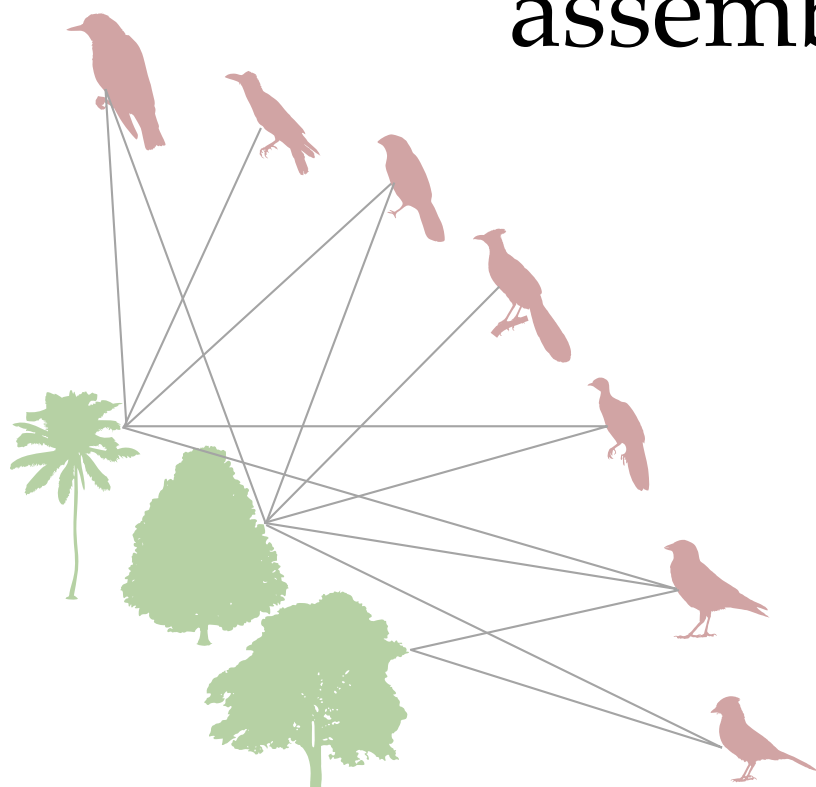# The roles of diet, speciation, and extinction on the diversification of birds, and on the assembly of frugivory networks

Gustavo Burin FERREIRA

# UNIVERSIDADE DE SÃO PAULO

## DOCTORAL THESIS

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# The roles of diet, speciation, and extinction on the diversification of birds, and on the assembly of frugivory networks

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*A thesis submitted to the*
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# Universidade de São Paulo

Tese de Doutorado

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# Os papéis da dieta, especiação e extinção na diversificação de aves e na montagem de redes de frugivoria

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*"You can't possibly be a scientist if you mind people thinking that you're a fool."*

Wonko the Sane, from Douglas N. Adams, in *So long, and thanks for all the fish (1985)*

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Gostaria de iniciar o texto pedindo desculpas, pois não sou tão bom com palavras quanto gostaria, e tenho certeza que as palavras abaixo não farão justiça ao sentimento que tenho para com todas essas pessoas. Peço desculpas também caso tenha esquecido alguém, mas essas coisas acontecem, infelizmente.

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I would like to start the text apologizing for not being as good as I would like with words, and I am sure the words below will not do any justice to the feelings I have towards everyone mentioned. I also apologize if I forgot someone, but these things unfortunately happen.

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# List of Abbreviations

**BiSSE**    **B**inary **S**tate **S**peciation and **E**xtinction
**MuSSE**    **M**ultiple **S**tate **S**peciation and **E**xtinction
**BAMM**    **B**ayesian **A**nalysis of **M**acroevolutionary **M**ixtures
**RPANDA**    **R** Phylogenetic **AN**alyses of **D**iversific**A**tion
**SP***var***    *Var*iable **SP**eciation and constant extinction rates
**EX***var***    *Var*iable **EX**tinction and constant speciation rates
**BOTH***cst***    **BOTH** rates *C*on*S*tan*T*
**BOTH***var***    **BOTH** rates *var*iable
**BOTH***exp***    **BOTH** rates *exp*onential

Dedicated to Tássia and
my to family for keeping
me sane, with my feet on
the ground, and without
whom this dissertation
would not be possible.

# Introduction

Despite the great interest in biodiversity, several questions related to the patterns and processes that determine diversity of a given clade or region still lack a consensual explanation (Coyne and Orr, 2006; Hillebrand, 2004; Mittelbach et al., 2007). This is partially due to our limited knowledge on the diversification dynamics of clades, which ultimately determines species diversity of lineages and different regions. Ultimately, the diversity of organisms is a result of speciation and extinction processes (Weir and Schluter, 2007; Mittelbach et al., 2007), which could be modulated by the existence of a limit in the total number of species that a certain region can harbor (Marshall, 2007; Rabosky and Hurlbert, 2015; Harmon and Harrison, 2015), or by a change in such limit (Marshall and Quental, 2016). Thus, if we aim to understand how diversity varies through time and/or space, it is mandatory to understand how the processes of gain and loss of species are temporally and spatially distributed, and which factors (biotic or abiotic) can affect speciation and extinction dynamics.

Biological interactions can play an important role on the diversification of organisms (Schluter, 2000; Futuyma, 2009; Levin et al., 2009; Grant and Grant, 2011; Soons et al., 2010; Hendry et al., 2009; De León et al., 2012; Nosil, 2012; Thompson, 2013). However, macroevolutionary studies have usually focused on a broad evolutionary perspective (e.g. phylogenies of big clades) while usually adopting a simple characterization of species interactions. The gap between diversification dynamics, and hence macroevolution, and ecological dynamics had also been accentuated by a somewhat, simplified view of ecological systems. For example, ecological studies usually focus on well-characterized interactions of a very few species, although more recently ecologists have been able to characterize large

ecological networks (Bascompte et al., 2003; Guimarães et al., 2006; Krishna et al., 2008; Heil et al., 2009; Melián et al., 2009; Davis et al., 2009; Díaz-Castelazo et al., 2010; Guimarães Jr et al., 2011; Olesen et al., 2010; Spotswood et al., 2012; Nuismer et al., 2013). Network theory-based approaches can augment our understanding of the ecological roles played by different species but still lacks an evolutionary perspective preventing us to fully understand how ecological interactions are assembled (Carnicer et al., 2009, Ricklefs, 2011, Ricklefs and Jenkins, 2011).

Therefore, the main goal of this dissertation is to investigate the evolutionary consequences of species interactions on diversity dynamics, the role of diversity dynamics in structuring ecological networks, and the ability of current phylogenetic methods (which are used to answer the other questions) in correctly estimating diversification dynamics. To address these topics, the dissertation is organized in three chapters, in which we investigated the following questions, respectively:

**1 - What is the effect of diet on speciation and extinction rates of birds?**

In the first chapter, we used Bayesian models of trait-dependent diversification and a comprehensive dietary database of all birds worldwide to assess speciation and extinction dynamics associated with different avian dietary guilds (carnivores, frugivores, granivores, herbivores, insectivores, nectarivores, omnivores, and piscivores).

**2 - How accurately do methods that solely rely on molecular phylogenies detect decline in diversity?**

In the second chapter, we evaluated the behavior of two recently developed methods (RPANDA and BAMM) under two scenarios of diversity decline (i.e. negative diversification rates at the present). In the first scenario we simulated phylogenetic trees where diversity decline is solely controlled by decreasing speciation, while in the second scenario it is solely determined by increasing extinction rates through time. We fitted both RPANDA

and BAMM to all trees at all time slices and compared the simulated and estimated rates to assess parameter estimate accuracy, potential biases and hence compare the performance of both methods. Lastly we compared their diversification rate estimates for a comprehensive dataset of 214 empirical trees.

**3- What is the role of speciation and extinction, if any, on building ecological networks? Are ecological network built in such a way that species belonging to lineages with different diversity dynamics play a distinct ecological role on those ecological networks?**

In the third chapter, we investigated the relationship between evolutionary turnover rates (extinction fraction) and ecological roles of species within interaction networks (here characterized by closeness and betweenness centrality measures). We expect that more central species would belong to lineages with a slower pace of evolution, i.e., those that are more reliable over evolutionary time and have been, therefore, a more predictable resource for plants to rely on.

# Chapter 1

# Omnivory in birds is a macroevolutionary sink

**BURIN**, Gustavo; **KISSLING**, W. Daniel; **GUIMARÃES**, Paulo R.; **ŞEKERCIOĞLU**, Çağan H.; **QUENTAL**, T. B.

## 1.1 Abstract

Diet is commonly assumed to affect the evolution of species, but few studies have directly tested its effect at macro-evolutionary scales. Here, we use Bayesian models of trait-dependent diversification and a comprehensive dietary database of all birds worldwide to assess speciation and extinction dynamics of avian dietary guilds (carnivores, frugivores, granivores, herbivores, insectivores, nectarivores, omnivores, and piscivores). Our results suggest that omnivory is associated with higher extinction rates and lower speciation rates than other guilds, and that overall net diversification is negative. Trait-dependent models, dietary similarity and network analyses show that transitions into omnivory occur at higher rates than into any other guild. We suggest that omnivory acts as macroevolutionary sink where its ephemeral nature is retrieved through transitions from other guilds rather than from omnivore speciation. We propose that these dynamics result from competition within and among

dietary guilds, influenced by the deep-time availability and predictability of food resources.

**Keywords**: Diversification, Macroevolution, Speciation, Extinction, Birds, Diet, MuSSE

## 1.2   Introduction

Variation of biodiversity across space and time is a trademark of the history of life on Earth and ultimately determined by speciation and extinction rates (Rosenzweig, 1995; Coyne and Orr, 2006). To better understand the dynamics of biodiversity we need to understand the roles of biotic and abiotic factors in determining speciation and extinction dynamics (Benton, 2009). While examples of abiotic factors affecting diversification dynamics are numerous (e.g. Condamine et al., 2013 and references therein), few studies have explored biotic influences on macroevolutionary rates across large spatiotemporal scales (Vermeij, 1987; Jablonski, 2008, Gómez and Verdú, 2012). Hence, the relevance of biotic interactions for diversification dynamics across deep time scales is still an open question.

Understanding the role of biotic interactions is a daunting task, given the myriad of interactions (e.g. antagonistic, mutualistic, competitive) that individuals of a given species can have with individuals of other species. However, characterizing and understanding the trophic habits of species is tractable and may also be of great importance to understand potential adaptive responses to food availability (e.g. Root, 1967) as well as the effects of biotic interactions on macroevolutionary dynamics (Price et al., 2012). As such, the diet of a given species can be used as a first order proxy to biotic interactions. It summarizes distinct morphological, physiological and behavioral traits of an organism, which jointly determine the way it interacts with the biotic and abiotic environment (Cooper, 2002, O'Donnell et al., 2012; Abrahamczyk and Kessler, 2014). For example, birds that attend army ant raids have to deal with the unpredictability of those raids, and have developed cognitive and behavioral adaptations to surpass these challenges (O'Donnell et al., 2012). Similarly,

many nectar-feeding species have evolved beaks that suit the morphology of the flowers on which they feed (e.g. Abraham-czyk and Kessler, 2014). Since flowering phenology is strongly constrained by seasonality, the variability in climate (e.g. in temperature) strongly determines geographic distributions of guilds such as nectarivores (Kissling et al., 2012a). More generally, the long-term availability of particular climates (Kissling et al., 2012b) as well as the spatio-temporal predictability of food resources (e.g. Karr, 1976, Fleming and Muchhala, 2008) might influence evolutionary radiations and diversity dynamics (Kissling et al., 2012b; Karr, 1976), with environmental instability setting a potential limit to the degree of specialization (Macarthur and Levins, 1967).

Dietary strategies have been crucial for understanding species formation because interspecific competition for similar food resources can explain character displacement and the evolutionary divergence of species (Brown and Wilson, 1956; Grant and Grant, 2006). Nevertheless, to date only few studies at macroevolutionary scales have tested how diets might affect diversification dynamics across whole clades (e.g. Price et al., 2012, Rojas et al., 2012; Cantalapiedra et al., 2014). The paucity of whole-clade investigations relating diet to macroevolutionary dynamics is partly due to the lack of data, but also due to methodological limitations. However, recently developed methods now allow us to explicitly address (Maddison et al., 2007, FitzJohn, 2012; Morlon, 2014) or indirectly assess (Rabosky et al., 2013; Rabosky, 2014) the relationship between trait evolution and diversification rates, and various authors have therefore analysed this relationship. Collectively, those studies revealed the effects of numerous traits on diversification dynamics, including self-incompatibility in Solanaceae (Goldberg et al., 2010), tank formation and photosynthesis type in bromeliads (Silvestro et al., 2014b), migratory behaviour in birds (Rolland et al., 2014), and diet in mammals (Price et al., 2012, Rojas et al., 2012). Hence, ecological and life history traits play a critical role for understanding macroevolutionary dynamics and broad-scale patterns of species coexistence (Morlon, 2014; Barnagaud et al., 2014).

One of the few papers that explicitly addressed the effect of diet on macroevolutionary dynamics has shown that coarse trophic levels (i.e. herbivores, carnivores, omnivores) are characterized by different diversification rates in mammals (Price et al., 2012). These results suggest that omnivorous mammals have lower net diversification rates than carnivores and herbivores, and that transitions into omnivory are more frequent than into other trophic levels. Using a finer diet classification within ruminants (i.e. giraffes, deer, buffaloes, antelope, etc.), it has further been shown that different feeding styles underwent differential diversification rates (Cantalapiedra et al., 2014). However, this analysis suggested that grazing and mixed-feeding (a combination of browsing and grazing) have both higher diversification rates and more transitions into and from these diets than browsing. Overall, these studies highlight the potential association between dietary guilds and diversification dynamics, but they also suggest that a more generalist diet (e.g. omnivory or mixed-feeding) might not have the same straightforward macroevolutionary outcomes at different lineages or hierarchical levels.

Birds represent a good model system for investigating the role of diet on speciation and extinction (Brown and Wilson, 1956; Grant and Grant, 2006), and more broadly, to understand the interplay between ecology and diversification. The clade Aves has an enormous taxonomic diversity (c. 10,300 species) with a large variability in ecological and life history traits (Şekercioğlu et al., 2004; Kissling et al., 2012a, Barnagaud et al., 2014). The recently published whole-clade bird phylogeny (Jetz et al., 2012) and the abundance of ecological information for Aves have allowed biologists to assess the evolutionary dynamics (either trait-dependent or trait-independent) of many bird lineages at different taxonomic levels (e.g. Huang and Rabosky, 2014; Garcia-R et al., 2014, Rolland et al., 2014). Moreover, different types of diet have evolved multiple times within the clade (Kissling

et al., 2012a). Dietary adaptations range from specialized feeders such as some insectivores (e.g. swifts and swallows), frugivores (e.g., oilbirds), seed predators (e.g., blue macaws), vertebrates (e.g., peregrine falcons), and carrion-feeders (e.g. vultures) that feed preferentially on one particular food type to omnivores such as the medium-sized, common raven Corvus corax (family Corvidae) which have a generalized diet by feeding on multiple food items, such as insects, fruits, seeds, vertebrates and carrion (Kissling et al., 2012a). Such variation in the degree of diet specialization is probably related to different physiological and anatomical adaptations required to deal with different food items (O'Donnell et al., 2012, Abrahamczyk and Kessler, 2014; Roggenbuck et al., 2014). For example, some nectarivorous and frugivorous species show specific preferences for different sugar contents related to enzyme activity and absorption rates (Martínez del Rio et al., 1992) which might eventually affect their food preference and hence their degree of specificity.

Here, we combine the most complete bird phylogeny (Jetz et al., 2012) and a comprehensive global dataset of the diets of the world's bird species (Şekercioğlu et al., 2004, updated with Hoyo et al., 2013) to investigate the potential effect of different diets on the speciation and extinction rates of birds, and the evolutionary transition rates between all dietary guilds. Given that shifts to new diets result in different ways of interacting with the environment (Root, 1967; Raubenheimer et al., 2009), and that such shifts might also affect the degree of specialization within a given lineage (Price et al., 2012, Cantalapiedra et al., 2014; Vamosi et al., 2014), we hypothesize that the evolution of different diets in birds will result in distinct speciation, extinction, and transition dynamics. Even though a simple classification of diet has been shown to affect diversification rates of mammals (e.g. Price et al., 2012), we know virtually nothing about the macroevolutionary effects of diet on such diverse groups of vertebrates such as birds where we have a more refined dietary categorization. Hence, investigating the role of diet on bird diversification will not only allow us to understand its effect on

this extremely diverse lineage but also help us to begin evaluating how general the observed effects of diets are for macroevolutionary dynamics across tetrapods.

For our analyses, we assigned each species to a different dietary guild based on its main diet (at least 50% of one particular food type; see also supplementary material for a sensitivity analysis regarding this dietary classification). When no item comprised more than 50% of the whole diet or if a given species consumed two food types equally, then it was considered an omnivore. By following this categorization we grouped species into carnivores, frugivores, granivores, herbivores, insectivores, nectarivores, omnivores, piscivores and scavengers. We then fitted Multiple State Speciation and Extinction (MuSSE) models in a Bayesian framework for 200 randomly sampled phylogenetic trees to incorporate phylogenetic uncertainty, and used the posterior distributions of diversification and transition rates to infer the relationship between diet and diversification (see also supplementary material for model testing, adequacy tests and sub-clade analysis). Additionally, we used network analysis to further quantify the evolutionary diet transitions among guilds and a principal component analysis of diet scores to assess the multi-dimensional similarity of diets. Our results indicate that dietary habits have influenced the diversification dynamics of birds, with omnivores experiencing higher extinction, lower speciation, and substantially higher transition rates into omnivory when compared to all other guilds.

## 1.3 Methods

### 1.3.1 Dataset

We used the bird phylogeny from (Jetz et al., 2012), which encompasses almost all bird species (9,993 species, available online at ). The tree was built using molecular data from 6670 species, and the remaining taxa with no molecular information were added to the phylogeny based on taxonomic information and simulated branching times from a pure birth (Yule) model

of diversification (Jetz et al., 2012). The distribution of these inserted species spans the entire tree and virtually all clades (Figure A.13). The addition of those species should therefore not bias diversification estimates and at best only homogenize any real differences between different traits, making our tests more conservative with respect to finding true differences in diversification dynamics among guilds. A distribution of 10000 trees with different topologies was obtained from the original paper (Jetz et al., 2012). To account for phylogenetic uncertainty, we randomly sampled 100 trees from this posterior distribution of trees for each of the two backbone trees, totalling 200 trees. Using these 200 trees diminishes any possible biases that the insertion process of species with no molecular data could bring into the phylogeny. We note that the two backbones from (Jetz et al., 2012) showed a similar amount of differences in topology then when both were compared to two other recently published high-order bird phylogenies (Figure A.24; for methods, see supplementary methods in Appendix A).

A comprehensive bird diet database (Şekercioğlu et al., 2004; updated with Hoyo et al., 2013) was used with numerical scores for different food types consumed by birds (including invertebrates; fruits; nectar; seeds; terrestrial vertebrates; fishes; carrion; plants (non-reproductive) and miscellaneous). The data came from over 250 ornithological books as well as peer-reviewed articles compiled in a global ornithological database by C.H.S. (Şekercioğlu et al., 2004; updated with Hoyo et al., 2013). The literature used includes synthetic works (e.g. Handbook of the Birds of the World, Birds of Africa, Birds of South America, Australia/New Zealand Handbook of Birds, Birds of Western Palearctic and all the books on bird families), which provide bird species accounts based on a summary of all literature on a particular bird species. Therefore, our diet classification was based on a comprehensive diet database that summarizes dietary preferences across a species range and across seasons. The scores of all diet items add up to 10 and represent the approximate proportion of each food type in the diet

of a given species. A species was classified into a specific dietary guild if it had one food item with a score >5 (for sensitivity analysis see figures A.19 - A.23). Species with only two equally consumed food items in their diet or with no food item with a score >5 were classified as omnivores. Thus, all species were classified into nine dietary guilds: carnivores (feeding predominantly on vertebrates), frugivores (feeding predominantly on fleshy fruits), granivores (feeding predominantly on seeds), herbivores (feeding predominantly on non-reproductive plant material such as leaves, roots and shoots), insectivores (feeding predominantly on insects or other invertebrates), nectarivores (feeding predominantly on nectar), piscivores (feeding predominantly on fish), scavengers (feeding predominantly on carrion) and omnivores (the species that do not have a predominant diet). After matching the taxonomy of species with dietary data with the phylogeny, we finally used a total of 9876 species in all analyses.

### 1.3.2   Model fitting and parameter estimates

Multiple State Speciation Extinction (MuSSE) models were fitted across all sampled trees (FitzJohn, 2012). This class of models estimates the parameter values (speciation, extinction and transition rates) associated with each trait state in a phylogeny. The models were implemented in a Bayesian MCMC framework to account for both phylogenetic and rate value uncertainties. Phylogenetic methods might underestimate extinction rates (Rabosky, 2010; Quental and Marshall, 2010), and to avoid rates to be equal to 0 (especially transition rates, that are prone to be very small in a multi-state model) we used three Cauchy distributions as hyperpriors. These hyperpriors have a location parameter fixed to 0 and the scale parameter is estimated from MCMC analysis. This allowed rates to be very small, but not zero. All parameters were independently estimated, i.e. with no constrains. A total of 1,500,000 steps (sampling every 1000th step) were necessary to achieve an acceptable convergence of the majority of the parameters. The Bayesian analysis was run for

separate trees in parallel on four computer servers. All analyses were conducted within the statistical environment R (R Core Team, 2016) using the diversitree package (FitzJohn, 2012) and a new script designed to implement the MCMC analysis (available at ).

There has been recently a debate over the performance of trait-based models (Maddison and FitzJohn, 2014; Rabosky and Goldberg, 2015). The main critiques are related to the low presence of true replicas. Strong phylogenetic signal and few events of state change in a given character could lead to pseudoreplication (Maddison and FitzJohn, 2014), and a high percentage of false positives in a class of trait-dependent speciation and extinction models due to rate heterogeneity throughout the tree could additionally bias rate estimates (Rabosky and Goldberg, 2015). Although the latter limitation has only been proven to be true for binary-state characters, some authors suggest that it is a common limitation among all xxSSE models (Maddison and FitzJohn, 2014; Rabosky and Goldberg, 2015).

As an alternative to the trait-dependent methods, a recent study by Huang and Rabosky, 2014 estimated speciation and extinction rates using BAMM (Bayesian Analysis of Macroevolutionary Mixtures – Rabosky, 2014), a trait-independent method that estimates these rates using reversible-jump MCMC to identify shifts in diversification rates. With the BAMM results a significant relationship between the degree of sexual dichromatism in birds and diversification rates was found using comparative methods. However, using BAMM as an alternative solution to xxSSE models does not seem to be fully adequate for our analyses and the phylogenetic structure of the diet traits. BAMM does not estimate transitions between states of the analysed character when estimating speciation and extinction rates, and these rates seem to have an important role for the macroevolutionary dynamics in our analyses, and more broadly in evolutionary dynamics. Additionally, given the phylogenetic overdispersion of omnivory in our phylogenetic trees (omnivore species usually appear as a isolated tip within a clade with species that belong to a more specialized dietary guild) and how BAMM operates (it

finds a node where a shift in rate is justifiable) we suspect that it
is virtually impossible to detect rate shifts associated with om-
nivory using BAMM. The reason is that within each group of
species that contains omnivores the statistical power to detect
any shifts in speciation and/or extinction rates for omnivorous
species would be insufficient. We therefore suspect that in such
a phylogenetic trait configuration the diversification rates ob-
tained with BAMM for omnivores would potentially be biased
in different directions depending on the diet of closely related
species. This would turn any posterior analysis unprofitable.
Lastly, a semi-parametric test to detect trait-dependent diversifi-
cation was proposed by Rabosky and Goldberg, 2015 that relies
on the rate estimates derived by BAMM to later estimate the re-
lationship between a binary (or continuous) trait and the diver-
sification rates. This test uses rate regime permutations to build
null distributions of correlation coefficients. Even though this
seems as an interesting alternative, this test was not used here
since it is currently not available for multi-state discrete charac-
ters (Rabosky and Goldberg, 2015, pg. 12).

To assess the reliability of our MuSSE results in relation to the is-
sues raised by (Rabosky and Goldberg, 2015) we performed four
additional analyses. In the first additional analysis, we tested if
rate heterogeneity captured by our empirical phylogenetic trees
might have led MuSSE to detect spurious relationships between
trait states and diversification. To do this, we simulated the evo-
lution of a discrete character with the same number of states
as in our empirical data set on 10 randomly selected empirical
bird trees, using the empirical transition rate estimates. We then
tested for a statistical association between those neutral char-
acters and the estimated rates (supplementary methods in Ap-
pendix A1) to see whether the model detects similar associations
between trait states and speciation and extinction rates.

In the second set of additional analyses (model adequacy), we
simulated 1000 trees using the rates estimated in our main em-
pirical analysis, to check whether the estimated empirical rate
values would generate a proportion of trait (diet) states com-
parable to the empirical proportions (supplementary methods

in Appendix A2). In the third set of additional analysis (sub-clade analysis), we ran separate MuSSE analyses for the four major bird orders (Passeriformes, Piciformes, Psittaciformes and Charadriiformes) on 10 trees to investigate if the macroevolutionary patterns associated with different diets as obtained from the whole tree analysis were also recovered at these sub-clades (see Appendix A3). In the fourth additional analysis, we investigated the extent to which our results were affected by our dietary classification scheme. We used a different classification scheme to categorize species into discrete dietary guilds and then estimated all diversification rates using the same procedure as in our main analysis using the 10 sampled trees (see Appendix AB). The complete description and results of these tests can be found in the supplementary methods.

