (Germany and Russia)	N,S,E	Dorofeev 1963; Mai 2001
<i>Pseudolmedia</i>	Middle Miocene (Iguincha Fm.)	S	Kowalski 2001
Family Rhamnaceae			
<i>Berchemia</i>	Middle Eocene (Hesse)	N,E,U+	Collinson et al. 2012
<i>Paliurus</i>	Oligocene (Crooked River), Miocene of Germany	E,F	Meyer & Manchester 1997; Mai 2001
<i>Rhamnus</i>	Maastrichtian (Hell Creek)	N,S,E,F,U+	Peppe et al. 2007
<i>Zizyphus</i>	Oligocene of Europe	N,S,E,F,U+	Mai 2001
Family Rosaceae			
<i>Adenostoma</i>	Late Pleistocene	N	Heusser 1978; Stock 1992
<i>Agrimonia</i>	Miocene	N,S,E,F,U	Mai 1995
<i>Amelanchier</i>	Middle Eocene (Okanogen Highlands)	N,E	DeVore & Pigg 2007; Schorn & Gooch 1994

<i>Cercocarpus</i>	Middle Eocene (Okanogen Highlands)	N	DeVore & Pigg 2007
<i>Cliffortia</i>	Mio-Pliocene	F	Scott 1995
<i>Comarum</i>	Miocene of Germany	N,E	Mai 1995
<i>Cotoneaster</i>	Miocene of Germany	E,F	Mai 1995
<i>Crataegus</i>	Middle Eocene (Okanogen Highlands)	N,E	DeVore & Pigg 2007
<i>Dryas</i>	Late Neogene (Arctic)	N,I,E	Matthewes & Ovendon 1990
<i>Eleopoldia</i>	Late Eocene (Florissant)	(extinct)	Wolfe & Wehr 1988; DeVore & Pigg 2007
<i>Filipendula</i>	Miocene	N,E	Mai 1995
<i>Fragaria</i>	Late Neogene (Arctic)	N,S,I,E+	Matthewes & Ovendon 1990
<i>Geum</i>	Late Neogene (Arctic)	N,I,E,F,U+	Matthewes & Ovendon 1990
<i>Hesperomeles</i>	Middle Eocene (Okanogen Highlands)	S	DeVore & Pigg 2007

<i>Holodiscus</i>	Late Eocene (Florissant)	N,S	DeVore & Pigg 2007; Schorn 1998
<i>Lyonothamnus</i>	Early Miocene (Coldwash)	N	Erwin & Schorn 2000
<i>Malus</i>	Late Eocene (Florissant)	N,E	DeVore & Pigg 2007
<i>Mespilus</i>	Mio-Pliocene (Saugbagger)	N,E	Mai 1995; Geissert et al. 1990
<i>Neviusia</i>	Middle Eocene (Princeton Chert)	N	DeVore et al. 2004; DeVore et al. 2005
<i>Oemleria</i>	Early Eocene (Republic)	N	Benedict et al. 2011; DeVore & Pigg 2007; DeVore et al. 2011
<i>Palaeorosa</i>	Middle Eocene (Princeton Chert)	(extinct)	Cevallos-Ferris et al. 1993; DeVore & Pigg 2007
<i>Photinia</i>	Early Eocene (Republic)	E	Wolfe & Wehr 1987; PBDB
<i>Physocarpus</i>	Miocene of Germany	N,E	Mai 1995; Matthewes & Ovendon 1990
<i>Polylepis</i>	Mid-late Miocene (Bolivia)	S	Gregory-Wodzicki et al. 1998
<i>Potentilla</i>	Late Oligocene (Creede)	N,S,I,E,F,U+	DeVore & Pigg 2007; Mai 1995; Matthewes & Ovendon 1990