### 1.3.3 Posterior distributions of rates

The posterior distributions of parameters from all 200 trees were combined into one single posterior distribution for every parameter (e.g. speciation, extinction and transition rates and hyperprior parameters, adding up to 93 parameters in total). For net diversification rates r (speciation – extinction), the posterior distribution was built by calculating r for each sample of the MCMC, resulting in the same 1,500 values for each state of the trait. For all posterior distributions of speciation, extinction, and net diversification rates the 95%, 90% and 80% credibility intervals (CI) (highest posterior density) were calculated. All results and discussion do not encompass rates from scavenger species because estimates were poor due to small sample size (33 species).

### 1.3.4 Comparison of rates of dietary guilds

To test whether or not speciation, extinction and net diversification rates of omnivores were significantly different from rates of all other guilds, we calculated the difference between each omnivore rate to the rate estimated for each other dietary guild.

These differences in speciation, extinction and net diversification rates were calculated at each sampled MCMC step, building posterior distributions of differences. These distributions were then compared and analyzed separately and the omnivore rate was considered different when the value 0 was not included in the credibility interval (CI) for each rate difference comparison (see figure 1.2).

The MuSSE analysis also allowed us to generate estimates for pairs of transition rates but not to explicitly test for any general asymmetry while considering all the transitions at the same time. Depending on how transition rates are organized among distinct dietary guilds, some guilds might constitute preferential routes of transition. In contrast, if there is no consistent pattern in the distribution of transition rates among guilds, no guild will show a higher transition rate into or from it. To evaluate if the empirical transition matrix significantly deviates from a null model where all transitions are expected to be balanced among nodes, we used a network theory approach. We depicted the transition rates as weighted links and dietary guilds as nodes of the transition network. If species from other guilds consistently shift to the same dietary guild, this latter dietary guild would show high levels of centrality in the transition network. In the transition network, eigenvector centrality describes how the transition rates lead, directly or indirectly, to a given dietary guild. We computed the eigenvector centrality of each dietary guild (Bonacich, 1972), which varies from 0 (peripheral dietary guild) to 1 (central dietary guild). Thus, a highly central dietary guild can be viewed as an absorbing state to which species from other dietary guilds may evolve by changing resource use. To verify the significance of these centrality values, we built a null distribution of centrality values by randomly assigning to each link a value sampled from the estimated transition rates without replacement for each of the 10000 replicas. We then compared the empirical centrality values to this null distribution and verified to which quantile the real value corresponded.

### 1.3.5 Diet similarity analysis

With the original diet scores for all species, we quantified the score frequencies of each food item within the diet of all omnivore species (supplementary figure 15). This was done to better characterize the diet of omnivorous species and to trace diet similarities between omnivores and all other guilds. We additionally performed a principal component analysis (PCA) using the full vector of diet scores (with each food item as a variable) to characterize omnivorous species and their multi-dimensional dietary similarity with other guilds (figure A.14). This allowed us to assess the distribution of dietary guilds in niche space with reduced multi-dimensionality. We also calculated the Euclidean distance between each possible pair of species in the orthogonal space created by the first three principal components (table 1.2). These distances were then averaged within and between each and all guilds for further comparison.

## 1.4 Results

### 1.4.1 Dietary guilds

Bird species are not equally distributed among dietary guilds. Both the total number of species and the phylogenetic signal strength differs among guilds (Table 1.1). This suggests that different dietary guilds might in fact have different diversification dynamics. The three most common dietary guilds are insectivores (55%), omnivores (12%) and frugivores (12%), and the least common is the scavenger guild (0.3%). Below we exclude scavengers from the results and discussion because their diversification rates were poorly estimated due to small sample size (33 species grouped in a few lineages such as New World and Old World vultures, some crows and a few phylogenetically isolated species). In general, all dietary habits seem to have multiple origins in Aves. However, there are at least two distinct evolutionary conservatism patterns in diets across the bird tree of life. Whereas omnivores are largely spread randomly across

the bird phylogeny, all other dietary guilds are phylogenetically clustered to some extent (Table 1.1, Figures A.1 - A.9).

TABLE 1.1: Number of species, percentage of total species per dietary guild, and mean phylogenetic signal of each dietary guild. Phylogenetic signal (measured as character dispersion D of a binary trait) was averaged over 10 random trees (5 from each backbone). Negative D values indicate phylogenetic clustering whereas highly positive values indicate phylogenetic overdispersion. Values not different from 0 indicate that the character evolves according to a Brownian Motion process, whereas D not significantly different from 1 indicates randomly distributed states on the tree. (*: values different from 1 but not from 0; **: values different from both 0 and 1; significance was the same for all trees).

| Dietary Guild | Number of Species (% of total) | Phylogenetic Signal (D value) |
|---|---|---|
| Carnivores | 280 (3%) | -0.2762* |
| Frugivores | 1141 (12%) | -0.03879* |
| Granivores | 824 (8%) | -0.02475* |
| Herbivores | 189 (2%) | 0.04889* |
| Insectivores | 5409 (55%) | -0.05087* |
| Nectarivores | 542 (5.7%) | -0.3661* |
| Omnivores | 1159 (12%) | 0.52702** |
| Piscivores | 232 (2%) | -0.13848* |

## 1.4.2   Diversification rates

Our results reveal that the net diversification rate of omnivores is lower than that of any other dietary guild (Figure 1.1). Underlying these dynamics is a lower speciation rate and a higher extinction rate of omnivores compared with other guilds (Figure 1.1). Additionally, the net diversification rates for all dietary guilds are positive except for omnivores, where the median value of the net diversification rate is negative (Figure 1.1). Even though the distribution of net diversification rates for omnivores includes zero (specifically when looking at the posterior distribution peak, Figure 1.1), this guild is the only one that has a large portion of negative values in its diversification rate posterior distribution. This reinforces the idea that omnivores have different dynamics, with net diversification rates being significantly lower than in other guilds.

The posterior distributions of all rates for almost all guilds are mono-modal, suggesting that parameter values well represent the estimated value for each rate. The main exception is the speciation rate for herbivores (Figure 1.1). Other distributions that are not mono-modal are the extinction rates for both insectivores and omnivores (Figure 1.1). In the case of herbivores, the distribution has a large uncertainty that results from combining mono-modal posterior distributions for individual phylogenetic trees that converged into different values. For insectivores and omnivores, the bi-modality of the extinction posterior distributions also arises from combining several mono-modal distributions from all sampled trees. However, this bi-modality represents the effect of phylogenetic uncertainty and not the non-convergence of estimates, reinforcing the importance of our implemented modeling framework which explicitly includes sources of phylogenetic uncertainty.
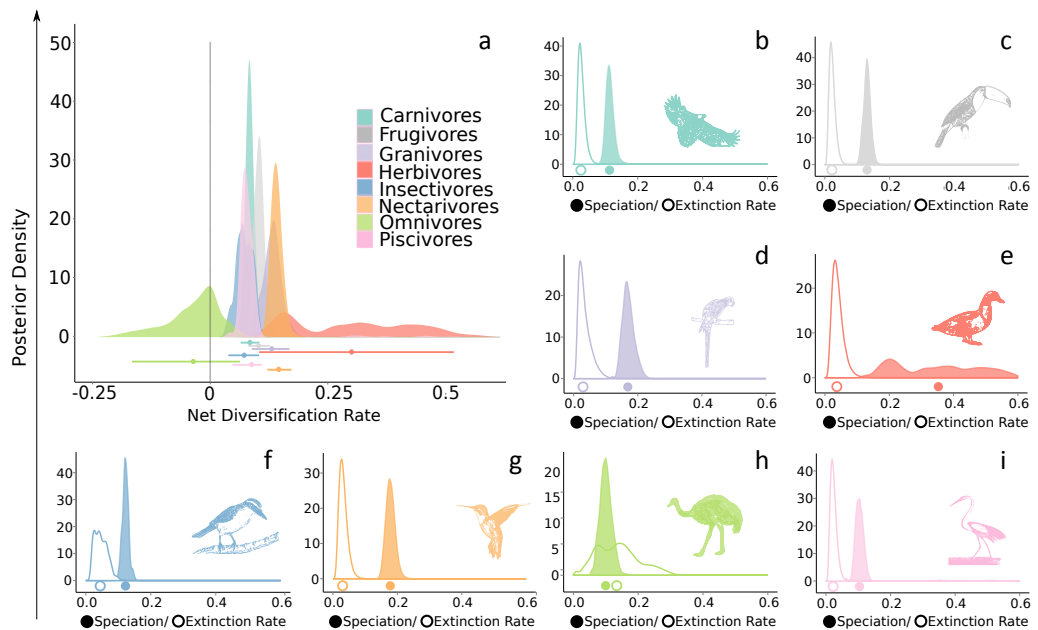


FIGURE 1.1: (a) Posterior distributions of net diversification rates for each dietary guild and (b-i) corresponding posterior distributions of speciation and extinction rates. Bars on (a) represent the 95% credibility interval of each distribution and the dots the median of the posterior distribution. In (b-i) colour-filled curves represent speciation rates and white-filled curves represent extinction rates. The filled and empty dots represent median values for speciation and extinction rates, respectively.

Figure 1.2 shows the credibility intervals at different significance levels (95%, 90% and 80%) for the posterior distributions of differences between the rates of all guilds as compared to those of omnivores. This reveals that net diversification, speciation and extinction of omnivores differ from other guilds in most cases (Figure 1.2). Omnivores show a statistically significant lower diversification rate than all other guilds except insectivores where this difference is marginal (Figure 1.2a). A similar pattern is found in speciation rates, where omnivore rates are lower than those of granivores, herbivores, nectarivores and frugivores (at 95% credibility interval (CI) for the first three guilds and 90% CI only for the latter – Figure 1.2b). Even though extinction rate differences are not as striking for some guilds as those for speciation rates (compare Figure 1.2c and Figure 1.2b), omnivores show higher extinction rates than carnivores, frugivores, granivores, nectarivores and piscivores (at a 90% CI). Omnivores also have extinction rates that are marginally higher than those of herbivores and insectivores.

Quantifying the transitions into different dietary guilds reveals a prevalence of transition rates into omnivores rather than into any other dietary guild (Figure 1.3; Figures A.11 and A.12). Herbivores and granivores show the highest transition rates into omnivory, insectivores almost no transitions into omnivory or any other diet, and other dietary guilds intermediate transition levels into omnivory. Overall, these results suggest that all dietary guilds preferentially shift into omnivores, except insectivores. This is also supported by a network analysis which shows that eigenvector centrality (a measure of whether network nodes —here dietary guilds— behave as preferential endpoints within a network) of omnivores is equal to 1, which is significantly higher than expected by chance (permutation test with 10000 permutations, p<0.0001 – Figure A.10). Estimates for all other guilds show centrality values that are not significantly different from the null model (Figure A.10). It is interesting to note that the estimates of transition rates into omnivory suggest that the overall rate of transition into omnivory (summing up the transitions from all guilds) is at the same order of magnitude as the speciation rates for other guilds (compare the side
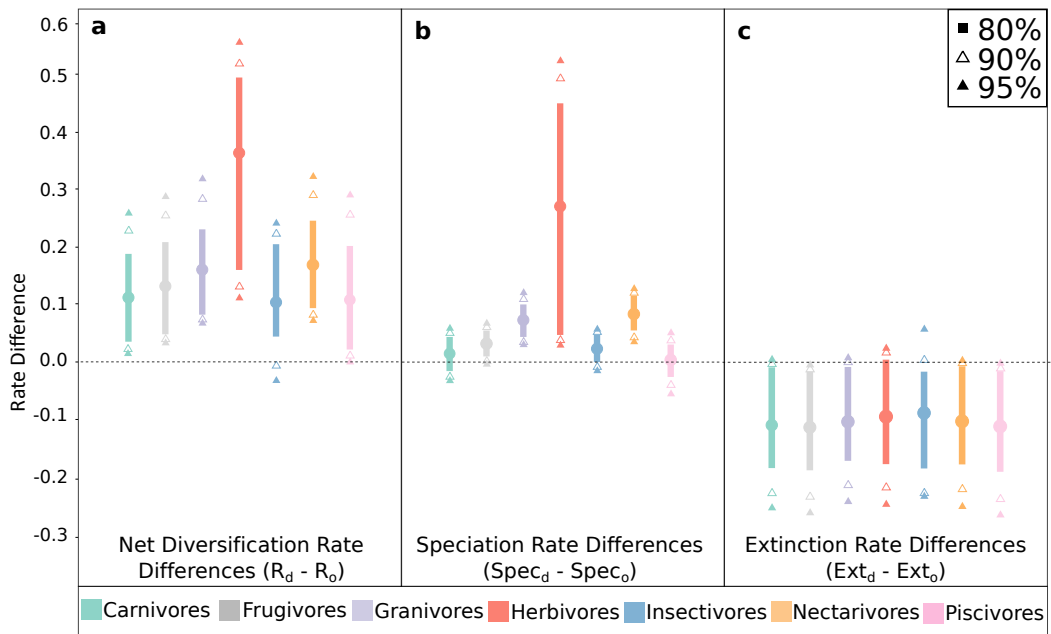
FIGURE 1.2: Differences between net diversification (a), speciation (b) and extinction (c) of all dietary guilds relative to omnivores. The differences in rates are calculated by incorporating phylogenetic uncertainty and therefore represent a posterior distribution of differences between the rate estimates of each guild compared to the rate estimate of omnivores. Different transparencies for the colors indicate different credibility intervals, and the dashed line indicates 0 (no difference). Positive values mean that the considered rate is higher for each guild than the same rate for omnivores. Omnivores generally show lower speciation and higher extinction rates, although differences are significant at different degrees of credibility depending on the guild.

panels of Figure 1.1 with Figure 1.3).

### 1.4.3 Dietary niche overlap

Each species has its dietary preferences described by a vector of diet items (i.e. vertebrates, fruits, seeds, invertebrates etc.) whose scores sum up to 10, and each of these scores represent the proportion that a given food item is consumed in the diet of a given species. To explore the multi-dimensional dietary similarity among guilds we used a principal component analysis (PCA) on the complete vector of diets for each species. This analysis shows that within the first three PCA axes the omnivores occupy intermediate positions relative to all other dietary guilds, having a considerable overlap with them. In contrast,

other guilds show little overlap with each other at least in one of the three PCAs (Figure A.14). Higher overlap of omnivores with other guilds is also reflected in the mean Euclidean distance between each species in the orthogonal space formed by the first three PCA axes (Table 1.2). Omnivorous species show greater mean distance within their own guild than do non-omnivorous species within their own guilds. Additionally, average distances between omnivores and species within each other guild are usually similar while the average distances between species of specialized guilds and of other guilds (including omnivores) can be highly variable and for many comparisons higher (Table 1.2). These results mean that omnivore guild is more centrally positioned in a coarse dietary space (see also figure A.14). Finally, we also explored the patterns of overlap between omnivores and species of other guilds. All omnivores include at least some insects in their diet (Figure A.15). Fruits and grains also show considerable prevalence in their diet, but carrion is rarely consumed by omnivores (Figure A.15). Overall, these results support the idea that diet overlap of omnivores with other guilds is high.

TABLE 1.2: Average Euclidian distances between species calculated using the first three axes of a principal component analysis on diet item scores per species within guilds (bold) and between guilds. Omnivores show higher within-guild average Euclidian distances than other guilds, suggesting that the diet similarity observed among omnivorous species is on average lower than diet similarity seen within any other guild. Numbers within parenthesis indicate standard errors.

| | Carnivore | Frugivore | Granivore | Herbivore | Insectivore | Nectarivore | Omnivore | Piscivore |
|---|---|---|---|---|---|---|---|---|
| **Carnivore** | **1.296** (**0.017**) | | | | | | | |
| **Frugivore** | 9.286 (0.008) | **2.375** (**0.005**) | | | | | | |
| **Granivore** | 9.335 (0.009) | 11.503 (0.004) | **2.455** (**0.005**) | | | | | |
| **Herbivore** | 3.723 (0.020) | 7.980 (0.009) | 6.770 (0.011) | **2.131** (**0.023**) | | | | |
| **Insectivore** | 9.134 (0.004) | 11.153 (0.002) | 11.749 (0.002) | 8.107 (0.004) | **1.782** (**0.001**) | | | |
| **Nectarivore** | 2.601 (0.011) | 10.469 (0.005) | 11.071 (0.006) | 5.381 (0.013) | 9.588 (0.002) | **1.575** (**0.008**) | | |
| **Piscivore** | 2.261 (0.017) | 8.405 (0.008) | 8.408 (0.010) | 2.613 (0.020) | 7.695 (0.004) | 3.707 (0.012) | **1.368** (**0.018**) | |
| **Omnivore** | 5.760 (0.008) | 7.470 (0.004) | 7.678 (0.004) | 4.133 (0.009) | 7.019 (0.002) | 7.052 (0.005) | 4.435 (0.008) | **4.337** (**0.004**) |

### 1.4.4   Model performance and adequacy

Our four auxiliary analyses showed that, in our particular case, it is very unlikely that the statistical methods (MuSSE) and the diet classification scheme produced spurious associations between diet and diversification dynamics. First, we show that simulations using empirical transition rates and no association between speciation/extinction rates and trait states do not recover the speciation and extinction dynamics seen in the empirical analyses (figures A.16 and A.17). Second, a model adequacy test suggested that the simulations using all estimated parameters produced a range of diet proportions that encompass the proportions of diets as observed in the empirical dataset (figure A.18). Third, the diversification dynamics observed in subclades of the whole phylogenetic tree showed partial concordance with our main results, especially that extinction rates of omnivores tend to be higher than those of any other dietary guild (figure A.19). The results for speciation and transition rates within species-rich sub-clades (Passeriformes, Piciformes, Psittaciformes and Charadriiformes) were inconclusive and difficult to interpreted (see supplementary results in Appendix A and figure A.19). Higher transition rates into omnivory were sometimes also recovered in these sub-clades, but for the subclade analysis, as opposed to the whole tree analysis, speciation rate became relatively more important on generating omnivore species than the transition rates. This change in relative importance (speciation being the main process of formation of new omnivore species) suggests that the speciation and transition dynamics are interrelated, making a comparison with the full phylogenetic tree not straightforward (see supplementary results in Appendix A for further discussion). Finally, we performed a fourth test to evaluate the sensitivity of our diet classification scheme. Using a more inclusive categorization of omnivory did not change our main results, i.e. that omnivory can be seen as a macroevolutionary sink (figures A.20 - A.24). Hence, for the analysis presented here we suggest that the MuSSE model provides reliable rate estimates and that the qualitative results and conclusions derived from the whole tree

analysis are robust. We therefore focus the discussion only on the main results.
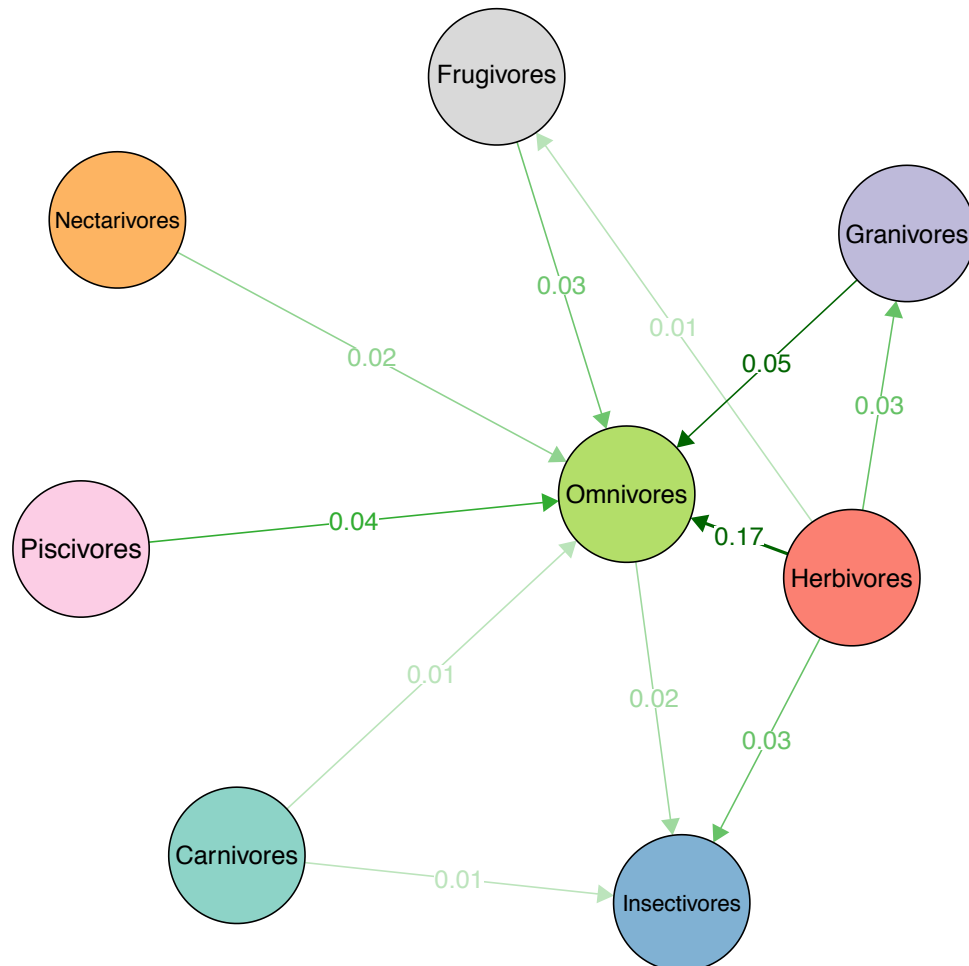


FIGURE 1.3: Network depicting the estimated transition rates (links) between dietary guilds (nodes). The intensity of each directed link is proportional to the median of the posterior distributions of transition rates. All transition rates smaller than 0.001 were omitted in the figure for better visualization. Numbers above the links correspond to the median value of the posterior distribution of the corresponding rate. Transitions towards omnivores are more common than any other direction of transition, and omnivory is the only guild that is significantly more connected than expected by chance (null model analysis, $p<0.0001$).

## 1.5   Discussion

Diet has a clear association with the diversification dynamics of birds. Most prominently, omnivores show lower (and even negative) net diversification rates compared to the positive rates of all other guilds (Figure 1.1). Our results suggest that this distinct evolutionary dynamic exhibited by omnivores arises from the interplay between significantly lower speciation rates and significantly higher extinction rates when compared to other guilds (Figure 1.2). Estimating speciation and extinction rates from molecular phylogenies has limitations (Rabosky, 2010, but see Beaulieu and O'Meara, 2015), but we highlight that our main conclusions are based on qualitative differences between omnivores and other dietary guilds rather than on the precise rate estimates. Interestingly, we further observed that transitions into omnivory occur at much higher rates than into any other guild (Figure 1.3) and that those transition rates occur in the same order of magnitude as the estimated speciation rates of other guilds. This result suggests that omnivory acts as a macroevolutionary sink where generalized diets are only transient. This sink behavior might be a more widespread pattern in tetrapods because similar dynamics have also been suggested for mammals (Price et al., 2012).

Lower speciation rates and higher extinction rates of omnivores in mammals (Price et al., 2012) were obtained by defining omnivory as eating similar proportions of plant and meat compared to two other trophic levels (i.e. carnivores and herbivores). However, at lower taxonomic levels within the mammalian tree of life such results differ among lineages. For instance, diversification rates have also been found to be lower for more generalized bat lineages that complement their frugivorous diet with other food items (i.e. nectar and pollen) relative to more specialized frugivore lineages (Rojas et al., 2012). In contrast, in ruminants the grazing and mixed-feeding strategies have both higher diversification rates than browsing (Cantalapiedra et al., 2014). In general, lower diversification rates of

omnivores could be explained by the ecological tenet that generalist species might be at a disadvantage when competing with specialists (Büchi and Vuilleumier, 2014). Such a "jack-of-all trades is a master of none" mechanism (species that can utilize several resources while performing poorly at utilizing specific resources; MacArthur and Pianka, 1966) could leave a signature at the macroevolutionary scale.

According to (Godoy et al., 2014), two main characteristics determine the coexistence probability of two or more species in the same place: niche overlap and competition asymmetry. We suggest that omnivorous species are at competitive disadvantage relative to species of more specialized guilds due to both factors. For niche overlap, our diet similarity analysis shows that omnivorous birds have a considerable degree of diet overlap with species from at least two other dietary guilds. In fact, omnivorous species have, on average, equivalent distances to other omnivorous species or to species belonging to other guilds (Table 1.2), indicated by similar average pairwise distances. Additionally, omnivory has a more central position than other guilds on all three PCA axes of the diet analysis, and always some degree of overlap with other dietary guilds (Supplementary figure 14). When considering competitive asymmetry, species within specialized dietary guilds should also show different levels of specialization. For example, within insectivores there are some highly specialized lineages. True antbirds (Thamnophilidae) are specialized on eating mostly terrestrial invertebrates escaping from army ant raids in tropical forests (O'Donnell et al., 2012), and flycatchers (e.g. family Tyrannidae) are highly adapted to catching their insect prey in flight. Dietary specialization therefore plays an important role for competitive dynamics and thereby might also influence evolutionary dynamics.

From an ecological point of view, several authors have proposed that the fitness of specialists (usually assessed via population size) is higher when compared to generalists (Wilson and Yoshimura, 1994, Straub et al., 2011). This can be explained by trade-offs between performing well at acquiring a narrow range of resources (e.g. hosts, food items, etc.) or having a

wide range of resources at the cost of being worse at acquiring them. When a specialist and a generalist species compete for the specialist's preferred resource, the specialist species should ecologically outperform the other (Straub et al., 2011). This explanation might be particularly true if resources are constantly available, e.g. in relatively stable or aseasonal environments. In contrast, specialists might be at disadvantage in places or at times where the preferred resource is scarce or unpredictable (Brown and Wilson, 1956; Wilson and Yoshimura, 1994).

If we expand this competitive scenario to a situation where omnivores share their resources with multiple different specialists, we hypothesize that over longer time scales omnivores would be systematically at a competitive disadvantage due to both high niche overlap and competition asymmetry. This would ultimately lead to very low abundances of generalist species (Straub et al., 2011) and possibly to local extinctions (Hardin, 1960). The simultaneous competition with multiple species might therefore translate into higher extinction rates at a macroevolutionary scale, resulting in a high macroevolutionary cost to omnivores. Assuming this scenario of multi-species competition, an omnivore would be a "jack-of-all-trades" (a species that can utilize several resources; MacArthur and Pianka, 1966) trapped in an arena of ecological competition with multiple competitors belonging to different guilds. Such a "master of none" mechanism (i.e. species perform poorly at utilizing specific resources; MacArthur and Pianka, 1966) would lead to macroevolutionary consequences at the species level, where the "jacks of all trades" should show low speciation and/or high extinction rates.

As outlined above, we suggest that higher extinction rates of omnivorous birds are the result of competition with species from multiple guilds. However, the generality of such a mechanism remains to be tested more widely given that a potential association between lower diversification rate and a more generalized dietary guild has so far only been examined in mammals (e.g. Price et al., 2012) and birds. Assuming that body size is a proxy for ecological niche (Bonner, 2011), mammals

might be responding to a similar mechanism as proposed here. Mammalian omnivorous species show both lower diversification rates (Price et al., 2012) as well as intermediate and overlapping body masses (i.e. intermediate and overlapping ecological niches) when compared to herbivores and carnivores (Price and Hopkins, 2015). Hence, inter-guild competition might be an overlooked mechanism that is potentially important to explain lower diversification rates of omnivorous species. Although species level mechanisms or outcomes were at first widely rejected as being drivers of macroevolutionary dynamics, they are now considered important mechanisms (6; Vrba, 1984; Rabosky and McCune, 2010) and the ever-growing empirical studies that show a pattern of trait-based diversification (Goldberg et al., 2010, Rolland et al., 2014; Cantalapiedra et al., 2014) suggest that it might indeed be a common phenomenon in determining the evolutionary success of lineages with different traits (Coyne and Orr, 2006; Rabosky and McCune, 2010).

Along with increased extinction rates, we also detected lower speciation rates of omnivores relative to other guilds. The mechanism behind the association between low speciation rates and omnivory is more elusive, but given that speciation and extinction rates are usually linked by the same mechanisms (Stanley, 1990, Gilinsky, 1994), it is possible that inter-guild competition might also play a role here. If each guild is an adaptive zone (sensu Van Valen, 1985) where the speciation process results in the crowding of this adaptive zone, then higher rates of speciation from multiple specialized guilds might result in a compound "crowding" effect that reduces speciation rates of omnivores at the macroevolutionary scale. Alternatively, the lower speciation rates of omnivores could also be explained by higher extinction rates at the population level, whereby populations experiencing high competition with multiple species are likely to go extinct. In this scenario, some populations that are going through a speciation process might not have enough time to be fully separated into two different species, resulting in lower speciation rates at the macroevolutonary scale, a process that might be referred to as 'ephemeral speciation' (Rosenblum et al., 2012).

Given the macro-evolutionary "costs" associated with omnivory (i.e. low speciation rates and high extinction rates), it might seem surprising that this dietary guild still constitutes such a considerable portion of extant bird diversity (1158 species, circa of 12%; see Table 1.1). From a deep-time perspective, a lineage with low diversification rates —especially those with negative rates— should eventually disappear or at best reduce its diversity due to species sorting (Leibold et al., 2004; Jablonski, 2008). We hypothesize the reason why omnivory has not disappeared lies in the high transition rates into omnivory.

Our results show that transition rates into omnivory are significantly higher than into any other dietary guild (Figure 1.3) and that they occur at the same order of magnitude as the speciation rates for other guilds. Moreover, network analysis reveals that omnivory is the most central guild and that diet shifts occur from all other dietary guilds into omnivory more than one would expect by random (Supplementary figure 10). This suggests that omnivore lineages preferentially originate at the macroevolutionary scale via transitions, and not through speciation. The reason why such transition rates are so high could depend on selection driven by resource competition at the individual level. Omnivory could be favoured at times or places with low abundance of a preferred resource or when resource availability is highly unpredictable (Macarthur and Levins, 1967; Wilson and Yoshimura, 1994). For instance, climate variability (e.g. seasonality) clearly influences resource availability and specialists might only survive if their resources are continuously available and highly predictable (Macarthur and Levins, 1967, Karr, 1976). For example, specialized nectarivores and frugivores only survive in places where seasonality is low and hence resource availability relatively constant (Kissling et al., 2012a). Granivores benefit in dry climates where seeds are constantly available, whereas insectivores perform well in the tropics where insects are available all year round (Kissling et al., 2012a). Hence, a low spatio-temporal predictability of resources as well as high environmental instability is likely to benefit omnivores by setting a limit to the degree of specialization (Macarthur and Levins, 1967). At macroevolutionary scales, this

will influence diversification dynamics and increase transition rates into omnivory.

A mixed-feeding diet has been shown to be beneficial for individuals belonging to different herbivore species across different animal groups (MacAarthur and Levins, 1964; Ballabeni and Rahier, 2000, Lefcheck et al., 2013). If individual-level selection is indeed an important factor for avian transitions into omnivory, we can expect ancestral lineages to feed on resources that were temporally limited, unpredictable, difficult to digest or with poor nutrition. In birds, most transitions into omnivory come from granivores and herbivores, and herbivores are represented with only few species (Table 1.1). Given such low frequency and the fact that feeding exclusively on leaves might represent a poor diet (Gaekde et al., 2002), selection pressure to add new, perhaps more nutritious, food items could indeed drive the evolution of omnivory from herbivorous ancestral lineages. In the case of granivores, it is more likely that resource availability plays an important role, but analogously to the hypothesis of transitions from herbivores this hypothesis remains to be properly tested. Interestingly, the transitions into omnivores (Figure 1.3) and the detailed information on their diets (Supplementary figure 15) suggest that transitions into omnivory systematically include the addition of insects. Insects might represent a predictable and protein-rich resource, but insectivory might also pose evolutionary challenges such as the digestion of lipids (Afik and Karasov, 1995) and the potential competition with more specialized insectivore species (O'Donnell et al., 2012).

We propose that the diversification dynamics of different dietary guilds are driven by resource competition caused by deep-time temporal and spatial changes in resource availability and predictability. These fluctuations in resource availability and predictability might create evolutionary pressures at two levels of organization. At the individual/population level, these fluctuations might promote transitions into omnivory in times of food resource scarcity by selecting individuals/populations that do not rely on single food items (Traveset et al., 2015). At

the species level, the same climate and resource fluctuations might result in more favorable conditions that would eventually bring back omnivore species in contact with species belonging to multiple dietary guilds. In times or places with relatively small changes in resource availability and predictability, the more specialized guilds can rapidly (re)colonize areas where omnivores emerged, possibly preventing the transitions of omnivores back into other more specialized guilds due to the velocity of migration in relation to selection. This would explain the higher extinction rates of omnivores. Such a selection mosaic (sensu Thompson, 2005) of resource distribution and competition would therefore mediate the macroevolutionary fate of omnivores and specialized dietary guilds (Price et al., 2012).

Even though it is challenging to directly test mechanistic hypotheses at a macroevolutionary scale, we suspect that such a competitive mechanism acting at both the species and individual level should not only result in specific macroevolutionary patterns (e.g. higher extinction rates of omnivores), but also in macroecological predictions. At broad spatial scales, we therefore predict that the spatial distribution of omnivorous species peaks in places where co-occurrence of specialized dietary guilds is low. For instance, the relatively stable, long-term (Cenozoic) availability of rainforest climates in South America (Kissling et al., 2012b) coincides with a low diversity of omnivores and high diversity of species belonging to specialized dietary guilds such as granivores, frugivores, nectarivores, insectivores and carnivores (Kissling et al., 2012a).

Expanding these ideas into the Anthropocene where human-driven global change is homogenizing biological communities and eliminating the resources of many specialist species, we expect that a shift in the competitive dynamics between generalists and specialist species will occur. Globally, generalist bird species are at a much lower risk of extinction than specialists, and in birds there is an observed positive relationship between increased specialization and increased risk of human-driven extinction (Sekercioglu, 2011). Hence, ongoing human-driven changes are likely to distort future macroevolutionary

dynamics by changing diversification rates and favoring generalist species at the expense of specialists.

Irrespective of the mechanism, our results support the notion that omnivory is a macroevolutionary sink, i.e. a transient state in bird evolutionary history. This dynamic seems to be affected by two different hierarchical processes. On the one hand, species sorting through higher extinction rates and lower speciation rates will lower species richness of omnivores through time. On the other hand, selection —presumably driven by changes in resource abundance and predictability— brings species diversity of omnivores back and results in higher transition rates into omnivory at the macroevolutionary scale. The ecological mechanisms behind these macroevolutionary dynamics are difficult to test, but the available data suggest that the interplay between intra- and inter-guild competition might lie at the heart of this macroevolutionary game of the "jack-of-all trades is a master of none".

# Chapter 2

# How well can we estimate diversity dynamics for clades in diversity decline?

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## 2.1 Abstract

The fossil record shows that the vast majority of all species that ever existed are extinct and that most lineages go through an expansion and decline in diversity. However, molecular phylogenies have largely failed to correctly infer extinction dynamics rendering themselves potentially unsuitable for detecting patterns of diversity decline, especially if we want to recover how rates have changed through time and the relative importance of changes in speciation and extinction in governing diversification dynamics. Two recently developed methods (RPANDA and BAMM) that permit extinction to be higher than speciation might be able to detect these decline patterns based solely on molecular data, although neither method have been thoroughly tested. Here we investigate the behavior of those two methods under two scenarios of diversity decline (i.e. negative diversification rates at the present). In the first scenario we simulate phylogenetic trees where diversity decline is solely controlled by decreasing speciation, while in the second scenario

it is solely determined by increasing extinction rates through time. Because phylogenetic trees might capture the clade diversity trajectory at different phases each tree was trimmed in different points in time to simulate molecular phylogenies with different underlying intensities of diversity loss. We fit both RPANDA and BAMM to all trees at all time slices to compare the simulated and estimated rates to assess parameter estimate accuracy, potential biases and hence compare the performance of both methods. Lastly we compared their diversification rate estimates for a comprehensive dataset of 214 empirical trees. Our results show that both methods perform equally well in the varying speciation scenario, and were able to properly reconstruct the diversification dynamics for the whole history of clade. For the varying extinction scenario rates at the present are reasonably well estimated, but both methods wrongly assign the variation in net diversification to a change in speciation instead of the simulated change in extinction. Diversification estimates for empirical trees revealed differences in the identification of declining clades between the methods: increasing extinction was identified in 67 and 13 out of 214 trees for RPANDA and BAMM, respectively and decreasing speciation rate was identified in 48 and 160 out of 214 trees for RPANDA and BAMM, respectively. We suggest that under a simple diversification scenario both methods might be able to estimate negative diversification rates at present, but could fail to infer how rates change at deep time and might need additional information in empirical analyses. This behavior of assigning the variation on net diversification rate to speciation when extinction varies challenge not only the idea that slow-downs in speciation are a common macroevolutionary phenomenon but also our hope for molecular phylogenies to properly estimate diversification dynamics when it is driven by changes in extinction rate.

**Keywords**: Diversification, Diversity Decline, Macroevolution, Speciation, Extinction, RPANDA, BAMM, Simulations, Vertebrates

## 2.2 Introduction

Understanding how biodiversity changes over geological time scales is of key importance to understand the mechanisms that shaped past and current biodiversity. Most species to ever exist on the planet have gone extinct, and extinction shapes clade-level diversity patterns as well (Raup, 1986; Foote, 2007; Liow and Stenseth, 2007; Quental and Marshall, 2013); Silvestro et al., 2015. Traditionally, paleontologists have assessed extinction and origination using the fossil record to understand the deep time processes that shape biodiversity. These studies have helped to clarify several extinction-related processes including mass extinction events and biodiversity rebounds (Roopnarine, 2006; Stanley, 2007), the possibility that diversity might regulate itself (Sepkoski 1978, 1979, 1984; Alroy, 1996), that the diversity dynamics of different clades might be interconnected (Liow et al., 2015; Silvestro et al., 2015) and the fact that the diversity decline might be controlled by both a drop in speciation as a rise in extinction (Gilinsky and Bambach, 1987; Quental and Marshall, 2013).

The fossil record provides the most direct way of estimating extinction and speciation through time (Nichols and Pollock, 1983; Quental and Marshall, 2009; Quental and Marshall, 2010), however the degree of incompleteness of the record may potentially limit inferences of such rates (Peters, 2005; Alroy et al., 2010). Over the last several decades methods that explicitly account for sampling and preservation biases have been developed (e.g. Alroy, 1996; Foote, 2007; Silvestro et al., 2014a; Starrfelt and Liow, 2016); however these methods still require a minimum amount of stratigraphic information. Hence many groups do not have a fossil record good enough to allow researchers to reliably describe patterns and infer processes that might govern biodiversity dynamics.

The advent of statistical methods that promise to estimate speciation and extinction rates solely from molecular phylogenies (Nee et al., 1994; Stadler, 2013b; Morlon, 2014; Rabosky, 2014)

and the unprecedented recent accumulation of molecular phylogenies represent an alternative with potentially a much broader taxonomic range than the fossil record. From simple constant-rate birth-death models (Nee et al., 1994) to complex bayesian models (Rabosky, 2014), through trait-dependent speciation and extinction (FitzJohn, 2012), these models have been heavily used in the past two decades. The use of those phylogenies have not only allowed researchers to evaluate the diversification dynamics of several types of organisms with a poor fossil record such as birds for instance (Huang and Rabosky, 2014; Burin et al., 2016), but also opened up the possibility for broader generalizations due to the paramount quantity of molecular data.

Several authors have cautioned against the ability of birth-death models to properly infer extinction rates (Rabosky, 2010, but see Beaulieu and O'Meara, 2015 and Rabosky and Goldberg, 2015) and hence properly detect diversity decline (Quental and Marshall, 2010). In fact, with few exceptions, most studies using molecular phylogenies either suggests very small extinction rates (e.g. Rabosky, 2014; Alencar et al., 2016) or that diversity is either increasing or at best plateauing (e.g. Morlon et al., 2010; Rabosky, 2014). These diversification patterns could be due to limitations inherent from the available data (Ricklefs, 2007; Barraclough and Nee, 2001), to a general interest in radiating lineages, but could also be due to the inability of the methods available at the time to properly detect decline in diversity from molecular phylogenies. Those patterns are clearly inconsistent with what we known from the fossil record, and this inconsistency has in fact spurred the development of new tools that allow extinction to be higher than speciation (Morlon et al., 2011; Rabosky, 2014).

Studies have suggested that molecular phylogenies alone are not enough to fully assess the diversification dynamics of clades (Quental and Marshall, 2010), especially if the clade of interest is thought to be in diversity decline (i.e. clades that had a

higher species diversity in the past than they have today) (Quental and Marshall, 2011). However, two recently developed methods are theoretically able to detect diversity decline in molecular phylogenies (Morlon et al., 2011; Rabosky, 2014). The first method is a likelihood-based model that allows the fitting and selection of multiple models on a priori selected trees (Morlon et al., 2011; Morlon, 2014); this method is implemented in the RPANDA package (Morlon et al., 2016), and we will refer to it as 'RPANDA' for simplicity. The second method, BAMM (Rabosky, 2014) relies on a reversible-jump MCMC algorithm to detect shifts in diversification rates and get average rates for the whole tree. As both methods were primarily tested using the cetacean phylogeny (Morlon et al., 2011; Rabosky, 2014), the contrasting results sheds light on their differences. In their initial study, Morlon et all (2011) showed that RPANDA recovered a diversity decline for Cetaceans and, across some sections of biologically relevant parameter space. Conversely, BAMM's cetacean rate estimates suggest expanding diversity (Rabosky, 2014). The fossil record on the other hand suggests that a drop in speciation is of primary importance in the decline dynamics not only for cetaceans (Quental and Marshall, 2010), but also for many other organisms (Gilinsky and Bambach, 1987; Quental and Marshall, 2013; Silvestro et al., 2015; Silvestro et al., 2014a). Given that molecular phylogenies allow researchers to indirectly estimate the contribution of speciation and extinction regimes, it is possible that such methods might have a difficult time in properly estimating their individual changes. Additionally, apart from Cetacea, other examples of diversity decline detected in molecular phylogenies either using the RPANDA or BAMM are extremely rare (see Discussion). In contrast clades declining in diversity comprise a pattern commonly seen in the fossil record. Although such rarity is not direct evidence, given what we know from the fossil record it is unlikely that almost all clades ever studied using molecular phylogenies belong to a dynamics of either expansion or equilibrium diversity (Quental and Marshall, 2010).

An additional challenge to the estimation of extinction from

molecular phylogenies lies in the changing phylogenetic signature of the diversification dynamics as the diversification process unfolds (Liow et al., 2010; Quental and Marshall, 2011). It is therefore possible that the success of birth-death methods in properly inferring the extinction and speciation regimes changes as times goes by. Despite the existence of methods that can now theoretically detect decline in diversity, and the explosion in diversification studies, the paucity of examples estimating diversity decline from molecular phylogenies is in strong contradiction with the overwhelming signal of decline seen in paleontological studies. Apart from those studies mentioned above, we are unaware of any other study that has systematically investigated the effect of time on our ability to infer the diversification dynamics, in particular for a decline scenario. We feel that none of those two methods were properly tested regarding their ability in estimating diversification rates in diversity decline, specially if we consider different moments of a given diversification processes. In fact only one study (Morlon et al., 2011) has directly investigated with simulations our ability to detect diversity decline, although with a parameter space a lot more restricted than the one used here (see methods). More importantly, if indeed those methods have a difficult time estimating extinction rates (Rabosky, 2010), their ability to unravel the separate dynamics of speciation and extinction under a scenario of diversity decline, where extinction clearly plays an important role, deserves full attention and a thorough investigation. If the current, state-of-the-art birth-death methods can reliably estimate diversification from molecular phylogenies, in particular the ability to distinguish expansion, equilibrium and decline diversity scenarios, they could allow researchers to scan the tree of life with no taxonomic limitation, opening up the possibility for broad generalizations.

Here we present a broad analysis to compare the ability of the two most recent and promising methods on estimating diversification dynamics, with special attention to their ability to detect diversity decline and properly infer the role of speciation and extinction on controlling such dynamics. We address three main questions: 1) Do any of the two recent frameworks (RPANDA

and BAMM) show a better performance when estimating rates of diversification under different scenarios of decline in diversity? 2) Can we use both methods to tell apart scenarios in which decline is caused by decreasing speciation rates from scenarios in which the decline is determined by increasing extinction rates, therefore being able to correctly reconstruct the diversity trajectory in deep time? 3) Does the ability of each method to properly infer changes in speciation and extinction rates, and their net result, depend on the intensity of the decline? To address these questions, we investigate a range of evolutionary scenarios over a comprehensive parameter space at different points in time in a clade's history to determine when declines in clade diversity are detectable and how reliable are the dynamics inferences. Under the light of the results from the simulation dataset, we analyzed a comprehensive dataset of empirical trees to address how both methods perform in "real world" scenarios.

## 2.3 Material and Methods

### 2.3.1 Workflow

The workflow for the simulation portion of our study consists of four major steps (Fig. 2.1). First, we simulated 2000 trees for each of two different diversification scenarios. In the first scenario the decline in diversity comes from varying (decreasing) speciation and constant extinction rates (hereafter called SP*var*), and the second scenario consists of constant speciation and varying (increasing) extinction rates (hereafter called EX*var*). Throughout this paper, we will consider a tree to be in decline in diversity if the estimated extinction rate is higher than the speciation rate at the present (i.e. at the tips of the tree). Second, we perform a "time travel procedure" wherein each simulated tree is trimmed in a pre-determined point in time to emulate what a given molecular phylogeny would look like in different phases of the decline process. Third, we fit both methods to the simulated trees, in order to obtain the diversification rates estimates. Finally, we analyze the performance of the models

by evaluating the relationship between estimated and simulated
rates.
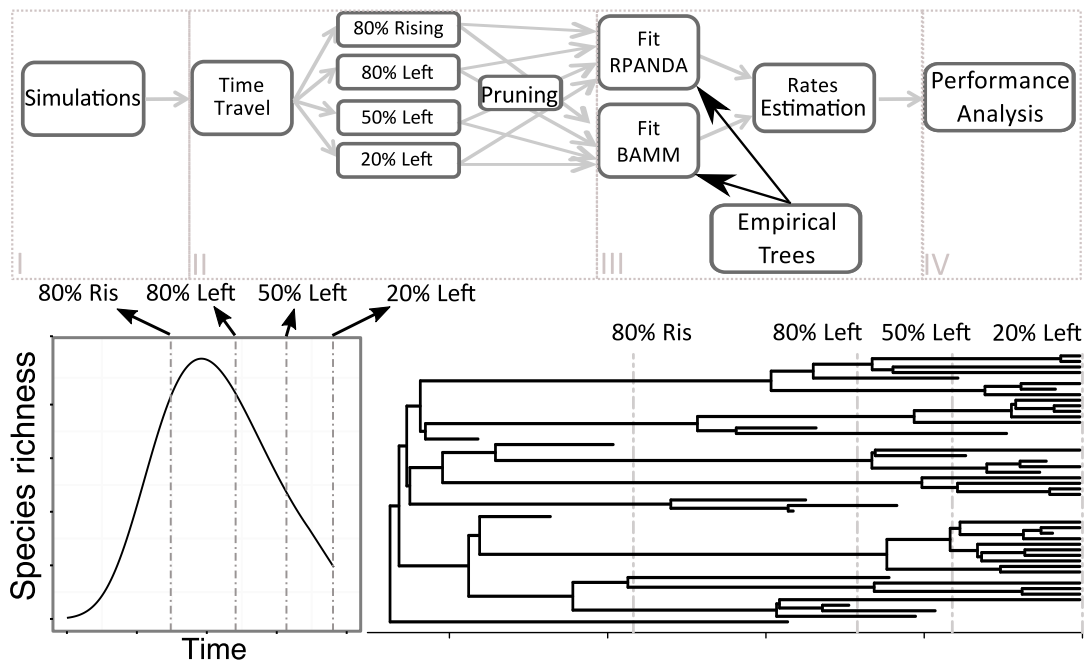


FIGURE 2.1: Schematic representation of the workflow of the study.
The top panel represents the main steps of tree simulation and rate es-
timation (with I - IV being the main sections of the protocol described
below), and the bottom panels show a cartoon example of the diver-
sity trajectory we simulated as well as an example tree showing the
time slices used on the study. (80% Rising = 80% of peak diversity in
the diversity expansion phase; 80%/50%/20% Left = 80%/50%/20%
of peak diversity in the decline phase).

**I: Simulations**

The first step consisted of simulating trees for two different di-
versification scenarios: the first scenario was characterized by
an exponential decline on speciation rates and constant extinc-
tion rates through time (SP*var*, 2.1), whereas the second scenario
consisted of constant speciation rates and saturating increase on
extinction rates over time (EX*var*, 2.1). We chose the saturating
increase instead of an exponential increase for the EX*var* sce-
nario so the variation in net diversification between both scenar-
ios would follow the same pattern. For these two scenarios, four
parameters (initial and/or final speciation and extinction rates)
were combined three by three according to each scenario: for

TABLE 2.1: Models of rate variation from the root to the tips and ranges of the uniform distributions from which each parameter was sampled in the two simulated scenarios (**SP*var*** and **EX*var***)

| | Rate Variation | | Parameter Range | | | |
|---|---|---|---|---|---|---|
| | Speciation | Extinction | $\lambda$ | $\alpha$ | $\mu$ | $\beta$ |
| **SP*var*** | $\lambda(t) = \lambda_0 e^{-\alpha t}$ | $\mu(t) = \mu$ | 0 - 10 (initial) | 0 - 1 | 0 - 2 (constant) | NA |
| **EX*var*** | $\lambda(t) = \lambda$ | $\mu(t) = \mu_f - (\mu_f e^{-\beta t})$ | 0 - 10 (constant) | NA | 0 - 10 (final) | 0 - 1 |

SP*var*, we used two parameters for speciation rates (initial speciation $\lambda_0$ and decaying rate $\alpha$) and one parameter for extinction rates $\mu$. In the second scenario (EX*var*), we used one parameter for speciation rates ($\lambda$) and two for extinction rates (initial extinction $\mu_0$ and increase rate $\beta$). These values were sampled randomly for each of the simulations (simulation process described below) from uniform distributions bounded by the values presented in 2.1.

Based on the range of values shown in Table 2.1, we simulated 2000 trees for each scenario. For each simulation, we followed the same three steps: (1) The three parameters necessary for the simulations were randomly sampled from uniform distributions with limits described in Table 1. With the combination of the three parameters, we calculated the time expected for the tree to reach its peak diversity, i.e., the time when speciation and extinction rates are equal ($t_{peak}$), as well as the expected maximum number of species. (2) We then estimated the time where the tree is expected to have only 20% of its diversity after passing its peak diversity, and designated this the total simulation time. (3) Finally, we ran each individual simulation using their three sampled parameters and the time of 20% after passing its peak diversity. For the simulations we used a script kindly provided by Dr. Hélène Morlon, that is available on github (). Should the simulated tree reach more than 20000 species at any point in time, or should the tree go extinct before the defined time, the sampled parameters were recorded, discarded and the steps 1-3 were repeated to generate all the 2000 viable trees.