<i>Prunus</i>	Early Eocene (Republic/Wutu)	N,S,E,F,U+	Benedict et al. 2011; Li et al. 2011; Cevallos-Ferriz & Stockey 1991; Manchester 1994
<i>Pyracantha</i>	Middle Eocene (Okanogen Highlands), later in Europe	E	DeVore & Pigg 2007; Mai 1995
<i>Pyrus</i>	Miocene of Germany	E,F	Mai 1995
<i>Rosa</i>	Middle Eocene (Eifel), also Okanogen Highlands (mid- late Eocene)	N,E,F	DeVore & Pigg 2007; Meyer & Manchester 1997; Tanai & Onoe 1961; Miki & Kokowa 1962; Tanai & Suzuki 1963; Wilde & Frankenhauser 1998
<i>Rubus</i>	Middle Eocene (Okanogen Highlands)	N,E,U+	DeVore & Pigg 2007
<i>Salmonensea</i>	Late Eocene/early Oligocene	(extinct)	Wolfe & Weir 1988
<i>Sanguisorba</i>	Pliocene (Netherlands)	N,E,F	Muller 1981
<i>Sibiraea</i>	Late Oligocene (Creede)	E	DeVore & Pigg 2007

<i>Sorbaria</i>	Middle Eocene (Okanogen Highlands)	E	DeVore & Pigg 2007
<i>Sorbus</i>	Middle Eocene (Okanogen Highlands)	N,E,F	DeVore & Pigg 2007; Tanai & Onoe 1961; Miki & Kokowa 1962; Tanai & Suzuki 1963
<i>Spiraea</i>	Early Eocene (Republic)	N,E	DeVore & Pigg 2007; PBDB
<i>Stephanandra</i>	Miocene of Germany	E	Mai 1995
<i>Stockeya</i>	Late Oligocene (Creede)	(extinct)	Wolfe & Weir 1988; DeVore & Pigg 2007
<i>Stonebergia</i>	Early Eocene (Okanogen Highlands)	(extinct)	Wolfe & Weir 1988; DeVore & Pigg 2007
<i>Vauquelinia</i>	Middle Eocene (Okanogen Highlands)	N	DeVore & Pigg 2007
Family Ulmaceae			
<i>Ulmus</i>	Oligocene (Bridge Creek),	N,E	Meyer & Manchester 1997; Mai 2001

Miocene in Europe

<i>Zelkova</i>	Oligocene (Bridge Creek) ,	E	Meyer & Manchester 1997; Mai 2001
	Miocene in Europe		

Family Urticaceae

<i>Boehmeria</i>	Miocene (Germany & Russia)	N,S,E,F,U+	Dorofeev 1963; Mai 2001
<i>Pilea</i>	Miocene (Germany & Russia)	N,S,E,F+	Dorofeev 1963; Mai 2001
<i>Urtica</i>	Late Oligocene (Germany)	NSIEFU+	Dorofeev 1963; Mai 1997; Mai 2001

Appendix IV – List of supplemental files contained in this dissertation and submitted through DRUM.

File name	Description
Alignmend BEAUti.nex	Multiple sequence alignment used to create phylogeny of the Rosales
BioGeoBEARS Chapter 3 code.r	R script (modified from BioGeoBEARS example script) with code added to conduct analysis for chapter 3
Biota.txt	Sample starting biota text file used for the clade simulation model of chapter 1
BiSSE Sim.r	Modifiable R code used to automate SpeciationExtinctionModel.c
Code_HSHR	R script for running the MuSSE analysis for chapter 2
Fossil_Ultra_Rosales.phy	Phylogeny of the Rosales with fossil taxa added for chapter 3
Genbank Accession Numbers.txt	Tab-delimited text file containing accession numbers of sequences downloaded from Genbank. Only non-rosaceous sequences are listed here; see Potter et al. (2007) for Rosaceae accession numbers.
Model.txt	Model parameters for the clade simulation model of chapter 1
MuSSE_HSHR.csv	Character state file used for MuSSE analysis for chapter 2
Rosales BEAUti Sorb +	BEAUti file used to run BEAST to generate the

Amel	phylogeny of the Rosales used in chapters 2 and 3
Rosales_Fossil_geog.data	Geographic distribution data for Rosalean living and fossil genera used in chapter 3
SpeciationExtinctionModel.c	Source code for the clade simulation model used in chapter 1

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