The simulations for both scenarios allowed us to explore two

different regions of the parameter space. Due to particular differences between the models for varying speciation and varying extinction and our desire to have a similar change in net diversification the values chosen for the uniform distribution from which extinction rates ($\mu$) was sampled were distinct from the range of values chosen to speciation rates ($\lambda$). It is important to note that in one scenario we have fixed extinction (or speciation) while in the other we had varying extinction (or speciation); hence it is difficult to compare the explored parameter spaces between the two scenarios (Fig. 2.2 panels a and b). Given the simulations limitations related to either phylogenies dying before the stipulated time or growing extremely large, the parameter space explored is constrained among certain values. We also note that in the varying extinction scenario (EX*var*) the final values of extinction can be extremely high and a lot higher than many empirical estimates. This is also the result of the model particularities where the only way to make the net diversification rate change in a similar fashion as in the other scenario (e.g. for this rate to be negative for the final part of the life of the tree, and to guarantee that the tree survives and diversifies) is to start with high values of constant speciation and a considerable rise in extinction from its initial value of zero. Although some of those final extinction rate values might seem unrealistic (in the order of 10 species per lineage per million years), for the purpose of model performance comparison they should not be a problem. For example, one could rescale the process to unfold at 10 times slower by decreasing the rates by a factor of 10. That would make the rate absolute values similar to empirical ones but the relative relationships between the rates would remain similar to the ones presented here. Lastly it should be noted that those extremely high extinction values are only experienced at the end of the simulation process.

**II: Time travel, pruning and summary statistics**

Since the historical information stored in a phylogeny changes through its evolutionary history, our studied assessed model performance at four different phases in the history of the clade.

Thus the following step of the protocol consisted of using the 2000 simulated trees that are in a late stage of decline that corresponds to 20% of its diversity after passing its peak diversity (hereafter called *20left*, which refers to the percentage of peak diversity remaining) and time-travelling back to the expected times when each of these trees would have had lost 50% and 20% of peak diversity (hereafter called *50left* and *80left*, respectively, which refers to the percentage of peak diversity left), as well as when the trees would have had 20% less species than at their peak diversity during the expansion phase (hereafter called *80rise*, which refers to the percentage of peak diversity attained at this time slice prior to the decline - see fig. 1 for all time slices). So, analogously to step (2) of the simulation step (see above), we estimated the time when the trees were expected to have reached 50% and 80% of the peak diversity in the decline phase and 80% of peak diversity in the expansion phase, and then used the function timeSliceTree from the paleotree package in R (Bapst, 2012) to slice the 2000 trees in the corresponding periods in the past to generate new trees. To properly do this we kept the extinct species in the original simulations (dropping them before time traveling would yield trees that were not the perfect representation of that tree at a given point in the past). After the time-traveling step for both scenarios, the extinct species were pruned from all of the 16000 resulting complete trees, and these trees were used in the final step of the workflow. Those trees represent what would be a molecular phylogeny had one capture the processes at that particular point in time.

We characterized all simulated trees at both scenarios and at all time slices using three frequently used features: number of tips, age of the tree, and the gamma statistics (Pybus and Harvey, 2000). The gamma statistics is known to be strongly dependent on tree size (number of tips); therefore, we used a version of the gamma value that is standardized in relation to the maximum possible value of gamma (Quental and Marshall, 2011) for a tree with the same number of tips, calculated according to equations (1) and (2):

$$\frac{\gamma}{\gamma_{max}} \tag{2.1}$$

$$\gamma_{max} = \frac{\sqrt{\frac{1}{12*(N_{tip}-2)}}}{2} \tag{2.2}$$

**III: Model fitting and parameter estimation**

Parameter estimation in RPANDA and BAMM reflect the differences in the underlying statistical frameworks of these methods. RPANDA's parameter estimation is based on a model selection approach, based on Maximum Likelihood estimation. In this approach, the user provides one or more models (functions) of rate variation through time, and RPANDA estimates the parameter combination that maximizes the likelihood of each model (Morlon et al., 2016). This is valid for both speciation and extinction. In contrast, BAMM is a Bayesian method that uses a reversible-jump MCMC algorithm to explore the posterior distributions of parameters, while it simultaneously tests for the presence of shifts in the diversification regime within the tree and test different diversification models for each regime (Rabosky, 2014). For each regime, BAMM estimates the parameters of an exponential increase or decrease in speciation (following the model present in the first cell of Table 2.1), and the parameters for a constant extinction model. In all cases model and parameter estimation, was restricted to trees with more than two tips (but note that the vast majority of trees had a lot more tips than that; see fig. 2.2). Based on the differences between the two methods, we adopted a slightly different approach for each one, which are described in the corresponding sections.

RPANDA — To estimate speciation and extinction regimes we performed model selection using RPANDA by testing all possible pairwise combinations between constant and time-varying speciation and extinction rates, using all the four rate variation models presented in table 1. We called each of the pairwise combinations as: BOTH*cst* (both rates constant); SP*var* (varying speciation and constant extinction); EX*var* (constant speciation and

varying extinction); BOTH*var* (both rates varying). Thus, for each of the 16000 trees (which include trees in all time slices) we provided the 4 model combinations and selected the best model based on the Akaike's Information Criterion corrected for finite sample sizes (AICc). RPANDA estimates the values for the parameters at the present and the rate of change for those models where one or both of the rates vary through time. To infer the rates at the origin of the clade we used the parameter estimates, the corresponded model, and the simulated time for each individual tree of interest. All RPANDA analyses were done in parallel within R environment (R Core Team, 2016) using the packages dplyr, foreach, doMC and RPANDA (Wickham and Francois, 2016; Analytics and Weston, 2015a, Analytics and Weston, 2015b; Morlon et al., 2016).

These fitting exercises included the true simulated combination of rate variation models plus 3 more (see 2.1). We used $\Delta$AICc greater than 2 to pick the best model, irrespective if it was the true simulated model. The best model was then used as the best estimate for each individual tree. We could have otherwise used only the simulated model but that would make the comparison with BAMM unfair given that in reality we do know which one is the true model and BAMM in fact cannot perform model test among different models provided by the user.

BAMM — To estimate the speciation and extinction regimes in BAMM we obtained the mean speciation and extinction rates at the tips and at the root of the tree, as well as the increase/decay parameter for speciation. The control files containing important information for BAMM such as prior parameters and chain length were set individually for each tree using parameters estimated using the BAMMtools package (Rabosky et al., 2014), and all BAMM analysis were run in parallel using the GNU parallel shell tool (Tange, 2011) and the latest BAMM version (2.5; Rabosky, 2014). After running BAMM, the resulting files were imported in R and processed to retrieve the rates using the package BAMMtools (Rabosky et al., 2014).

We should also note that the scenario with only varying speciation (SP*var*) yields the most direct comparisons between the

methods, given that the current version of BAMM does not allow a test for varying extinction rates. Even though the varying extinction scenario (EX*var*) is only implemented in RPANDA, we decided to also use BAMM to estimate rates under this scenario not only to compare the methods, but more importantly to understand the behavior of both methods in a potentially more complicated scenario. This is justified given that it is an evolutionary plausible scenario, and from a given molecular phylogeny there is no a priori justification to exclude such scenario as a potential one.

Empirical trees —We fitted both RPANDA and BAMM to 214 empirical trees. The trees used here are the same as the trees used by Lewitus and Morlon, 2016, and include trees of all five major vertebrate groups (fishes, amphibians, reptiles, birds and mammals). For RPANDA, we fitted all four models used in the simulation analysis plus a fifth model that represented an exponential increase in both speciation and extinction (hereafter called BOTH*exp*). Different from our simulations, which only had diversity decline, a scenario of increasing expansion in diversity is possible. For BAMM, we estimated the set of parameters for each tree individually using the BAMMtools package for R. Since there was only one tree (Muridae, 680 species) slightly larger than the recommended size for the "expected number of shifts" parameter to be set as 1, we used 1 for all trees. The estimated rates were then summarized following the same protocol as for the simulated trees, the only addition being that for the empirical trees we estimated the values for each parameter via model averaging, in addition to analyzing the results for the best selected model ($\Delta$AICc > 2; only the best model was considered for trees with $\Delta$AICc < 2). These estimates consisted in the parameter values in each of the four models averaged by their respective Akaike weights. We do not know which model is the true model that shaped the diversity of each empirical clade, whereas for the simulated dataset we knew the true model in each scenario. Therefore, we used the model averaging approach only for the empirical estimates. Lastly, we fitted linear models to the each of the estimated rates of both methods (speciation, extinction and net diversification) both at the

tips and at the root to help us better understand the differences between the parameter estimates.

**IV: Performance Analysis**

All the results from the parameter estimation for all 16000 trees were tabulated, and used to evaluate the performance of the two methods both visually through estimated by simulated plots, and using goodness of fit metrics such as sum of squared deviations from the perfect fit (when estimated = simulated). Additionally, we considered that a tree was in diversity decline (hereafter called only "decline") when the extinction rate at present is higher than the speciation rate at present for all analyzed time slices.

## 2.4 Results

### 2.4.1 Simulations

Our results indicate that the collection of viable trees allowed us to greatly expand the parameter space explored by Morlon et al (2011) and explore the total parameter space delimited by the values present in table 1 in a comprehensive manner (figure 2.2a and b). Our simulations also resulted in trees with similar size and depth distributions for both scenarios (figure 2.2c and d), with trees ranging from 2 to more than 6000 species, and from 3.3 to 100 million years of age. Hence the simulations of both scenarios resulted in a virtually indistinguishable distribution of phylogenies with respect to total time and richness. The branching patterns on the other hand are very different. The standardized gamma statistics distributions of both scenarios have very little overlap (figure 2.2e), being predominantly negative for SP*var* and positive for more than 98% of the trees at EX*var*.
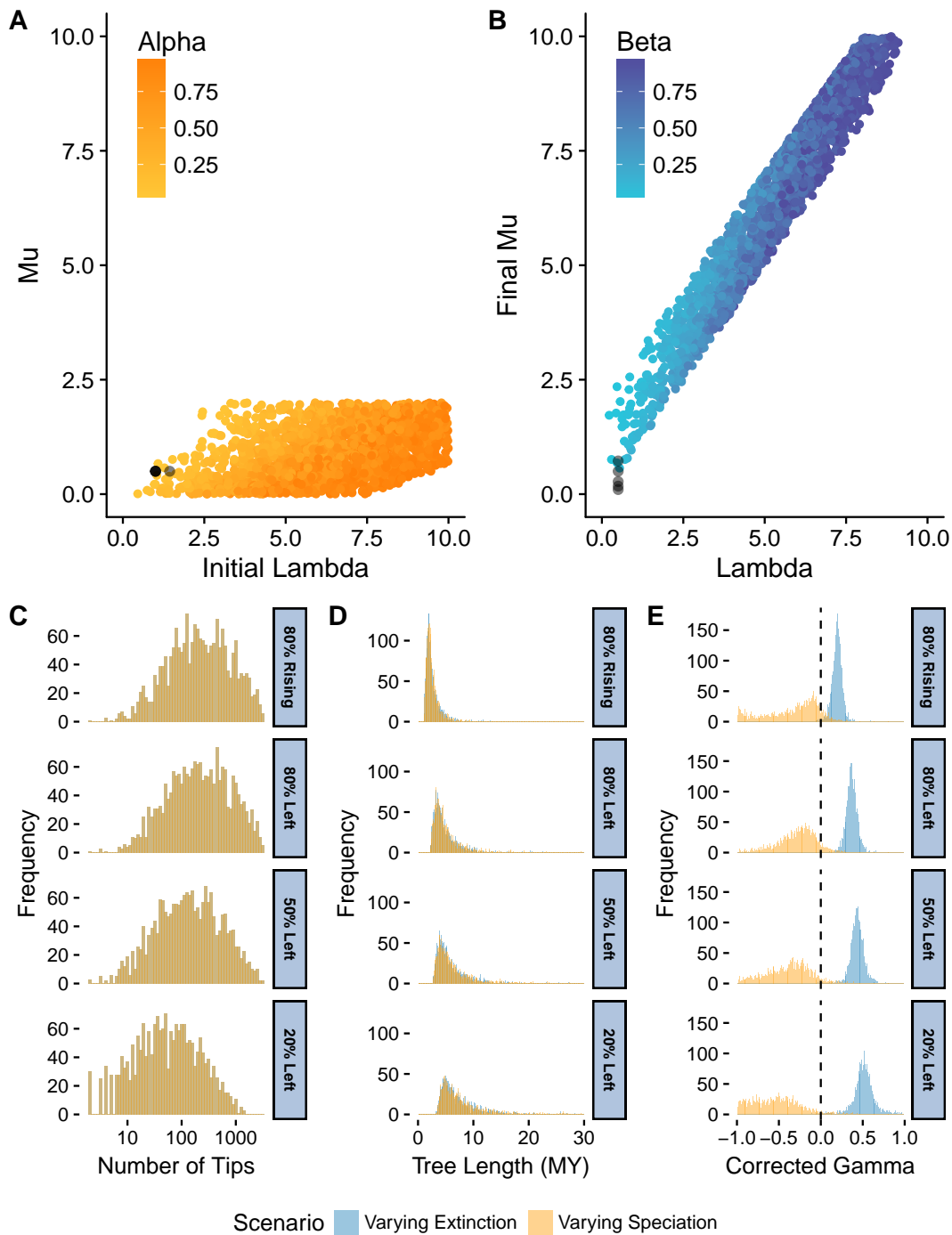
FIGURE 2.2: Explored parameter spaces and simulation results. a. Parameter space explored in the SP*var* scenario. b. Parameter space explored in the EX*var* scenario. c. Distribution of number of tips in the viable trees of both scenarios. d. Distribution of tree depth (in million years) in the viable trees of both scenarios. e. Distribution of the corrected gamma statistics calculated for all the simulated trees from both scenarios. The black points in panels a and b represent the parameter combinations used by Morlon et al., 2011.

### 2.4.2 Fitting

We present the results of three out of the four time slices (*80rise*, *80left* and *20left*, respectively). The results for the *50left* time slice are qualitatively similar to the ones presented below and hence are only presented in the supplemental material (figs. B.1-B.4). The predominantly positive estimated values of net diversification rates for the *80rise* time slice indicate that there is no bias towards falsely detecting decline for both methods in both scenarios (panels a and d of figures B.1 and B.2), nor any bias in estimating individual rates of speciation and extinction (figs. B.3 and B.4 panels a, d, g and j). Hence we focus on the two other time slices, which represent our main interest in diversity decline.

SP*var* — RPANDA selects the "true" model for the vast majority of the trees (91% for the *80left* time slice and 87.5% for the *20left* time slice - Table 2.2). The good performance of RPANDA on estimating net diversification is due to the non-biased and accurate estimation of both speciation and extinction rates at present (Fig. 2.3 panels b, c, g, h and i, and figs. B.1, B.3, B.4, and B.5), with a very small bias for both rates in the smaller trees (figs. B.3, and B.4). Extinction rate is frequently estimated to be very close to zero when the BOTH*cst* model is selected. Thus, RPANDA does not detect decline for a few trees in both time slices, especially when the best model selected is BOTH*cst*. RPANDA estimates of net diversification show little bias for both time slices (*80left* and *20left* - figs. B.1, and B.5). When the most complex model (BOTH*var*) was selected, the estimates of net diversification are highly negative, overestimating the pace of diversity decline for those trees (fig. B.1 panels B, and C), especially for moderately sized trees.

In the SP*var* scenario, RPANDA detected a single best model for the majority of trees (table 2.3). Additionally, it is worth noticing that even when more than one model were equally likely, the true model was among the best models for the vast majority of trees (table B.1).

TABLE 2.2: Number of trees for which RPANDA choses each of the four tested models as the best model in both scenarios. First row indicates the true simulated model in each scenario. Numbers in bold show the instance where the correct model was chosen.

| Model | SP*var* | | | EX*var* | | |
|---|---|---|---|---|---|---|
| | *80rise* | *80left* | *20left* | *80rise* | *80left* | *20left* |
| BOTH*cst* | 335 | 79 | 108 | 673 | 222 | 443 |
| EX*var* | 69 | 1 | 3 | **10** | **10** | **34** |
| SP*var* | **1538** | **1821** | **1749** | 1210 | 1635 | 1376 |
| BOTH*var* | 58 | 99 | 140 | 107 | 135 | 147 |

TABLE 2.3: Number of trees for which RPANDA choses each number of equally likely models based on the AICc differences ($\Delta$AICc > 2)

| Number of Equally likely models | SP*var* | | | EX*var* | | |
|---|---|---|---|---|---|---|
| | *80rise* | *80left* | *20left* | *80rise* | *80left* | *20left* |
| 1 | 1282 | 1466 | 1601 | 856 | 1125 | 1274 |
| 2 | 641 | 530 | 368 | 912 | 795 | 637 |
| 3 | 73 | 3 | 18 | 190 | 68 | 77 |
| 4 | 4 | 1 | 13 | 42 | 12 | 12 |

Similarly, BAMM is able to detect decline (negative diversification at present) for most trees in both time slices (fig. B.1 panels e, and f). However BAMM produced slightly negatively biased estimates (fig. B.1 panels e, and f, and fig. B.8). This bias is more evident for small trees (up to 100 tips), and also at the *80left* time slice (fig. B.8). Interestingly, both speciation and extinction rates seem to be overestimated for trees up to 1000 tips, and this bias is seen more clearly at the *20left* time slice although the number of trees is small and hence biases harder to infer (fig. 2.3 panels e, f, k, and l, and figs. B.6 and B.7). Surprisingly, our results indicate that this bias seems to be stronger for speciation rates than for extinction rates (fig. B.6 and B.7). Nevertheless, the biases in both rates seem to be coupled, i.e., the overestimation in both rates for the same tree is proportional, since the net diversification rates are much less biased than each rate alone (fig. B.8).
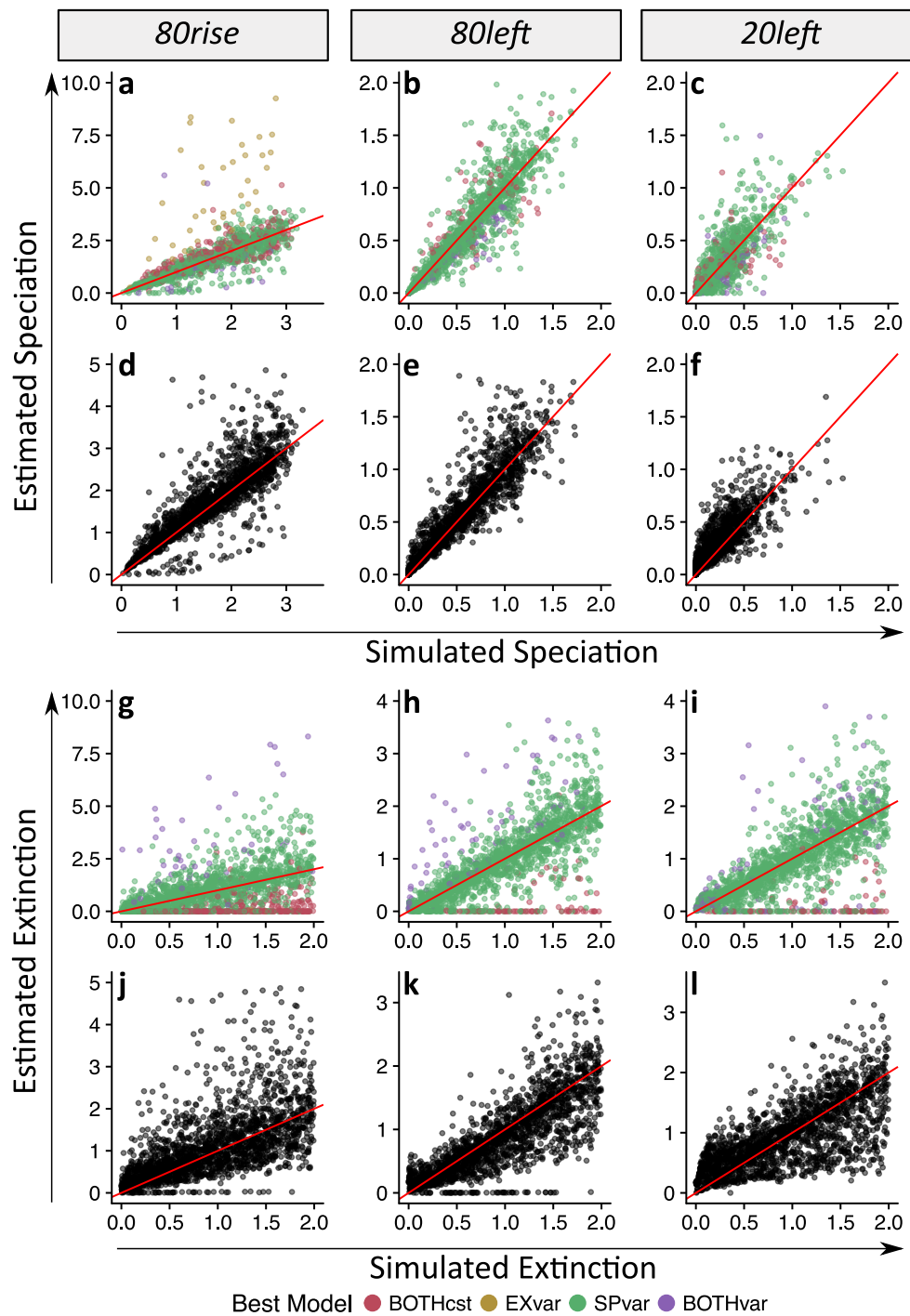
FIGURE 2.3: Estimated versus simulated speciation rates at present (panels a-f) and estimated versus simulated extinction rates at present (panels g-l) for the SP*var* scenario for RPANDA (panels a, b, c, g, h, and i) and BAMM (panels d, e, f, j, k, and l). Estimates are for the *80rise* time slice (left column), *80left* time slice (middle column), and *20left* time slice (right column). For all RPANDA panels (a, b, c, g, h, and i), colors denote the best model selected, and in all panels the red line denotes the 'perfect fit' (estimated rate equal to the simulated rate). The y-axes were rescaled to values that contained at least 95% of the trees for better visualization.

The two methods estimated different amounts of extinction experienced by the clade. For example, in the *80left* and the *20left* time slices RPANDA does not seem to be too affected by the increased amount of historical extinction, showing a similar ability to detect negative diversification in both time slices (although the number of trees for which the method chooses the simplest model - BOTH*cst*- increases at the *20left* time slice - table 2.2). Conversely, BAMM seems to benefit from the increased relative importance of extinction, detecting decline for more trees at *20left* than at *80left* time slice (fig. B.1 panels e, and f).

For both methods, the estimated speciation and extinction rates at the root of the trees (reconstructed values for RPANDA and estimated values for BAMM) are very similar to the simulated values, regardless of the time slice for both methods (figure B.9). RPANDA tends to overestimate speciation rates at the root more than BAMM, probably as a consequence of those rates being the result of an extrapolation using the selected model, and also influenced by the propagation of the error in the estimates of the rate at the present and the decay/increase parameter. This overestimation is greater when the best model selected has variation in extinction rates (BOTH*var*). Accordingly, estimated extinction rates at the root are underestimated when the BOTH*var* model is selected, being very close to 0.

EX*var* — For the varying extinction scenario (EX*var*), both methods perform worse in estimating the net diversification rate estimates. RPANDA rarely selects the "true" model as the best model (table 2.2); at both the *80left* and *20left* time slices the varying speciation model (SP*var*) is the preferred model for most trees (table 2.2), followed by the model with both rates constant. In this varying extinction scenario it is also worth noting that the method fails to detect the true simulated model for about 99.6% of the trees at the *80left* time slice and for about 98.3% at the *20left* time slice. Additionally, in the EX*var* scenario RPANDA detects a single best model for much less trees than in the other scenario (table 2.3). Moreover, for the trees for which one or two models were selected as best ($\Delta$AICc < 2), the true (simulated)

model is almost never among them (table B.1). Lastly, the estimates under the true model in this scenario (EX*var*) are biased towards underestimation for both speciation and extinction at present (fig B.10 panels G-L). This underestimation is more severe for extinction rate, and these biases combined make estimates of net diversification rates at the present to be positive under the true model for the majority of the trees (fig B.10 panels I, and L). Hence RPANDA seems unable to detect varying extinction rates.

Although RPANDA detects diversity decline (negative diversification rates at present) for most trees with the best model, in the EX*var* scenario it does by selection the wrong model (see table 2.2). It is interesting to note that RPANDA shows two distinct biases for net diversification rate estimates: it either estimates net diversification rates to be considerably more negative than the simulated values (regardless of tree size), or it tends to estimate this rate to be a lot less negative, or even positive, for a considerable amount of trees, especially those trees up to 1000 tips (fig. B.13). Nevertheless, the estimates for both speciation and extinction rates are non-biased when we look at all estimates together (figs. B.11, and B.12). This implies that for any given tree RPANDA estimates of at least one of the two rates at present for most trees is considerably different from the simulated one (even accounting for the inherent stochasticity of the process, that makes the realized rates to be not exactly the same as the simulated rates).

Like RPANDA, BAMM is able to detect negative net diversification rates for most trees, even if the implemented model is not the correct one (BAMM only has varying speciation rate and constant extinction). However, BAMM estimates of net diversification rates seem to be slightly less biased in all tree sizes (fig. B.16). For BAMM the bias seems to be unidirectional, where estimates of net diversification rates tend to be less negative than the simulated values (fig. B.16). This bias difference is clearer for small trees. Speciation and extinction rates are slightly underestimated at the *20left* time slice for trees up to 100 tips (figs. B.14 and B.15).
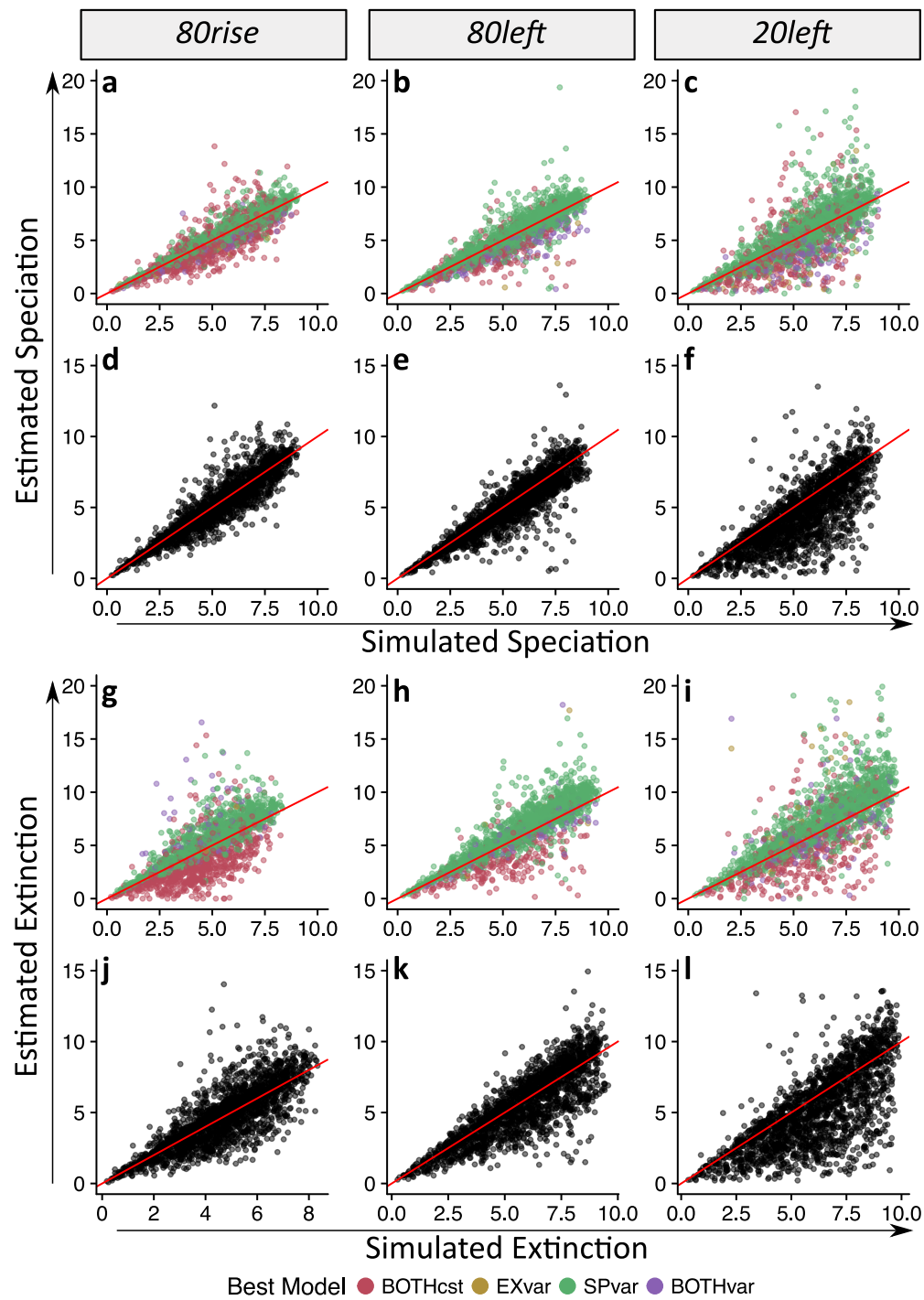
FIGURE 2.4: Estimated versus simulated speciation rates at present (panels a-f) and estimated versus simulated extinction rates at present (panels g-l) for the EX*var* scenario for RPANDA (panels a, b, c, g, h, and i) and BAMM (panels d, e, f, j, k, and l).  Estimates are for the *80rise* time slice (left column), *80left* time slice (middle column), and *20left* time slice (right column).  For all RPANDA panels (a, b, c, g, h, and i), colors denote the best model selected, and in all panels the red line denotes the 'perfect fit' (estimated rate equal to the simulated rate).  The y-axes were rescaled to values that contained at least 95% of the trees for better visualization.

Overall both methods seem to be more likely to detect diversity decline at the *20left* time slice than at the *80left* time slice. Interestingly RPANDA seems to detect negative diversification more often than BAMM at the *80left* time slice, but the opposite happens at the *20left*. At *80left* time slice RPANDA fails to detect decline for 201 trees, and BAMM fails to detect decline for almost a quarter (446) of the trees. Conversely, RPANDA fails to detect decline for 160 trees and BAMM for 316 trees at the *20left* time slice (fig. B.2).

In the EX*var* scenario, speciation rates at present are reasonably well estimated in both methods (Fig. 2.4) although the net diversification rate is poorly estimated). However, both speciation and extinction rates at the root are very poorly estimated (figs. B.17 and B.18). In fact both methods infer a considerable drop in speciation and a relatively constant extinction at both time slices for most trees, although the simulated model had constant speciation rate and variable extinction. RPANDA only correctly estimated extinction rates at the root for the few trees for which models with varying extinction rates were selected (143 trees for *80left* and 181 trees for *20left* - table 2.2); on the other hand, BAMM does not allow for extinction to vary, which forces the method to estimate root extinction to have the same values than in the present.

### 2.4.3 Analysis of empirical trees

The analysis of empirical trees revealed that both methods do not recover the same diversification dynamics for the same collection of trees. RPANDA indicates a decline in diversity (net diversification smaller than -0.01) for 67 of the 214 analyzed clades, whereas BAMM detects decline for only 13 clades from the same dataset (see also figure B.19). Moreover, for only 8 trees was a negative net diversification rate inferred from both methods (see also figure B.19). This difference in assigning a negative diversification for a different number of trees is likely to result from very different estimates of extinction rate at present (figure 2.5b and 2.5c), here also revealed by a very low statistical association between extinction rate estimates at present (table 2.4).
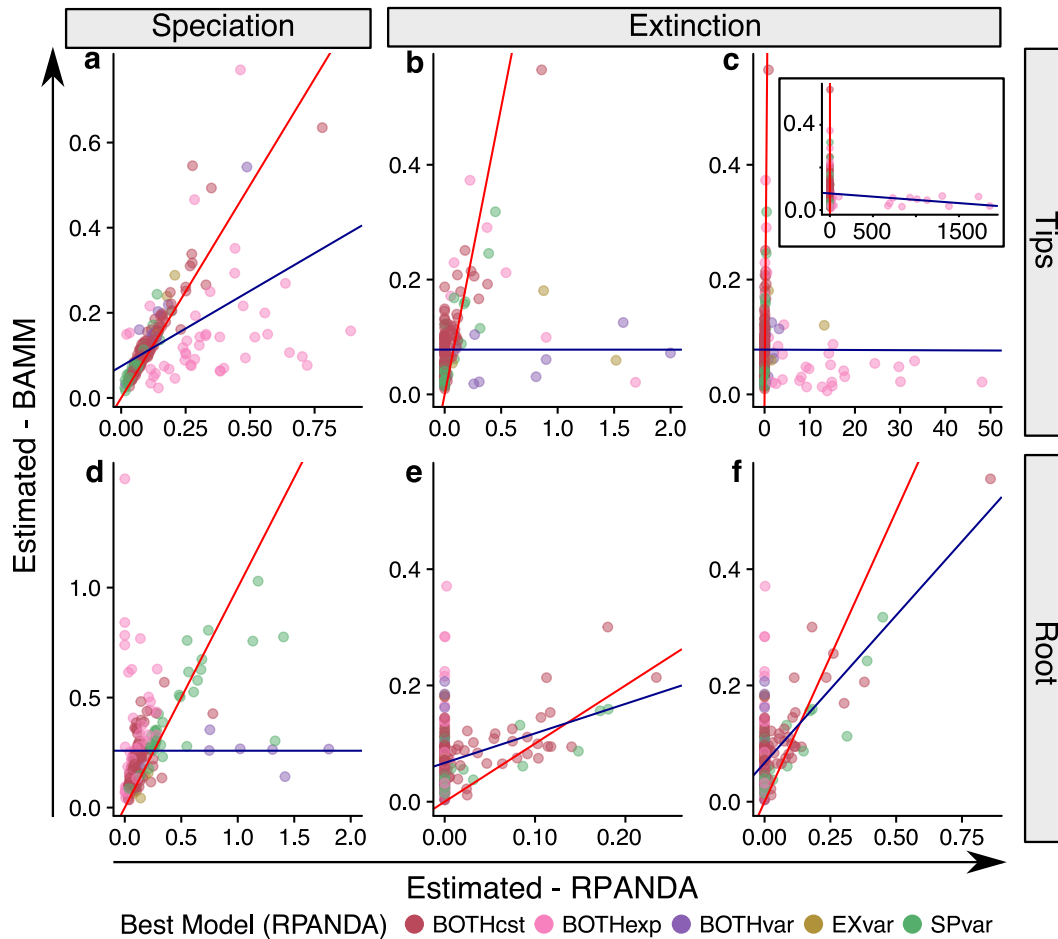
FIGURE 2.5: Estimated rates for BAMM (y axis) and RPANDA (x axis) for (a and d) speciation rates at the tips and the root respectively, and for (b - c and e -f) extinction rates at the tips and the root respectively. The x-axis of panels b and e were rescaled for better visualization, since there are estimated extinction rates from RPANDA that are greater than 10 events/lineage*MY (up to more than 1500 in the detail of figure c). The red line represents the perfect correlation (estimates from BAMM and RPANDA are equal), and the blue line represents a linear fit between the two variables. R2 values are shown in table 4. Speciation rates are similar between the two methods, whereas extinction can be quite distinct between the two methods.

TABLE 2.4: Estimated $R^2$ for the linear regression between rate estimates of BAMM and RPANDA for each rate and at each point in time (tip or root). Tip represents estimates at present and "root" at the start of the history of the clades. Values in bold are significant (p < 0.05), and values in both bold and italic are considered being small regardless of being significant (p < 0.05).

| | λ | | μ | | Net Diversification | |
|---|---|---|---|---|---|---|
| | Tip | Root | Tip | Root | Tip | Root |
| Full Dataset | **0.278** | -0.004 | 0.009 | **0.418** | **0.23** | -0.003 |
| Without BOTH*exp* | **0.876** | -0.006 | 0.012 | **0.602** | **0.33** | -0.004 |
| Without varying extinction | **0.861** | **0.629** | **0.7** | **0.692** | **0.239** | **0.433** |
| Only varying extinction | ***0.05*** | -0.009 | 0.018 | 0.019 | ***0.122*** | 0.003 |

The lack of correlation between extinction rate estimates at present might visually seem strongly influenced by the fitting of one particular model, BOTH*exp* (see Fig. 2.5), but even after removing the trees that fit this model the correlation is still very low and non-significant (see "without BOTH*exp*" results for "Tip" on Table 2.4). We note that the model BOTH*exp* (exponential increase in both rates) resulted on quite high extinction rates at present (31 trees with extinction rates higher than 5 events/lineageMY), and sometimes on very unrealistic estimates (see the eleven outliers on the sub-panel on figure 2.5c). Those likely represent poor estimates albeit coming from the best model (e.g. for the 11 trees with extinction rates higher than 500 events/lineageMY, in 8 trees the ΔAIC is higher than 2 for the next best model). We also note that about half (23 out of 43) of those trees which fitted the BOTH*exp* model tended to show small rates of extinction through most of the clade's history and that the very high rates at present are produced by a recent and abrupt rise in extinction (fig. B.23). This reinforces the idea that although those might be the best model they might not be a good model for those trees. Lastly, RPANDA frequently estimated very small values for extinction rates at present (e.g. 113 trees with extinction estimates equal or less than 0.01), while BAMM extinction rate were infrequently estimated to be so close to zero (e.g. 2 trees with extinction estimates

equal or less than 0.01). RPANDA on the other hand suggested a broader variation in extinction rates for the same collection of empirical trees than BAMM (figure 2.5). This discrepant extinction pattern clearly reflects the lack of correlation on extinction estimates between both methods.

Estimates of extinction rate at the root between the two methods are correlated (figure 2.5e and table 2.4), but it is important to consider some key model aspects that might facilitate this association. In RPANDA, three (EX*var*, BOTH*var*, BOTH*exp*) out of the five tested models are strongly constrained to start with very low (or zero) extinction rates. The other two models (SP*var*, BOTH*cst*) are basically the same scenarios allowed in BAMM. Hence this high association is somewhat driven by those trees that fitted those two models, and by the fact that extinction rates are usually estimated to be low at the root or constrained to be zero (figure 2.5). As expected if we consider only models that vary extinction, we see that the association is lost (table 2.4).

Speciation rates at present were estimated to be reasonably similar between both methods (figure 2.5a; table 2.4), especially if we remove the trees that RPANDA fitted the BOTH*exp* model which typically resulted in very high, and some times unrealistic, extinction rate estimates (table 2.4). The correlation between the estimates of net diversification at present are, as expected, somewhere in between (figure B.19; table 2.4). One should note that the surplus of trees with negative net diversification rates when using RPANDA comes, from the most part, from those trees that fitted models with increase in both rates, the BOTH*exp* model (43 out of 67 trees; see also table B.2).

When looking at the dynamics through time the discrepancy between the two methods is clearly accentuated for speciation. While RPANDA finds more instances of diversity decline (67 vs 13; see also figure 2.6) than BAMM, most of those trees with negative diversification rates derived from the RPANDA analysis do not show a decrease in speciation (note on figure 2.6a that most cases which the best model suggests diversity decline -red and light green points- are in the quadrants of rise in speciation, above zero on the y-axis). In fact, only 16 out of the 67
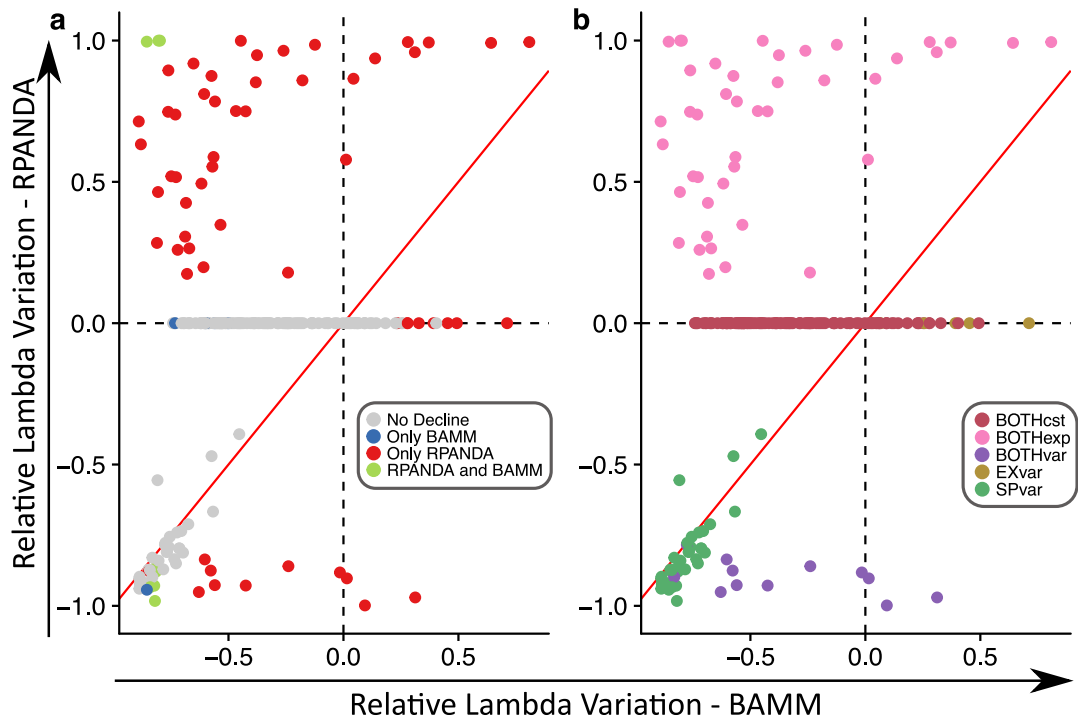
FIGURE 2.6: Relative speciation rate variation, calculated as [lambda at tips - lambda at root]/max(lambda at tips, lambda at root) of RPANDA as a function of the same index for BAMM. Positive values indicate an increase in speciation towards the present, whereas negative values indicate decreasing speciation rates through time; 0 indicates constant rates. a: Points are colored according to which model detected decline for each empirical tree; b: Points are colored according to which model was selected as the best model by RPANDA. It is possible to notice that the points that deviate the most from the perfect association (red line) have models with varying extinction rates as the best model, and that the points that represent a model that is the same as the model used by BAMM fall very close to the red line (green dots on panel b).

trees (23%) for which RPANDA detected diversity decline have a drop in speciation rate (figure 2.6a- red and green points below zero on the y-axis; table B.2). BAMM on the other hand, inferred a decrease in speciation for all 13 trees which it inferred diversity decline (blue and light green points in figure 2.6a). More striking, if we look to all empirical trees (not only those that were inferred to be in diversity decline), RPANDA suggests that the vast majority of trees (166 out of 214 – 77%) fitted models where speciation was either constant (123 out of 214 - 57%) or increasing (43 out of 214 - 20%), not decreasing (figure 2.6a). BAMM on the other hand suggested that the majority of empirical trees (160 out of 214 – 75%), irrespective if those are or not in diversity decline, showed a relative decrease in speciation comparable to the changes in rates estimated by RPANDA (figure 2.6a; most points below zero on the y-axis). As expected, this discrepancy is also reflected in the estimates of speciation rate at the root where we see no association between speciation rate estimates at the root (figure 2.5 and table 2.4), even if we remove the results from the BOTH*exp* model (table 2.4). It is interesting to note that if RPANDA fits a model that is implemented in BAMM (e.g. SP*var*), then the estimates are quite similar (green points in figure 2.6b). In fact if we plot the estimates derived solely from SP*var* model in RPANDA against the BAMM estimates, we see, as expected, a very good association (fig. B.20).

As expected, the association between diversification rate estimates is lower at the root than at the present (fig. B.19; table 2.4). It is worth mentioning that very few empirical trees (5 for RPANDA and 13 BAMM) suggest negative net diversification at the root (fig. B.19) and that BAMM only detected rate shifts for 14 empirical trees. We also note that when we used model averaging to get estimates derived from RPANDA to compare it to the estimates from BAMM we find the same results as presented here with the best model (figs. B.21 and B.22; table B.3).

## 2.5 Discussion

The fossil record shows that most of the organisms that roamed the planet are now extinct (Raup, 1986). It also shows that some extant groups were more diverse in the past than they are today, and that full lineages have gone extinct (Foote, 2007; Liow and Stenseth, 2007; Quental and Marshall, 2013; Silvestro et al., 2015). This overwhelming rock evidence of extinction contrasts with: (i) the phylogenetic perspective of diversification that usually suggests extremely low extinction rates (Quental and Marshall, 2010); (ii) a similar signature (at least when using a simple metric) between clades on equilibrium and clades experiencing diversity decline (Quental and Marshall, 2011); (iii) the view that extinction rates should not be estimated from molecular phylogenies (Rabosky, 2010). Although the development of new methods (Morlon et al., 2011; Rabosky, 2014) allow diversity decline to be estimated in principle, the question of whether extinction dynamics can be properly estimated from molecular phylogenies remains contentious (Nee et al., 1994; Rabosky, 2010; Quental and Marshall, 2010; Morlon et al., 2011; Beaulieu and O'Meara, 2015; Rabosky, 2016, Moore et al., 2016; Rabosky et al., 2017). By the virtue of knowing the true dynamics, simulation studies should be very valuable on investigating our ability to detect negative diversification rates based solely on molecular phylogenies, but to date only one exist that apply recently developed methods to a wide range of parameter space (Morlon et al., 2011).

### 2.5.1 Simulation perspective on our ability to infer negative diversification rates

Morlon et al (2011) suggested that RPANDA was able to detect diversity decline. However this study was limited in several important respects: (i) parameter space was restricted relative to biologically relevant values of speciation and extinction (ii) it did not consider method performance as a function of time towards clade decline (iii) it only examined performance of a single method. Hence we believe our results greatly contribute to

our understanding of how well we can detect diversity decline using molecular phylogenies not only because it is the first to test the ability of BAMM to detect negative diversification rate, but also because it expands the findings by Morlon at al (2011). Unexpectedly, we now show that even when the wrong model is chosen (even if we consider the general dynamics given by BAMM which does not directly fit models), the overall inference of negative net diversification at present is not strongly affected, at least for the scenarios simulated here. Moreover, our results indicate that the different phase of a tree's history (our scenarios at *80rise*, *80left*, *50left* and *20left* time slices) has only a slight impact on the ability of both models in detecting diversity decline in the both simulated scenarios.

This is surprising given that the phylogenetic overall signature of diversification dynamics (the branching patterns) changes as the diversification processes unfolds and the clade ages, a pattern previously revealed by changes in the gamma statistics (Liow et al., 2010; Quental and Marshall, 2011). It is also worth mentioning that both methods are able to properly infer the positive diversification rates when the dynamics is still in the diversity rise phase prior to reaching the peak diversity (the *80rise* time slice). The fact that the overall branching signal changes as the dynamics unfolds (Liow et al., 2010; Quental and Marshall, 2011) allied to the fact that the tested methods are able to infer negative diversification at present suggest that the methods studied here might be able to infer the dynamics in the recent past. It is important to note that this does not guarantee that the overall inference of the temporal dynamics and the accuracy of estimates of individual rates are always reliable.

### 2.5.2    Can we properly infer the diversification dynamics of clades in decline?

Our simulation results confirms the finding of Morlon et al (2011) that if one is simply interested in detecting diversity decline, here inferred by a recent negative diversification rate, both methods might be appropriate if the assumptions undertaken here are met by the empirical data. On the other hand, our

results suggested that the accuracy of the methods in depicting the temporal dynamics, either by choosing the best model (in the case of RPANDA) or by estimating the rates at both the present and at the root of the trees (in the case of BAMM) varied drastically according to the scenario explored. We clearly show that when extinction was allowed to vary (EX*var* scenario), both methods performed worse than when extinction was held constant (SP*var* scenario). This is not surprising for BAMM given that varying extinction rate is not implemented (although it could have inferred variation in extinction rates by detecting shifts in diversification regimes), but the inability of RPANDA, which does not have such limitation, to infer varying extinction rates suggests that this limitation might be more related to the nature of the data than to the method or implementation used.

Under the EX*var* scenario, speciation rate estimates at the root (fig. B.17) are significantly higher than the true values for both BAMM and RPANDA, and both methods suggested a significant drop in speciation rate (figure 2.4 and fig. B.17) when in reality speciation was constant. Moreover, the prevalence of models chosen by RPANDA with varying speciation in the simulated varying extinction scenario (EX*var*) indicates that RPANDA detected variation in net diversification but explained it as dynamically changing speciation rate. Given that those methods rely on indirect inference of the past, the amount of information available for both methods becomes thinner as we move towards the root of the tree. In fact both RPANDA and BAMM showed greater associated error for parameters at the root regardless of the simulated scenario (figures B.9 and B.18), a pattern similar to what was found by Moore et al. (2016). This might not be surprising but we argue that it represents one important aspect of the two methods, and (likely) the nature of signal in phylogenetic data sets. Methods based on molecular phylogenies could be seen as binoculars with limited range: they allow researchers to infer important aspects of the recent history of a clade, but it loses power and focus as one tries to look towards the deep past.

On the other hand, it is interesting to note that the gamma statistic (Pybus and Harvey, 2000) for those simulated trees under the EX*var* scenario are virtually all positive (fig. 2.2), not negative as one would expect for a declining speciation rate scenario (Rabosky and Lovette, 2008), at least when extinction rate is relatively low with respect to speciation rates (Quental and Marshall, 2009). Although time could have easily eroded this signal for lineages under the saturation (Liow et al., 2010), the results shown here (see also Quental and Marshall, 2011) suggest that for a scenario of declining diversity driven by a temporal drop in speciation rate the gamma values should remain negative irrespective of how much history has been unfolded. Hence although fitting complex models to the varying extinction simulated scenario suggested a scenario of varying speciation, the signal revealed by the gamma statistic would strongly caution against this interpretation given that virtually all trees under this scenario had a positive gamma value. We note that the signal of gamma tells us nothing about how extinction varies through time, neither if a given clade is in decline of diversity or not (Quental and Marshall, 2010), but we suggest that gamma statistics coupled with BAMM or RPANDA could improve our ability to detect diversification dynamics when clades are in decline. While BAMM and RPANDA are able to detect negative net diversification rates, gamma values could help indicate if the decline does indeed comes from a scenario of significant decrease in speciation rate (see results, Fig. 2.2).

### 2.5.3 Comparing the performance of both methods in empirical phylogenies

The diversification dynamics inferences on empirical trees suggest that the two methods behave very differently and infer very different dynamics for the collection of clades analyzed here. This is especially evident when we compare extinction rates at present (figure 2.5 b and c), although not surprising given that BAMM, differently than RPANDA, forces extinction to be constant. This different treatment of extinction dynamics clearly affected the ability to detect diversity decline, and depending

on the method used one would have a very different view of how common is diversity decline in the real world (31% vs 6% of clades in diversity decline, for RPANDA and BAMM respectively). This casts serious doubts on our current ability to estimate extinction rates (Rabosky, 2010) and, more importantly to the argument here, detect diversity decline based on current available methods.

Given what we know from the fossil record (Quental and Marshall, 2010; Silvestro et al., 2014a; Sakamoto et al., 2016), and the fact that RPANDA is more flexible (e.g. user can supply a different models such as exponential or linear variation in extinction), it would be reasonable to expect that that RPANDA performs better than BAMM in detecting decline. On the other hand, our results from the simulated dataset show no clear evidence of differences in performance between both methods, at least on the simple scenarios simulated here. Moreover, we do not know the true diversification history behind the empirical trees, so it would be premature to say that RPANDA estimates for the empirical trees are better than BAMM, but the comparison is informative nonetheless.

Apart from our ability/inability to infer diversity decline from molecular phylogenies it is also interesting to note the discrepancy of speciation dynamics between both methods. Our analysis suggests that although speciation rates are reasonably similarly estimated at present also for the empirical trees, the deep time dynamics of speciation is, for most clades, inferred to be very different depending on the method used: BAMM tends to suggest an overwhelming drop in speciation, irrespective if the lineages were in diversity decline or not, RPANDA does not. It is particularly important to note that this discrepancy between the two methods is specially striking when at least one of the methods suggests diversity decline (compare the colored points to the grey points in figure 6a). Moreover, this discrepancy seems to be driven by the important difference on how the two methods model extinction rates because most discrepant estimates in speciation dynamics come from those cases where RPANDA inferred changes in extinction (figure 2.5 b-c).

Our RPANDA speciation results on the empirical trees are also in direct conflict with what was found previously in terms of speciation dynamics (McPeek, 2008; Phillimore and Price, 2008; Morlon et al., 2010; Quental and Marshall, 2010). Previous work has suggested that a decrease in speciation rate would be a pervasive phenomenon in nature, either indirectly by looking at the gamma statistics (McPeek, 2008; Phillimore and Price, 2008) or, more importantly, directly by fitting complex models (Morlon et al., 2010). That said, it is important to note the differences in those approaches: the method used in Morlon et al. (2010) is based in a coalescent model that did not allow (at least in that particular paper) extinction rates to be higher than speciation rates, whereas RPANDA (Morlon et al., 2011) used in our study is based in a birth-death model that allows net diversification to be negative. Taken together, these results either suggest that: a drop in speciation is a common phenomena and that speciation dynamics is misfit by RPANDA for clades in diversity decline; or that a drop in speciation is not so prevalent and RPANDA properly recovered diversity decline for the empirical trees analyzed here.

One could argue that the collection of trees analyses by Morlon et al (2010) and the ones analyzed here are not identical, but given the large number of trees analyzed in both studies we suspect this would not explain this difference. More importantly, gamma statistics for empirical phylogenies suggest that the vast majority of trees have a negative gamma (171 out 214, about 79%) and of those about 41 % reject the null model of constant diversification rate (see table B.4). This suggests that a drop in speciation could be a rather common phenomena in the empirical trees analyzed here. On the other hand model fitting for RPANDA suggests that a drop in speciation is less common (about 48 of 214 trees, circa of 22%). This prevalence in speciation drop is also found in the BAMM analysis here, but we should note that RPANDA, as expected due to its model selection framework, is more conservative to infer a drop in speciation rate than BAMM.

The discrepancy in rate estimates from both methods could potentially result from rate heterogeneity in the empirical phylogenies and how the methods deal with it (e.g. radiating subclades that would mask a potential diversity decline of a complete clade - see Rabosky, 2014). In fact the cetacean analysis done by Morlon et al (2011), which recovers diversity decline for some lineages, implicitly incorporated potential rate heterogeneity by sub-dividing the whole clade based on their ecology, and analyzing those clades (which included paraphyletic ones) separately. We suspect this does not explain the discrepancy in both methods because our results show that only 14 out of 214 analyzed trees showed significant rate heterogeneity among the tree. Nevertheless, we highlight that by allowing researchers to arbitrarily "break" the tree into sub-clades and to test different models (scenarios) of rate variation RPANDA can be an important tool for hypothesis testing in macroevolution.

### 2.5.4 Final remarks: how reliable are estimates of diversification dynamics.

The last decades have witnessed the constant development of new comparative methods (FitzJohn, 2012; Morlon et al., 2011; Rabosky, 2014), and the turmoil of optimistic and pessimistic views on how well can we infer diversification dynamics solely from molecular phylogenies. This field has recently arrived to its final frontier, the idea that one could detect diversity decline, a scenario where the recent is experiencing more extinction than speciation even though no direct information on extinction is stored in phylogenies. Only one study (Morlon et al., 2011) has explicitly test the ability of those models on properly detect negative diversification rates, and only a few empirical studies have in fact detect this scenario. In addition to showing to be possible to detect diversity decline, our study reveals important caveats to interpreting the diversification signal such as detecting the rate variation scenario behind the diversity decline for instance. Nevertheless, we think the "jury is still out" on this matter.

Here, for the first time to our knowledge, we explicitly test the ability of BAMM (Rabosky, 2014) to detect negative diversification rates. Although our simulation results suggest that we might be able to answer the simple question "are we able to detect diversity decline or not", we also show that the inferred dynamics might be utterly wrong, and that the empirical pattern of drop in speciation previously thought to be prevalent might in fact result, at least in part, from model "misbehavior" by mistakenly attributing changes in extinction to changes in speciation. It is important to see our simulations results bearing in mind all assumptions and simplifications made in our study. We simulated simple scenarios without rate heterogeneity among lineages, which might be a reasonable assumption for small or medium size clades.

When we compare the performance on empirical trees, which by definition, do not need to follow the simple dynamics used in our simulations, we recover very different views of diversification dynamics, in particular the deep time dynamics. This reinforces our argument that we should question the ability of current methods to properly infer not only the past dynamics, but also if clades are or not in diversity decline. After all the two methods tested here would lead to very different estimates of diversity decline prevalence.

Irrespective of the true underlying diversification dynamics in empirical trees, the great discrepancy between the two methods (and to previous gamma statistics results) casts doubt on our ability to simultaneously infer past dynamics and current dynamics, especially for clades experiencing diversity decline. Furthermore, based on our results we reinforce that researchers should try to use external sources of information (e.g. fossil record when available) when trying to reconstruct diversification dynamics in deep time. This might be especially relevant when there is evidence for considerable variation in extinction rates. Nevertheless both methods indeed allow us to detect decline of diversity in the present. Therefore we suggest that simple auxiliary tests such as the gamma statistic may enhance our power to interpret the results of complex evolutionary models

for deeper time scales, in particular for clades with poor fossil record. Although we remain pessimistic about our ability to properly infer the diversification dynamics in deep time of clades experiencing or not diversity decline, we believe that our results might help map the scenarios where those models are more likely to be close to reality. Additionally, and perhaps more optimistically, we suggest that current phylogenetic methods might properly infer very recent dynamics.

# Chapter 3

# The Role of Diversification Rates on the Assembly of Frugivory Networks

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## 3.1 Abstract

Biological interactions are a key aspect determining how communities are organized. However, most studies with an evolutionary perspective focus on one or few pairs of species at a time. Although network theory provides tools to assess the dynamics of multiple species interacting with each other, those studies typically lack an evolutionary perspective. Here we investigated the relationship between evolutionary turnover rates (extinction fraction) and ecological roles of species within frugivore interaction networks (closeness and betweenness centralities). We hypothesize that more central species would belong to lineages with a slower pace of macroevolution, i.e., those that are more stable over evolutionary time and, therefore, are a more reliable resource for plants. We found a significant negative association between the ecological role a species play in frugivory network and the diversification dynamics associated to that species for temperate networks. This suggests that species belonging to evolutionary unreliable lineages are restricted to more peripheral roles in the ecological network . Additionally, we found that annual precipitation and precipitation seasonality modulate this relationship in the temperate region. In this case

an increase in precipitation and in precipitation seasonality, led to a stronger association between ecological role and diversification dynamics. No significant association between ecological role and evolutionary dynamics is recovered for tropical networks, suggesting that this evolutionary effect to be only relevant where the availability of potential dispersers is both phylogenetically and numerically more restricted. We propose that in tropical regions, where the richness of frugivorous bird species is a lot higher, the evolutionary reliability of specific disperses lineage is not relevant because there are plenty opportunities for plants from several different lineages, even if each individual disperser lineages is considered evolutionary unreliable. In temperate networks on the other hand, plant species depend strongly on the presence of a few disperser species and hence the evolutionary reliability of their lineages ends up playing an important role in network assembly. In summary, we recover an association between a local ecological structure and a long-term evolutionary effect, which suggests that evolutionary reliability might be relevant to understand current structure of ecological networks

## 3.2   Introduction

Since the publication of "On the origins of species" by Charles Darwin in the 19th century, biological interactions have been widely studied as one of the motors of diversification. Particular interest has been paid to competitive interactions (Schluter, 2000), and the well-studied Galapago's finches illustrate very well the importance of intra-specific and inter-specific competition on species and morphological diversification (Futuyma, 2009; Levin et al., 2009; Grant and Grant, 2011). In this case, different species in the genus Geospiza posses different beak morphologies and different lines of evidence suggest that these differences were selected in response to an evolutionary pressure imposed by the competition for different food resources (Soons et al., 2010; Grant and Grant, 2011). Additionally studies within populations of the same species suggest that competition for

food resources can also result in disruptive selection (Hendry et al., 2009; De León et al., 2012) and morphological differences, illustrating the first steps of the process of ecological speciation (Nosil, 2012; Thompson, 2013).

Similarly, predation and parasitism have also been implied as evolutionary forces playing an important role in diversification. For example, the escape-and-radiate coevolution hypothesis, originally proposed to describe the interaction between plants and herbivore insects, states that the evolution of defense against natural enemies result in the radiation of those plant lineages into several species (Ehrlich and Raven, 1964). This radiation then sets the stage for a subsequent radiation of insect lineages that subsequently evolve resistance to those defenses (Ehrlich and Raven, 1964). Therefore antagonistic interactions might in fact act as a diversification motor resulting in diversification of lineages and morphological evolution.

Even though competition, parasitism and predation have been shown to structure natural communities (Thébault and Fontaine, 2010, Lavergne et al., 2010) and act as evolutionary motors (Switzer et al., 2005; Futuyma and Agrawal, 2009; Hendry et al., 2009; De León et al., 2012; Nosil, 2012; Thompson, 2013) less attention has been paid to mutualistic interactions. Mutually beneficial interactions, like pollination or seed dispersal, are probably as frequent as antagonistic interactions and hence must also be a relevant evolutionary force. In fact the vast majority of species throughout the world are believed to be involved in at least one mutualistic relation (Levin et al., 2009). However this type of interaction has only recently been fully acknowledged as a fundamental force generating and maintaining current and past biodiversity patterns (Levin et al., 2009). According to Levin (2009) mutualisms can be seen as a biological market (see also Noë and Hammerstein, 1994) where each species offers some "product" that it is easy for it to produce in exchange for some other resource that cannot be easily produced by itself. Within this "market", relationships between species are created with varying degrees of dependence for each participant.

Mutualistic interactions between animals and plants represent important examples of such mutualistic relationships. For example, vertebrates (especially birds) represent very important fruit dispersers in tropical forests (Jordano, 1992). Its importance is highlighted by the fact that around 70-94% of tropical woody plant species are dispersed by vertebrates (Jordano, 1992), and by the fact that about 30% (> 3000) of all bird species have fruits at least as part of their diet and therefore may act as seed dispersers or predators (Kissling et al., 2009).

Due to observational and methodological limitations, (such as extensive fieldwork) most studies of species interactions focus on two, or at the very best, few species at a time. Therefore these studies only partially capture the relevance of species interaction given that species in the wild form multi-species interaction networks. More recently, ecological studies have in fact investigated large ecological networks (Bascompte et al., 2003; Guimarães et al., 2006; Krishna et al., 2008; Heil et al., 2009; Melián et al., 2009; Davis et al., 2009; Díaz-Castelazo et al., 2010; Guimarães Jr et al., 2011; Olesen et al., 2010; Spotswood et al., 2012; Nuismer et al., 2013) and have shown that these networks usually have non-random structures which reflects inherent properties of the communities such as degree of network modularity and nestedness.

From these networks it is thus possible to analyze the properties and the consequences of these interactions in a broad ecological scale. For example, many networks have ben shown to be highly modular networks, composed by subsets of species, which weakly interact with other subsets of the same network (Olesen et al., 2007). Others have shown to be highly nested indicating the existence of specialist species, which directly interacts with only a subset of species, which on its turn interact with more generalist ones (Bascompte et al., 2003). Unfortunately the vast majority of current studies consider the network as a static (under an evolutionary perspective) object, evaluating them solely in ecological time scales (Carnicer et al., 2009). It has become clear that we need more integrative studies of

ecology and evolution to properly understand several ecological patterns (Ricklefs, 2011; Ricklefs and Jenkins, 2011) and the study of species interaction and ecological networks should be no exception. A few fossil networks have been characterized (Roopnarine et al., 2007, Roopnarine, 2010; Dunne et al., 2008), but those are far from being able to fully integrate an historical perspective to properly understand what are the evolutionary forces that build ecological networks.

The fossil record and/or molecular phylogenies provide the needed historical information, but these two types of data have rarely been integrated into ecological network studies of extant taxa. Although molecular phylogenies do not directly store information of extinct species, the development of mathematical tools have allowed the estimate of speciation and extinction rates (Harvey et al., 1994, Stadler, 2009; Morlon et al., 2011; Condamine et al., 2013; Stadler, 2013a for a review of several tools). In fact, recently developed methods (Rabosky, 2014; Morlon et al., 2016) might even allow us to identify decline in diversity (extinction rates higher than speciation rates) using solely molecular phylogenies. The performance of these very recent methods have been recently tested and the results are encouraging (but see chapter 2). Lastly, related methods have been developed enabling us to map specific traits (e.g. different ecologies) on phylogenies and assess how those might affect the speciation and/or extinction rates of lineages (Paradis, 2005; FitzJohn et al., 2009; Pyron and Burbrink, 2012; Rabosky et al., 2013) as well as potentially reconstruct past ecologies (Pagel, 1999; FitzJohn, 2010; FitzJohn, 2012; Lartillot and Delsuc, 2012). For example; Price et al., 2012 have shown that dietary adaptations strongly affect diversification rates in mammals. These authors show that herbivores diversify faster than carnivores and omnivores, and also that the transitions between these three diet strategies happen at different paces, where the highest rate of change is from herbivory to omnivory. In the first chapter of this dissertation, we found that omnivorous bird species show smaller (even negative) net diversification rates when compared to other dietary guilds (Burin et al., 2016), and that species richness is maintained at high levels due to high transition rates into omnivory.

Therefore, we infer that omnivory acts as a "macroevolutionary sink".

Given that mutualisms with plants have shown to be very important on the diversification of vertebrates (Gómez and Verdú, 2012), that the diversity and strength of ecological interactions might change through time, and that those interactions shape ecological networks (Díaz-Castelazo et al., 2010), we should expect that the ecology of different species might affect the diversity dynamics of different lineages and that different diversity dynamics of different lineages might be a relevant historical aspect when ecological networks are assembled. Here we used both molecular and ecological data to investigate the role of diversification dynamics on structuring extant frugivore ecological networks. We hypothesized that species belong to a lineage with a lower pace of diversification (low extinction and low speciation rates) would be a more reliable resource for plants, and therefore would play central roles in the networks, whereas more peripheral species would no have such evolutionary restrictions. We also expect that the regional pool of species might influence and modulate this potential relationship between the species ecological roles and the background rates. In other words, it is possible that background rates have an "absolute" effect (e.g. only species belonging to lineages with a given value of rates play a given ecological role) or that the effect of background rates is relative to what is regionally available (e.g. species that play a central role are the ones with the lowest rates among those in the region).

## 3.3 Methods

### 3.3.1 General Approach

To investigate the potential effect of diversification rates on building current ecological networks we first characterized each frugivore species with respect to its potential ecological role in the network and then estimated the speciation and extinction rates related to each bird lineage using an almost complete

molecular phylogeny (see below). We then tested for a correlation between the network metric and the macroevolutionary rate (see figure 3.1 for a cartoon version of the general approach) using phylogenetic generalized least square tests (PGLS - Martins and Hansen, 1997). Phylogenetic correction was used because the network metrics showed significant phylogenetic signal.
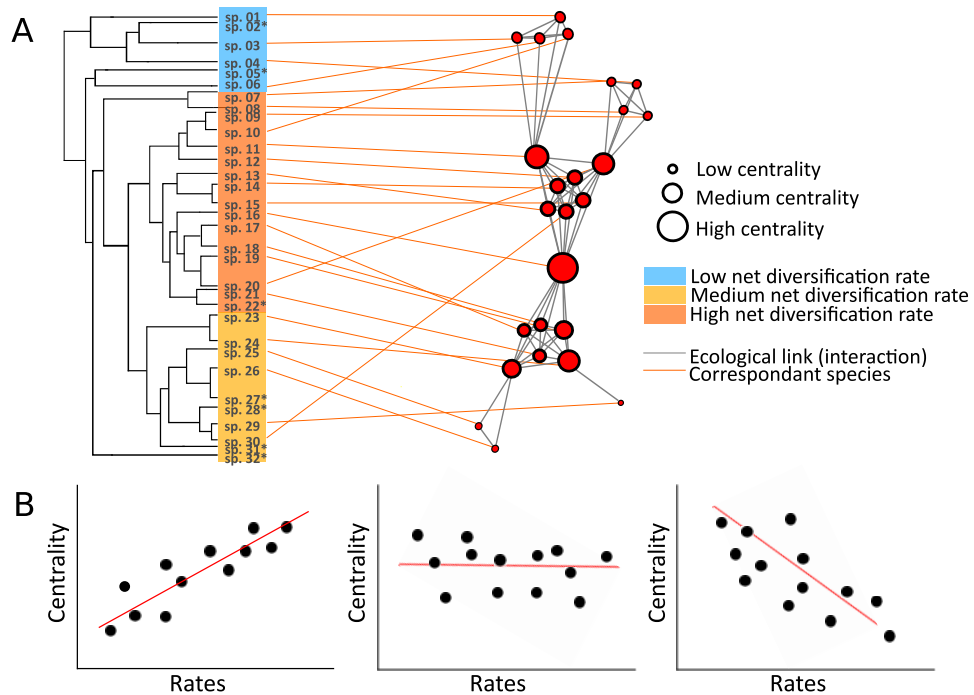


FIGURE 3.1: Schematic view of hypothetical phylogeny and network, showing the species correspondence between the two types of data. Species with an * are species for which no network data is available. B) Possible correlations between diversification rates (speciation and extinction) and centrality values.

Instead of speciation and extinction rates themselves, we used as our evolutionary metric called "epsilon" which is an extinction fraction. This is nothing more than the relative magnitude of extinction with respect to speciation rate. This rate is typically described as "turnover" rate and gives a sense of how labile a given lineage is. To our purposes, this better represents what we would call evolutionary reliability of a given lineage.

### 3.3.2   Diversification Rates

To estimate speciation and extinction rates we used the most recent and virtually complete bird phylogeny (Jetz et al., 2012). The phylogeny comprises the vast majority of bird species (9993 species in the phylogeny from an estimated total of 10,064 species – 99.3%) (http://www.birdlife.org/). To tavoid any potential bias that introduced by adding species withoud DNA sequences (using a birth-death algorithm) on our estimates of speciation and extinction rates (Rabosky and Goldberg, 2015), we used the tree that contains only species with molecular data was available. We analyzed the bird molecular phylogeny using a novel Bayesian framework (BAMM v. 2.5; Rabosky, 2014) to estimate the rates of speciation and extinction while explicitly taking into account the sampling fraction of species. The incompleteness (about 1/3 of species without DNA data) was accounted for by informing the percentage of missing species within each clade of the maximum clade credibility tree obtained by Jetz et al. (2012). Rabosky (2014) have developed an algorithm that finds subtrees within a phylogeny which share speciation and extinction rates through a bayesian framework using reversible-jump Markov Chain Monte Carlo sampling. This model allows us to identify groups with similar diversification dynamics. As output, this method detects sub-clades that share similar diversification dynamics and to a certain degree also the rates of speciation and extinction associated to each tip of the phylogeny.

Since BAMM is a method built within a Bayesian framework, each diversification shift configuration has an associated posterior probability, and each configuration can assign different diversification rates to a particular species or clade. Since we do not know which is the true configuration (and there is no practical need to know it), we will use the mean rates averaged by the marginal posterior probabilities of each distinct shift configuration. Lastly, we calculated our rate of interest (epsilon - extinction fraction) dividing the mean extinction rate by the mean speciation rate for each species. This rate is typically described

as "turnover" rate and gives a sense of how labile a given lineage is. To our purposes, this better represents what we would call evolutionary reliability of a given lineage.

### 3.3.3 Ecological Networks

To evaluate the ecological role of different species we used 34 different frugivory networks compiled by Pigot et al., 2016 that comprise both temperate and tropical areas and a total of 546 unique bird species (838 total unique interactions). Some networks were simple binary networks (11 networks) but others were quantitative networks (23 networks) that measured the strength of each interaction. To characterize each species ecological role within the compiled networks we investigated the different properties of nodes and edges (species and interactions, respectively). We calculated both closeness and betweenness centralities. Such measures will provide us with information related to the position each species takes part on the network as a whole (Blüthgen et al., 2008; Spotswood et al., 2012). To be able to combine the ecological roles estimated for different networks (that have different properties such as number of species, connectance, etc.) into a single analysis, we obtained z-scores (Olesen et al., 2007) for each species metric by network. This was done by first calculating the difference between the centrality of each species to the average centrality for the network it belongs, and then dividing this difference by the standard deviation of the centrality values for the respective network. Both centrality values were calculated with the quantitative networks (N = 23) and with binary networks (N = 34, which include the binarized quantitative network by assigning 1 to existing interactions regardless of the intensity).

Some species (N = 154) are present in more than one network. Using all centrality values for a given species in the same analysis could add undesired phylogenetic pseudo-replication to our analysis, and could possibly mask any important signal. Therefore, we generated 100 datasets where in each one we sampled one centrality value for species that were present in multiple networks. For each of these 100 datasets we proceeded with the
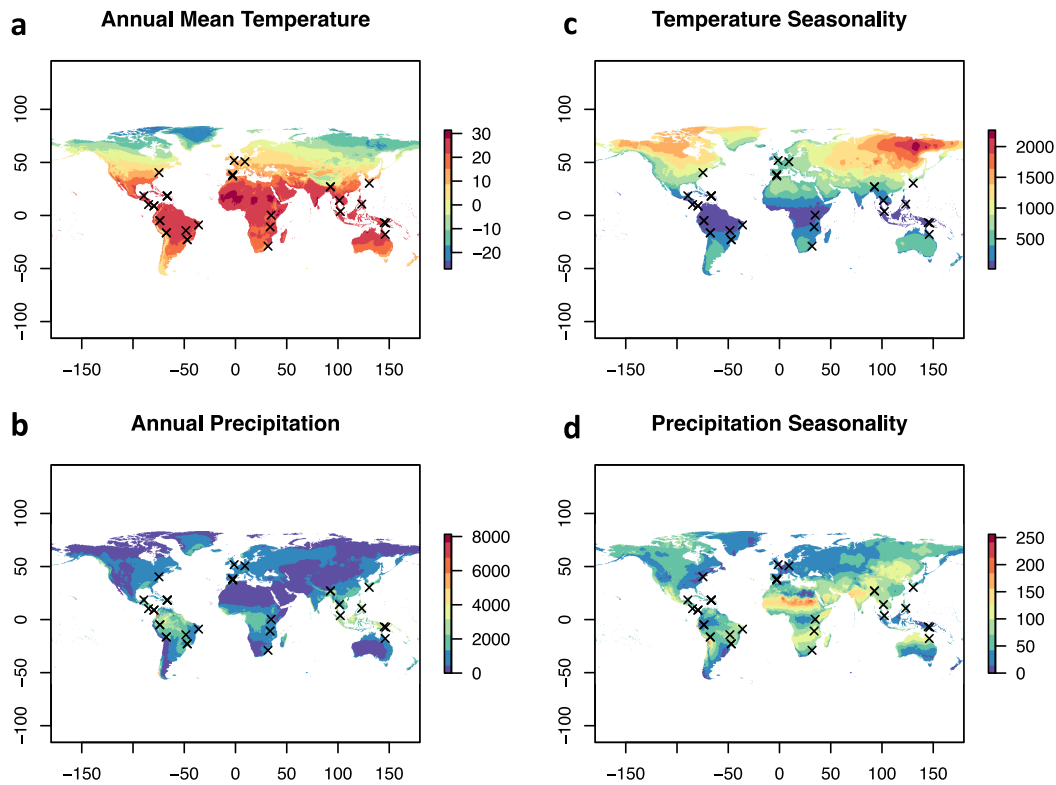
FIGURE 3.2: Global maps of the four environmental variables used. a) Annual Mean Temperature, b) Annual Precipitation, c) Temperature Seasonality, d) Precipitation Seasonality. The "x" indicate the location of the networks compiled by Pigot et al. 2016. Note that the location of some networks fall very closely to each other, and are difficult to visualize individually.

standard approach described above, and the results are shown using the mean parameter values and mean p-values (see table 3.1 in results).

### 3.3.4 Co-Factors

Because both the intensity and quality of ecological interactions are known to vary between latitudes, landscapes and even altitudes (Roslin et al., 2017) we analyzed tropical and temperate networks separately and used several climatic variables as co-factors. All models were tested using annual mean temperature, temperature seasonality, annual precipitation and precipitation seasonality as environmental co-factors (figure 3.2). The climatic data were obtained from the WorldClim database version 2.0 (Fick and Hijmans, 2017).

Furthermore each network was also characterized regarding their degree of modularity and nestedness. Modularity values, as well as the null distribution for modularity were obtained using the software MODULAR (Marquitti et al., 2014), and the nestedness values (NODF2) were calculated using the nested function in the R package bipartite (Dormann et al., 2009; R Core Team, 2016). The null models are essential for characterizing both modularity and nestedness because these two metrics are highly dependent on the number of species and the connectance of the networks. Therefore, we calculated the z-score of the two metrics by comparing the empirical values with the mean and standard deviation of random networks generated using the same number of species and connectance of each empirical network.

Both types of co-factors (environmental and network traits) and their respective interactions will be used to test our hypothesis, i.e. 6 models for each latitude (Temperate and Tropical) and for each metric (closeness and nestedness), totaling 24 models. These 24 different models will be tested using the centrality values calculated both from the binary network dataset and the quantitative dataset to assess how much information is lost when not taking into account the intensity of interactions. Lastly, we also calculated the z-score values for epsilon in the same way we did for the centrality metrics, and repeated the model testing using these transformed values instead of the raw rates. This allowed us to test if it is the absolute magnitude of the evolutionary rates that matter or if it is the relative rates among the regional pool of species. For each of the 6 types of model within each latitude zone (tropical vs temperate) and each metric, we used a significance threshold of 0.0083 as a corrected value for the multiple comparisons.

## 3.4 Results

### 3.4.1 Diversification Rates

Our most comprehensive database (34 binary networks) is consisted of 546 bird species, spread through out the bird phylogeny (figure 3.3). Those species belong to 61 families and 11 orders, with a predominance of passeriform species (407 species). From those 546 species, 78 does not have molecular data available and were therefore not in the molecular phylogeny. We did not include these species in the correlation tests, but they were used to calculate the z-score centrality (see next section). The best shift configuration from BAMM indicated 28 diversification regime shifts in the phylogeny (figure 3.4). We should note there is even more rate heterogeneity between species since we used the rates averaged across all shift configurations. In fact when we calculated the epsilon values for all the species used in the correlation analysis, we see quite a range of values (figure 3.5).

### 3.4.2 Network Metrics

There are substantial differences regarding the data and the metric we use to characterize the ecological roles of species within networks. Figure 3.7 shows both the closeness and betweenness centrality values for each species calculated when using the binary (x axes) and quantitative (y axes) network data (network size-corrected values on panels a and b, and z-scores on panels c and d). It is possible to note that the while closeness values are consonant within networks regardless of the dataset used, the association for betweenness values is much weaker (figure 3.7 panels a and b), due to the large number of zeros for betweenness centrality. This large amount of very small values are linked to the fact that almost all networks are not significantly modular (table C.1). This pattern is maintained also when we look the z-scores of the values, where the z-scores of closeness centrality seem to be more correlated within networks than do the z-scores of betweenness centrality (figure 3.7 panels c and
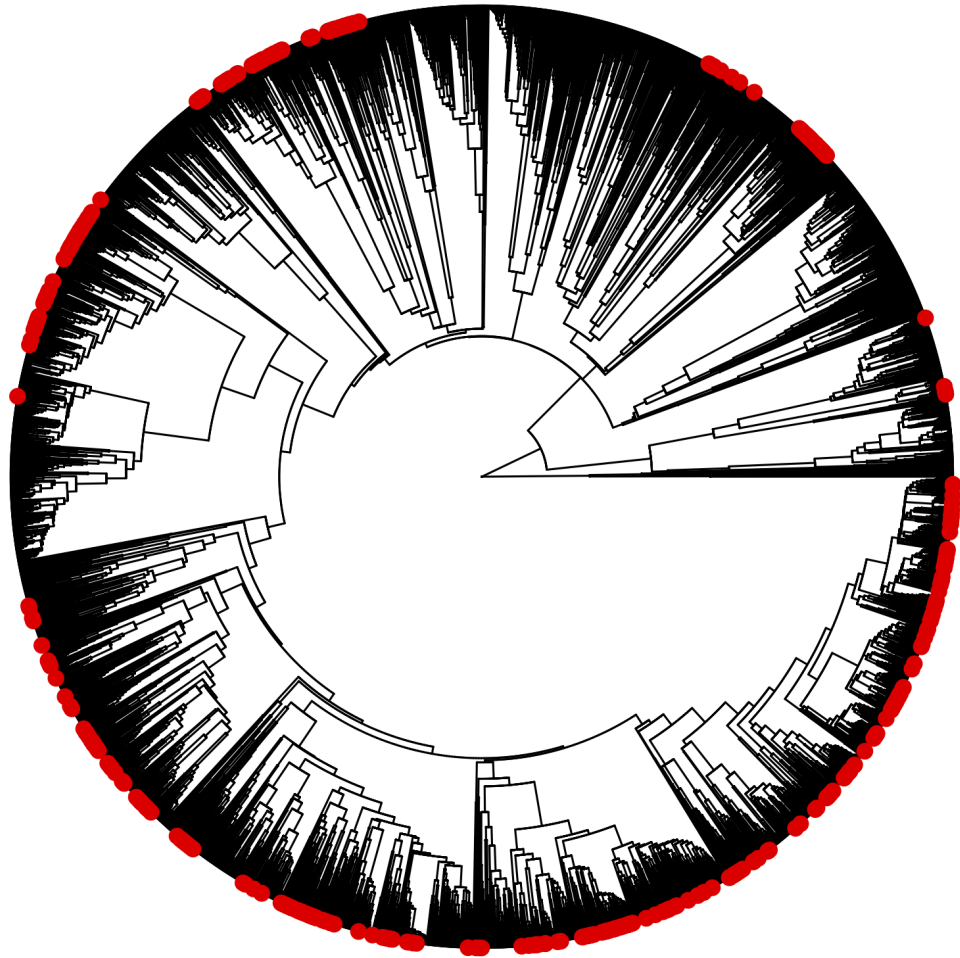
FIGURE 3.3: Distribution of species with network data in the molecular phylogeny of birds.

d). Information (number of species, number of interactions, location, etc.) about all networks, as well as estimates of nestedness and modularity are present in table C.1. Interestingly, closeness and betweeness are not associated in a linear fashion (figure 3.6), which suggests they potentially measure different ecological aspects.

None of the PGLS tests using betweenness centrality were significant after a posteriori corrections for multiple testing (figures 3.8-3.9). However, we found significant correlations between closeness centrality and extinction fraction associated with water availability parameters. For temperate networks
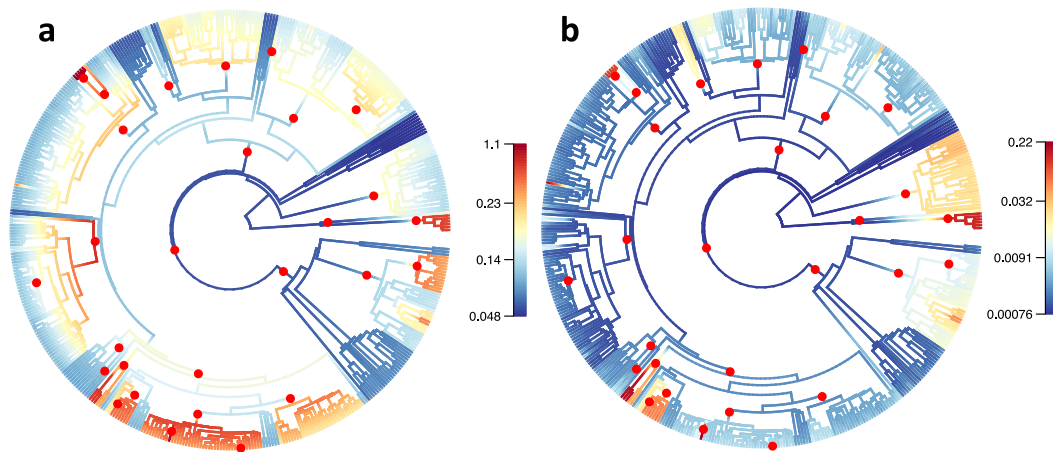
FIGURE 3.4: Diversification rate distribution (a: speciation, b: extinction) on the pruned phylogeny containing only the species that are present in the networks. The red circles indicate shifts in diversification regimes.

the strongest significant correlations between closeness centrality and extinction fraction where found when annual precipitation and precipitation seasonality were used as the co-factors, in both cases for the quantitative dataset. For annual precipitation all three parameters (extinction fraction, annual precipitation and the interaction between the two) were significant ($p < 0.003$), whereas for the precipitation seasonality, only the interaction parameter was significant ($p < 0.004$) (table 3.1; figure 3.9). For tropical networks, only the model that contained annual mean temperature as a co-factor for the binary dataset was recovered as significant (see table 3.1), and only the interaction parameter was below the significance threshold ($p < 0.006$).
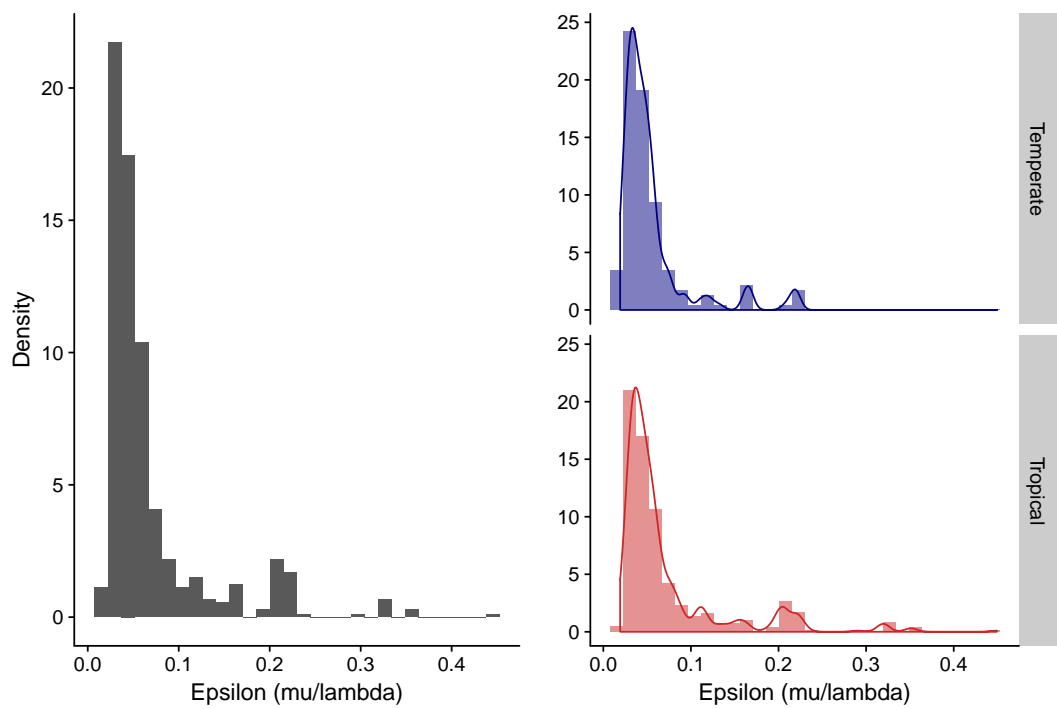
FIGURE 3.5: Histogram showing the variation of epsilon: bars in black represent all analyzed species combined, and the blue and red bars represent the rates for species present in temperate and tropical networks, respectively.
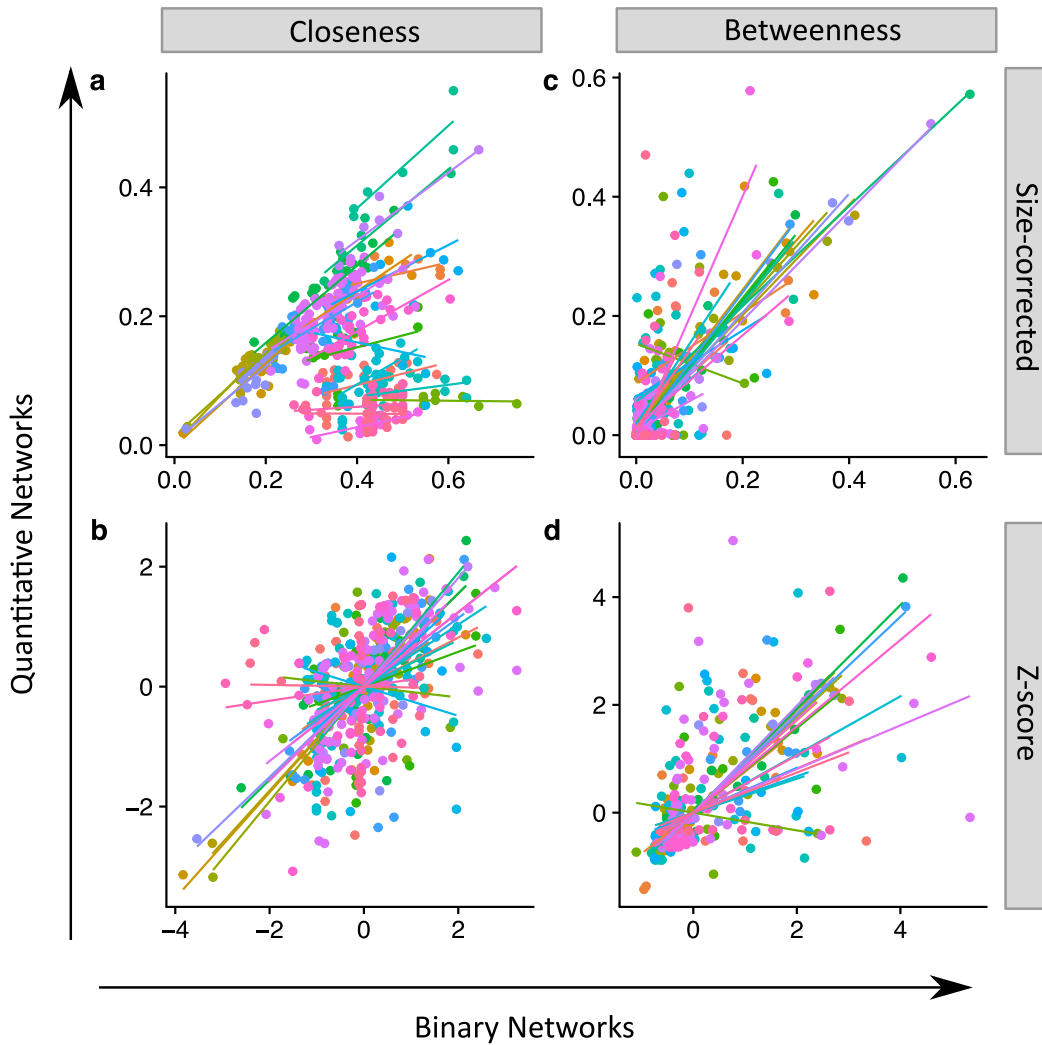
FIGURE 3.6: Betweenness versus closeness centrality z-score values for a) binary networks, and b) quantitative networks. Due to the large amount of zeroes for betweenness centrality (which drives the mean close to this value), we see a plateau around 0 in the y-axis for small closeness values.

TABLE 3.1: Results from phylogenetic generalized least squares tests (PGLS). Here we show only the models that were at least marginally significant (without a posteriori correction for multiple comparisons), whose names are indicated by the co-factor. All tests here follow the formula: $centrality \sim epsilon * cofactor$. *: marginally significant (p < 0.05, without correcting for multiple comparisons); **: significant (p < 0.0083). The most significant model (with all three parameters significant) is highlighted in bold.

| Model | Latitude | Network Type | Intercept | | Rate | | Climate | | Interaction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Parameter Mean | P-value Mean | Parameter Mean | P-value Mean | Parameter Mean | P-value Mean | Parameter Mean | P-value Mean |
| Annual Mean Temperature | Temperate | Quantitative | -0.704 | 0.687 | 46.340 | 0.024 | 0.077 | 0.439 | -3.784 | 0.010* |
| **Annual Precipitation** | **Temperate** | **Quantitative** | 1.217 | 0.373 | **-28.792** | **0.004**** | **-0.014** | **0.002**** | **0.335** | **0.0001**** |
| Modularity | Temperate | Quantitative | 0.671 | 0.670 | -14.608 | 0.184 | 0.167 | 0.462 | -8.240 | 0.035* |
| Nestedness | Temperate | Quantitative | -0.280 | 0.573 | 6.458 | 0.107 | 0.042 | 0.449 | -0.926 | 0.035* |
| Precipitation Seasonality | Temperate | Quantitative | -0.537 | 0.708 | 17.832 | 0.077 | 0.159 | 0.401 | -6.666 | 0.005** |
| Temperature Seasonality | Temperate | Quantitative | 0.635 | 0.680 | -43.909 | 0.046* | -0.001 | 0.584 | 0.069 | 0.029* |
| Temperature Seasonality | Tropical | Binary | -0.093 | 0.942 | 1.169 | 0.600 | 0.001 | 0.333 | -0.028 | 0.006** |
| Temperature Seasonality | Tropical | Quantitative | -0.200 | 0.885 | 4.346 | 0.105 | 0.002 | 0.217 | -0.039 | 0.046* |
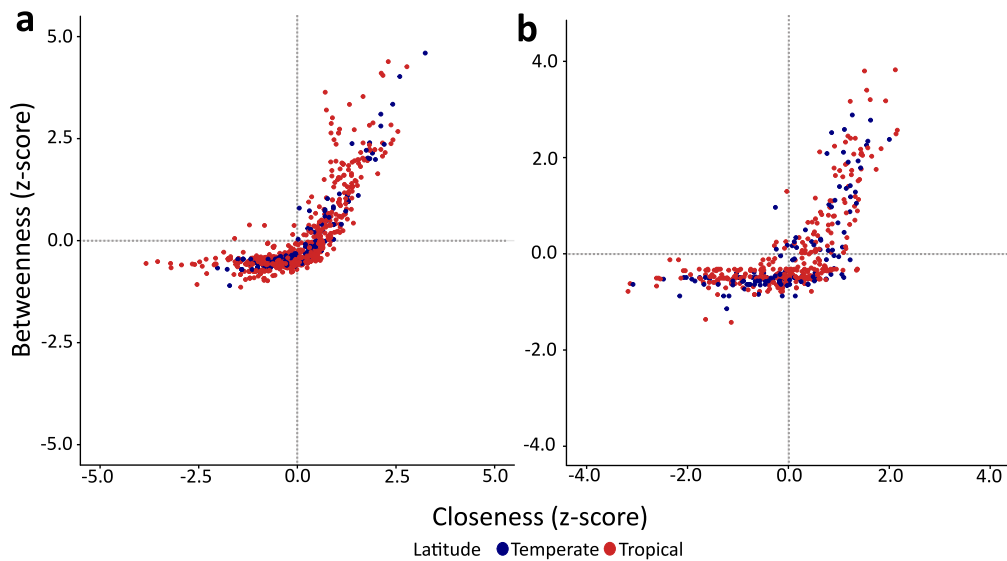
FIGURE 3.7: Comparison between centrality values for both size-corrected and z-score values calculated using both the binary (x axes) and quantitative (y axes) datasets. Panels a and b show closeness and panels c and d show betweeness. Colors in each graph denote a different network, and the lines indicate a linear trend for each network.

According to the most significant model, both extinction fraction and annual precipitation have a negative correlation with closeness centrality, and the interaction between epsilon and precipitation is positive (table 3.1). This means that the greater the annual precipitation for a given temperate network, the less negative is the relationship between extinction fraction and closeness centrality (figure 3.11). In the model with precipitation seasonality as the co-factor, the only significant relationship is the interaction between the co-factor and extinction fraction (in this case negative), which suggests that there is no significant relationship between epsilon and closeness centrality for places with low to average precipitation seasonality, and that the slope of this relation changes toward negative values as rainfall seasonality increases. The same can be said about the effect of temperature seasonality in tropical areas, meaning that the slope of the relationship between closeness and epsilon changes toward negative values as seasonality in temperature increases. We also note that all significant or nearly significant correlations, after multiple test correction, involved the raw values of epsilon,

FIGURE 3.8: Relationship between z-score values of betweenness centrality for binary networks and: a) raw extinction fraction (extinction/speciation), and b) z-score values of extinction fraction (deviations from mean rates divided by standard deviation of rates, both for each network). Temperate networks consistently show negative correlations, and tropical networks show positive correlations, although none of them are significant.

and that no correlation was found when using the z-score transformed epsilon (table 3.1). Lastly, we note that most significant or nearly significant correlations involved the temperate region (table 3.1).

It is worth noticing that out of the 24 performed tests using both data from binary and quantitative networks, only one test was significant using data from the binary networks (even when considering the tests that were significant without accounting for multiple comparisons), and still only the interaction parameter was significantly different from 0 (table 3.1). Additionally, even if we also consider the tests that were marginally significant (without accounting for multiple comparisons) in a conservative scenario, it is important noticing that all significant tests are related to closeness centrality (table 3.1). Additionally, similarly to Mello et al., 2015, we did not find a significant correlation between diet specialization and centrality (figures C.1-C.2).

FIGURE 3.9: Relationship between z-score values of betweenness centrality for quantitative networks and: a) raw extinction fraction (extinction/speciation), and b) z-score values of extinction fraction (deviations from mean rates divided by standard deviation of rates, both for each network). Temperate networks consistently show negative correlations, and tropical networks show positive correlations, although none of them are significant.

## 3.5 Discussion

The vast majority of fruits we see today are dispersed by birds (Jordano, 1992), and this association is widespread in different biomes throughout the planet (figure 3.2). In fact, bird and plant evolutionary histories have been linked through their ecological interactions for millions of years and have resulted in adaptations in both sides of this interaction (Snow, 1981). Our results indicate a potential influence of the evolutionary reliability on the assembly of ecological networks that dependents whether the network is found on tropical or temperate environment. We suggest that in temperate regions species that belong to evolutionary unreliable lineages typically do not play a central role (higher values of closeness) on frugivore networks. Conversely, species that belong to evolutionary reliable lineages might end up being either more central or peripheral within its ecological network. Such association is modulated by water availability, shown here by a significant interaction between epsilon and both annual precipitation and precipitation seasonality.
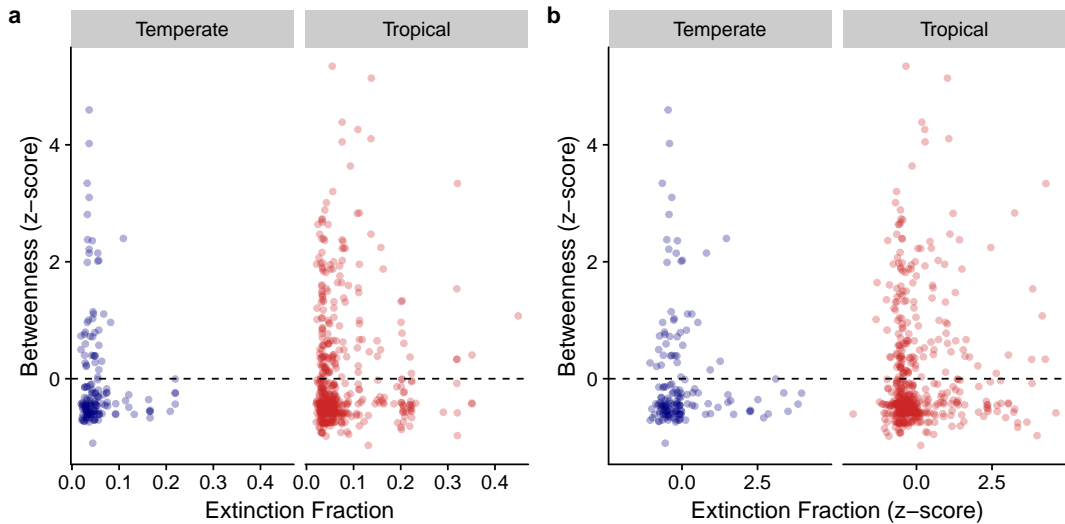
FIGURE 3.10: Relationship between z-score values of closeness centrality for binary networks and: a) raw extinction fraction (extinction/speciation), and b) z-score values of extinction fraction (deviations from mean rates divided by standard deviation of rates, both for each network). Temperate networks consistently show negative correlations, and tropical networks show positive correlations, although none of them are significant.

Water availability is known to help trigger different phenological phases of plants, and the effects of lack of enough water in the soil might last for years after a drought event (Bréda et al., 2006). Thus, low water availability might impose severe restrictions to fructification, and therefore change the tempo and duration of the fructification phase as well as the amount of fruits (Kissling et al., 2007; Waide et al., 1999; Field et al., 2005). So ultimately water regimes might strongly influence the timing of such interactions, the amount of resources for dispersers, and consequently the reliability of partners in the long run (Thompson and Willson, 1979. For temperate regions where water is not as abundant as in the tropics, we see evidence that places with lower the annual precipitation might prevent unreliable evolutionary partners to enroll a more central positions in ecological networks. This is supported by the most significant model (table 3.1), in which both epsilon and annual precipitation have negative correlation to centrality, and the interaction between the rate and the climate shows that high annual precipitation acts on erasing this negative association. Similarly, the significant
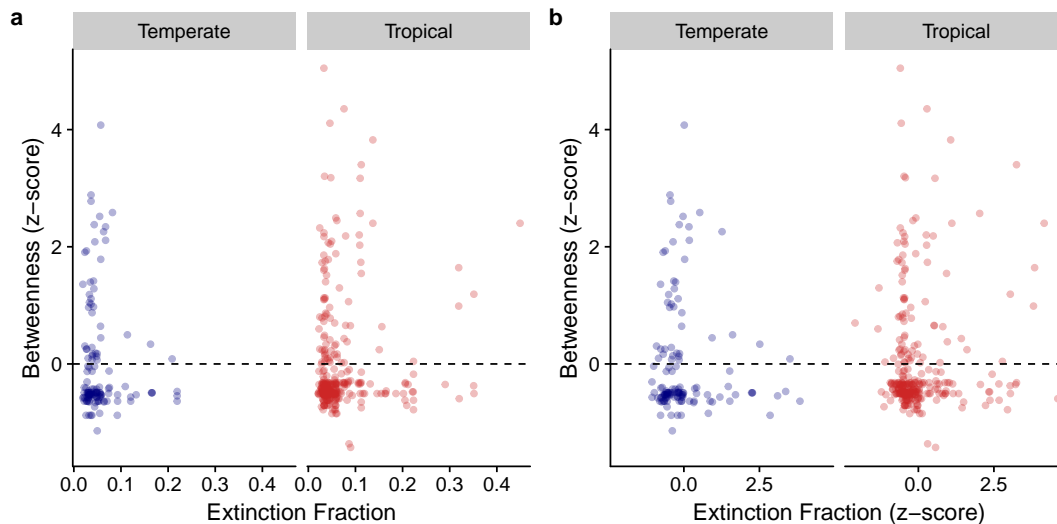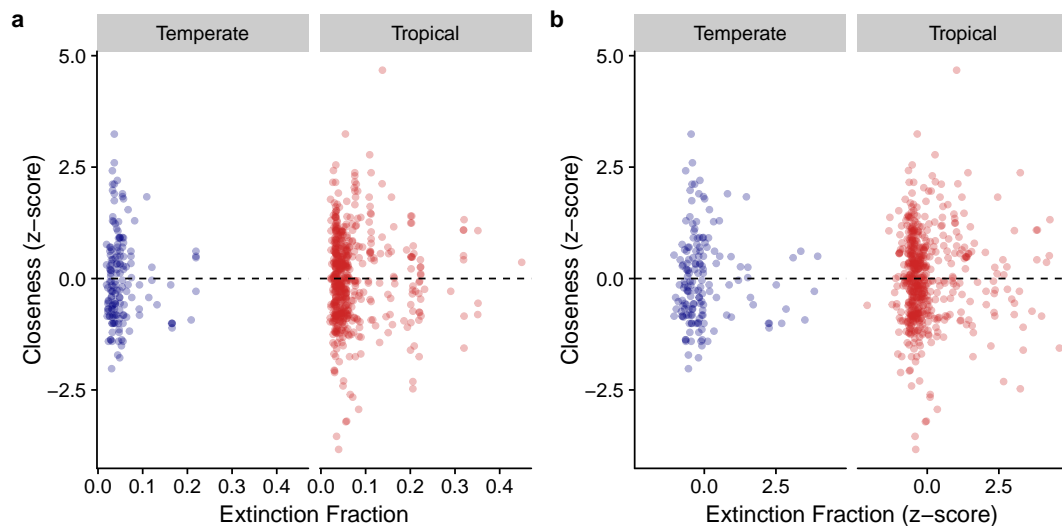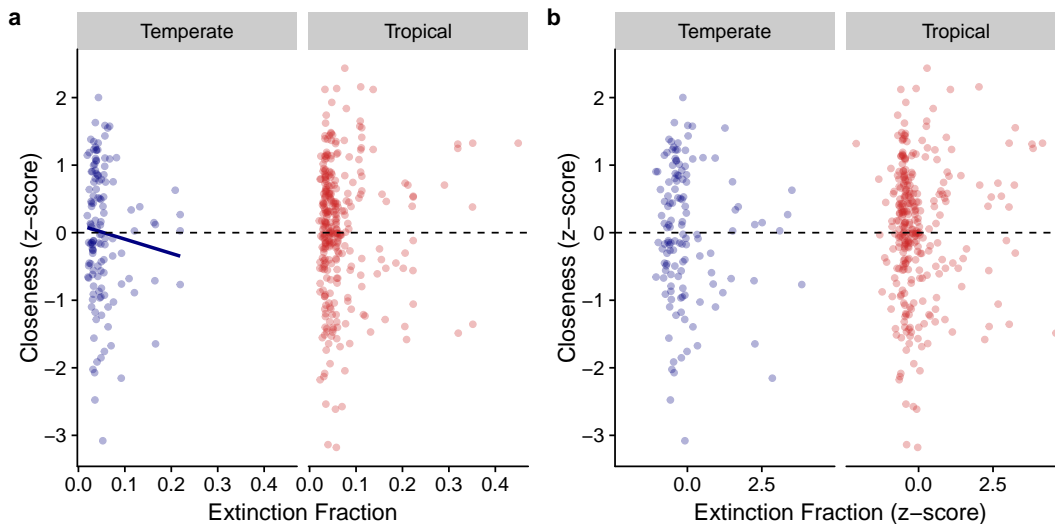
FIGURE 3.11: Relationship between z-score values of closeness centrality for quantitative networks and: a) raw extinction fraction (extinction/speciation), and b) z-score values of extinction fraction (deviations from mean rates divided by standard deviation of rates, both for each network). Temperate networks consistently show negative correlations, and tropical networks show positive correlations, although none of them are significant.

interaction between epsilon and precipitation seasonality reinforces the idea that water availability modulates the relationship between epsilon and closeness. In this case, the higher the seasonality the less likely it is for evolutionary unreliable species to assume more central roles in the network (table 3.1). Under this water availability hypothesis we expect fructification to be different among different places with different water regimes, leading to perhaps shorter fructification periods and/ore less fruits in places with less and more seasonal water regimes. This would affect the assembly of frugivores and the establishment of such interactions, which could also leave spatial pattern of such association between water regimes and dispersers availability.

In fact; Kissling et al., 2012a found that net primary productivity (estimated using actual evapotranspiration) and precipitation are positively correlated with frugivore bird species richness for different biomes, whereas climate seasonality has a negative relation with richness. Thus, as temperate climates tend to show lower precipitation and higher seasonality than tropical climates (Hurlbert and Haskell, 2002; Currie et al., 2004),

temperate biomes have lower frugivore species richness than tropical ones (Kissling et al., 2012a). The opposite effects of annual precipitation and precipitation seasonality on the correlation between centrality and extinction fraction indicate that the more similar the climate of a temperate region is to a "stereotypical" tropical climate, the less significant the association between ecological role and evolutionary dynamics (positive interaction coefficient associated to negative individual parameters - table 3.1). In fact, it is important to highlight that most correlations for tropical regions are not significant, with the exception of the interaction between epsilon and temperature seasonality (table 3.1).

This potential influence of resource availability on modulating the role of evolutionary rates on network assemblage is also reflected in our results describing how temperature seasonality modulates the relationship between closeness and epsilon in the tropics. Low climatic seasonality (especially in temperature) is typically associated with tropical climates (Hurlbert and Haskell, 2002; Currie et al., 2004), hence the significant negative interaction between epsilon (extinction fraction) and temperature seasonality in tropical regions suggests that the higher the seasonality the more negative the association between closeness and epsilon. In other words, the more similar the climate of tropical networks gets to an archetypical temperate locality, in terms of temperature seasonality, the more likely we see the relationship recovered for temperate networks.

It is curious to note that evolutionary reliability is only relevant on assembling networks in the temperate zone and not in the tropics. We suspect this is due to a higher diversity of frugivorous bird in the tropics (Kissling et al., 2012a) and the fact that frugivore birds in the tropics are, on average, more specialized in fruits than birds that eat fruits in the temperate zone (Wheelwright, 1988). When looking at our own data, we in fact capture a higher degree of frugivory in tropical species (figure C.2), which suggests that the frugivore networks studied here are in fact very different in nature, and their assembly should reflect differences not only in environment but evolutionary history

(which determines diversity) between the tropics and the temperate zone.

We argue that a bigger and phylogenetically more diverse pool of frugivore species in the tropics would permit species belonging to evolutionary unreliable lineages to engage into more central roles in tropical ecological networks. In this case if a species goes extinct and no other species within the same lineage is present, this role could be taken (or is already also done) by a species in a different lineage. We could refer to this pattern to some sort of "evolutionary benefit of the commons", where ecological redundancy among several unrelated lineages overcomes the evolutionary unreliability of a single lineage. In the temperate zone on the other hand, the pool of disperser species is a lot smaller, and potentially phylogenetically more restricted. Hence species belonging to lineages that are evolutionarily less reliable do not establish a more central role. This somehow evokes a mechanism of species sorting. Our data indeed suggests that the tropics have a more phylogenetically diverse pool of frugivores, comprising 43 bird families from eight Orders, while the temperate networks contains species from only 16 families from three orders.

Here we envision species sorting acting as a filtering process, which would result on a network being structured around more reliable lineages, and rendering species that belong to evolutionary unreliable lineages to end up in the periphery of the network. Individual selection could cement the interaction among reliable species and reinforce the empirical association we described here between evolutionary reliability and ecological role. It is worth noting that temperate species are not strongly frugivorous, that fruits are not available all the time, and that the more central temperate species are not necessarily the most frugivore species in the temperate zone networks (figure C.2). We argue that this reinforces the idea that reliability and not host-plant specificity is indeed an important aspect to the assembly of temperate networks. Irrespective of the nature of selection (individual or higher level) we do recover an association between a local ecological structure and a long-term evolutionary effect,

which suggests that evolutionary reliability might be relevant to understand current structure of ecological networks.

Other interesting aspects are worth mentioning. First the strongest correlations between evolutionary aspects and ecological aspects for temperate regions are those using a quantitative dataset and not binary one. The discrepancy between the quantitative and qualitative ecological datasets highlight that the frequency of interactions, used as a proxy for interaction strength, not only changes the way we describe the role a species play within a network (figure 3.4), but also affect our ability to understand the potential mechanisms responsible for building those ecological roles. The idea that different datasets might lead to different ecological interpretations of species is also evident on the absence of correlation between the binary and quantitative measures of betweenness (figures 3.6-3.8). One should note that quantitative measures of ecological interactions are not free of problems, and that those might be especially sensitive to interaction sampling in the field.

Another aspect of our results worth mentioning is the fact that most significant interaction between evolutionary reliability (epsilon) and a centrality measure happened with closeness and not with betweenness. A closer look at the centrality measure their definition and ecological meaning of those metrics might help understand this. The closeness centrality represents the sum of the shortest distances (here measured by the number – and weights in the quantitative dataset - of links connecting species) between a given focal node (here species) to all other nodes (here species) in the same network (Bavelas, 1950; Sabidussi, 1966; Mello et al., 2015). Therefore a bird species with higher closeness centrality is typically directly linked to more plant species and indirectly to more dispersers, than one with lower closeness value. Hence high centrality species that are evolutionary reliable typically guarantee a partner for many plant species and, perhaps help hold the whole network together, as expected by our hypothesis. A species with high betweenness centrality connects different parts (such as modules)

of a network (Mello et al., 2015), and hence would have the potential to hold a similarly important ecological role. We should note though, that almost all of our networks did not show significant modularity (table C.1). Hence it might not be surprising that, for the collection of trees we analyze, the betweenness centrality does not depict important variation in species' ecological role. In fact, many species show betweenness values that are zero, and we only see an association between closeness and centrality for values of betweenness that are considerably higher than zero (figure 3.7). A future avenue would be to estimate the ecological role of species using other metrics (degree, eigenvalue, katz, page-rank, etc.) and representing a more "global" role using orthogonal projections of all metrics with principal component analysis (PCA) (Sazima et al., 2010).

Lastly, the lack of significant correlations between centrality and the z-score values of diversification rates is also noteworthy (table 3.1). By using the raw and z-score values for epsilon, we are in fact testing whether there is a general mechanism underlying the assembly of the networks (the absolute diversification dynamics matters) or if the species sorting process is more related to the available pool of species. In the second case to play central roles within a network a species would preferentially come from lineages that have the slower pace in relation to the other species present in the area. Our results indicate that the mechanism that sorts species seems more general. We note that this is somewhat a weak statement given that most of our correlations are somewhat weak and that many co-factors are not significant.

We should also say that our correlations strongly depend on our ability to estimate evolutionary rates. There is an ongoing debate about whether it is possible or not to estimate extinction rates from molecular phylogenies (Rabosky, 2010; Beaulieu and O'Meara, 2015, Rabosky, 2016). Nevertheless, our results from chapter 2 indicate that both speciation and extinction rates (and consequently net diversification rates) can be well estimated, even in a scenario of decline of diversity. We also note that if the rates are well estimated relative to each other (which is less demanding than asking for the absolute true values), then the

general pattern and interpretations described here should be the same.

We acknowledge that we tested simple climatic variables and that future improvements may come from generating better, more complex models, as well as from new attempts to characterize the ecological role of frugivorous species by using multidimensional centrality components. Nevertheless, we believe the results presented here represent an important advance linking ecological and evolutionary dynamics of bird-plant interactions. We showed that that stricter, more seasonal climatic conditions restrict species belonging to evolutionarily unreliable lineages, to occupy central roles in frugivory networks. Additionally, our results showed that this evolutionary effect is absent in tropical networks possibly because the tropics have a richer and phylogenetic more diverse pool of disperser species, generating an "evolutionary benefit of the commons" which might overcome any negative effect that evolutionary reliability of specific lineages might impose on network assembly.

# Conclusions

In each of the three chapters of this dissertation, we addressed different aspects of important macroevolutionary questions. Our results provided new information about the roles of diet on the diversification of birds (chapter 1), as well as preliminary insights on the processes behind the assembly of frugivory networks (chapter 3). Additionally, we were able to extensively test methods that are widely used to estimate speciation and extinction in a scenario commonly overlooked by neontologists (chapter 2).

The results from the first chapter suggest that omnivory is associated with higher extinction rates and lower speciation rates than other guilds, and that overall net diversification is likely to be negative. Trait-dependent models, dietary similarity and network analyses also showed that transitions into omnivory occur at higher rates than into any other guild. Based in all these results, we suggest that omnivory acts as macroevolutionary sink where its ephemeral nature is retrieved through transitions from other guilds rather than from omnivore speciation. We propose that these dynamics result from competition within and among dietary guilds, influenced by the deep-time availability and predictability of food resources.

In the second chapter, we show that both methods perform equally well in the varying speciation scenario, and were able to properly reconstruct the diversification dynamics for the whole history of clade. We also showed that for the varying extinction scenario, that rates at the present are reasonably well estimated, but both methods wrongly assign the variation in net diversification to a change in speciation instead of the simulated change in extinction rate. Diversification estimates for empirical trees revealed differences in the ability of those two methods in identifying a declining in diversity: increasing extinction

was identified in 67 and 13 out of 214 trees for RPANDA and BAMM, respectively and decreasing speciation rate was identified in 48 and 160 out of 214 trees for RPANDA and BAMM, respectively. We suggest that under a simple diversification scenario both methods might be able to estimate negative diversification rates at present, but could fail to infer how rates change at deep time and might need additional information in empirical analyses. This behavior of assigning the variation on net diversification rate to speciation when extinction varies challenge not only the idea that slow-downs in speciation are a common macroevolutionary phenomenon but also our hope for molecular phylogenies to properly estimate deep-time diversification dynamics when it is driven by changes in extinction rate.

Lastly, in the third chapter we found a significant association between the ecological role a species play in frugivory network and the diversification dynamics associated to that species belongs in temperate networks, but not in tropical networks. Additionally, we found that climatic variables (namely annual precipitation and precipitation seasonality) modulate this relationship in the temperate regions. In this case an increase in precipitation and in seasonality, led to a stronger association between ecological role and diversification dynamics. We propose that in tropical regions, where the richness of frugivorous bird species is a lot higher, the evolutionary reliability of specific disperses lineage is not relevant for plant species because there would be plenty opportunities from several different lineages, even if each lineages is considered evolutionary unreliable. In temperate networks on the other hand, plant species depend strongly on the presence of a few disperser species and hence the evolutionary reliability of their lineages ends up playing an important role in network assembly. In the temperate zone species belonging to evolutionary unreliable lineages are restricted to more peripheral roles in the ecological network.

We believe the results and discussions present on this dissertation can help us better understand the roles of speciation and extinction in shaping current biodiversity. Moreover, the results

also highlight some future avenues for new studies, such as investigating the role of dietary specialization on diversification, testing for complex effects of climate and dietary specialization in the assembly of interaction networks, as well as detecting limitations of current phylogenetic methods that may foster further method development.

# Appendix A

# Supplementary Material - Chapter 1

## A.1 Supplementary Figures
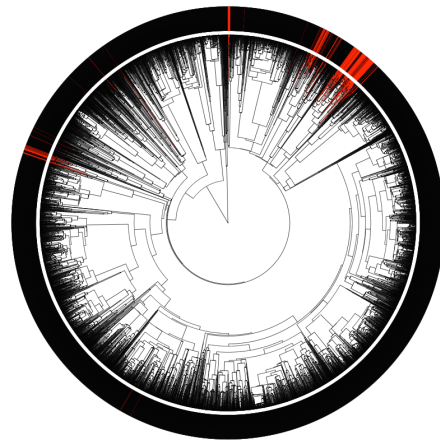
FIGURE A.1: Distribution of carnivore species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.
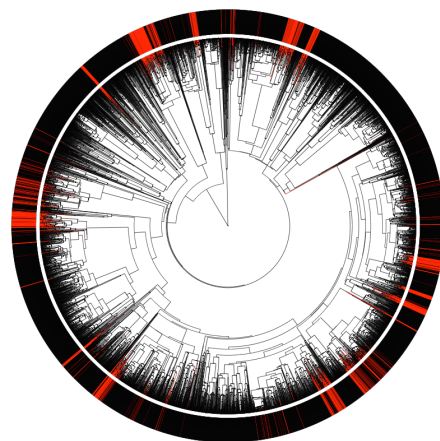


FIGURE A.2: Distribution of frugivore species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.

FIGURE A.3: Distribution of granivore species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.



FIGURE A.4: Distribution of herbivore species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.
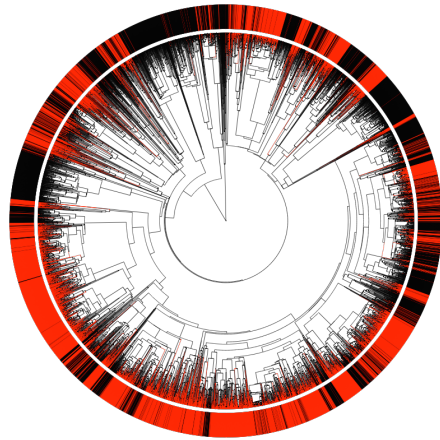
FIGURE A.5: Distribution of insectivore species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.
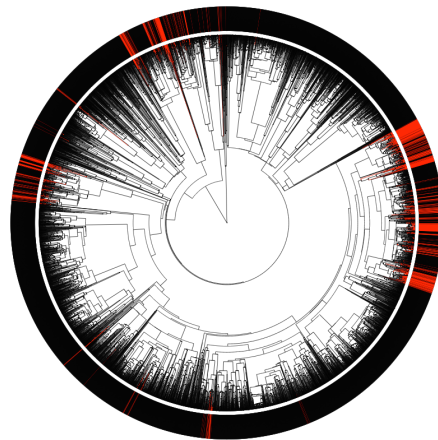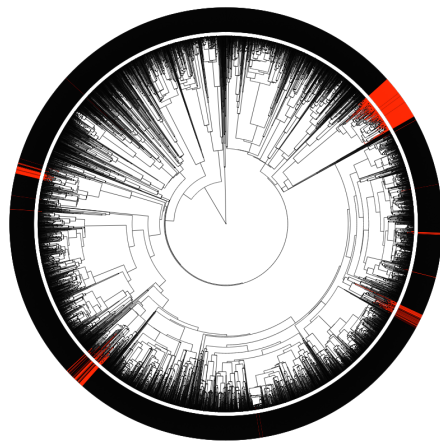


FIGURE A.6: Distribution of nectarivore species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.
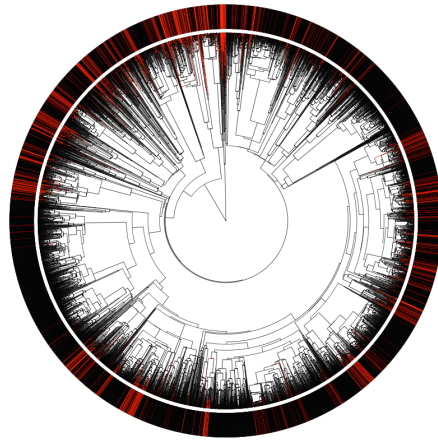
FIGURE A.7: Distribution of omnivore species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.
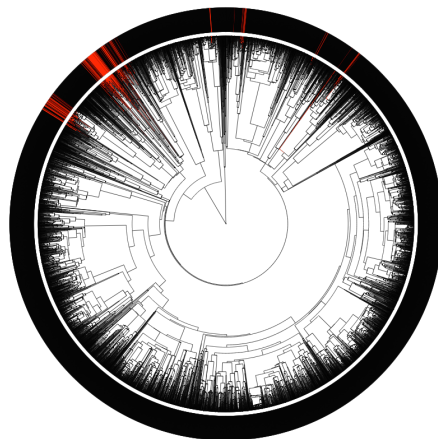


FIGURE A.8: Distribution of piscivore species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.
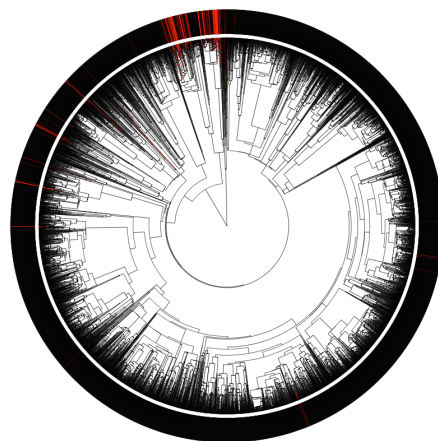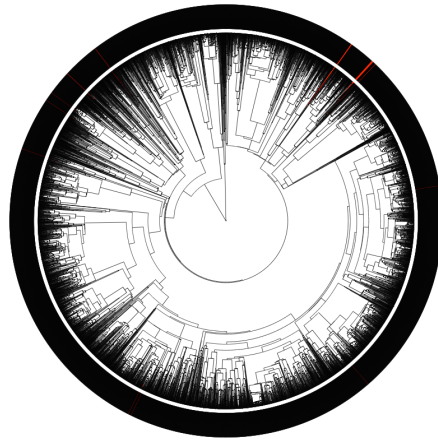
FIGURE A.9: Distribution of scavenger species within the Jetz et al. phylogeny. The phylogeny presented here was randomly sampled from the 10000 trees from the collection using the Ericson backbone.
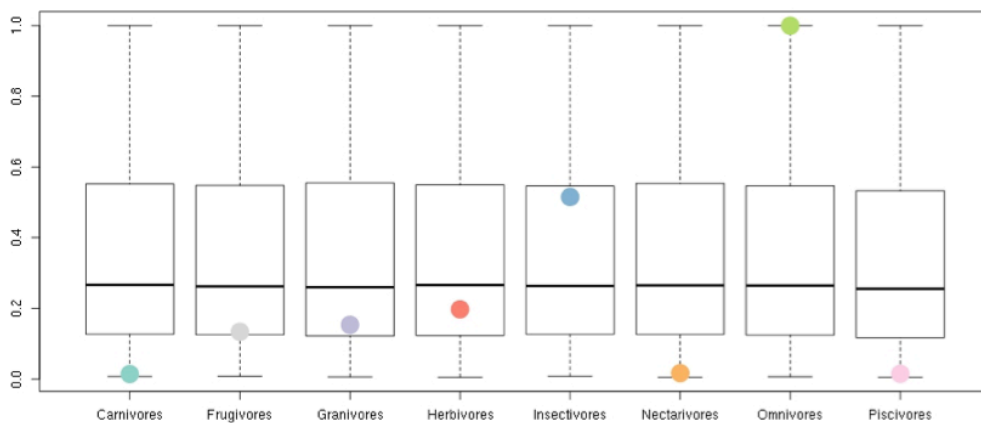


FIGURE A.10: Boxplots of null distributions of centrality values for each node in the transition network. The dots represent the calculated values for the data. Horizontal lines represent mean values, whereas the intervals indicated by dashed lines and ticks represent 1.5 times the interquartile range from the first (lower limit) and third (upper limit) quartiles.
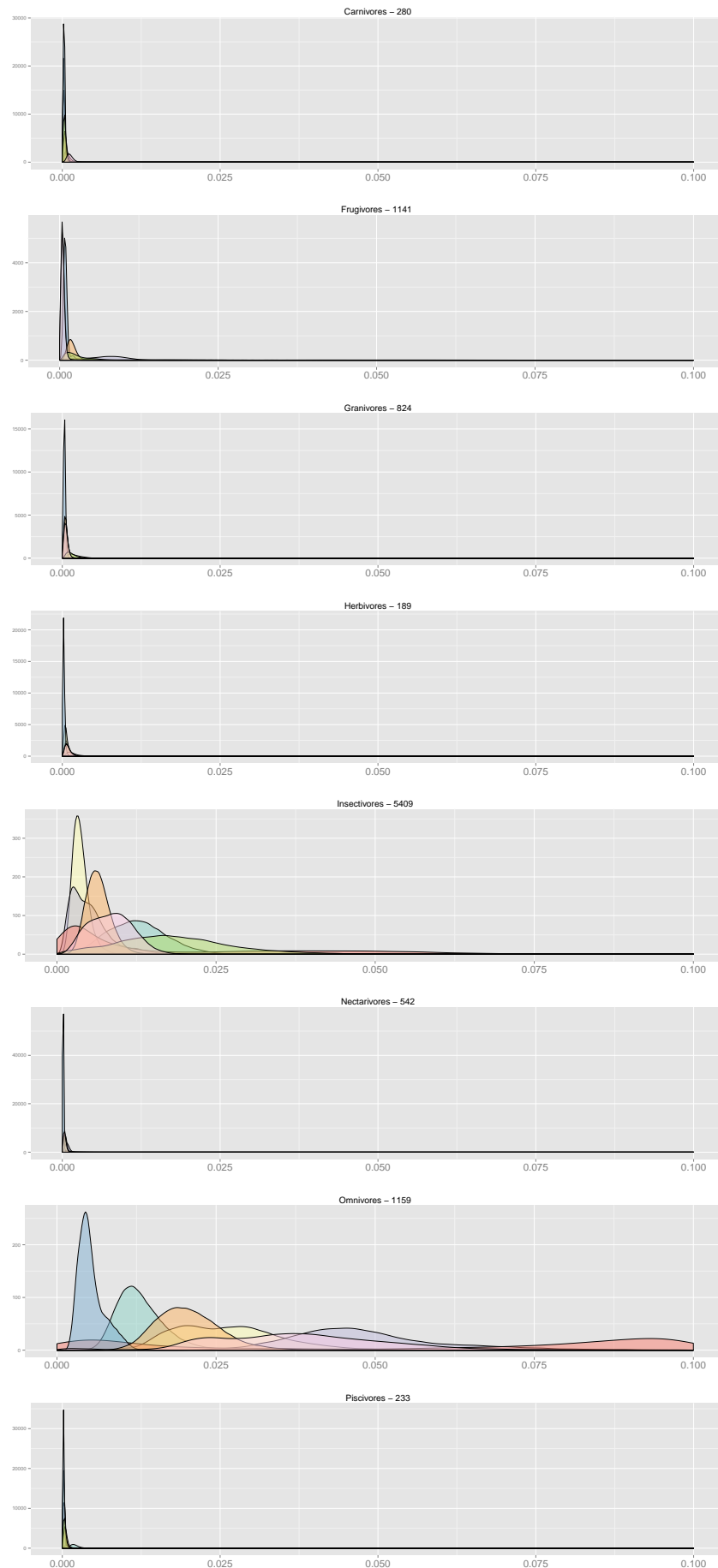
FIGURE A.11: Posterior distributions of transition rates into each one of the diets coming from all other guilds. X-axis is truncated for better visualization.
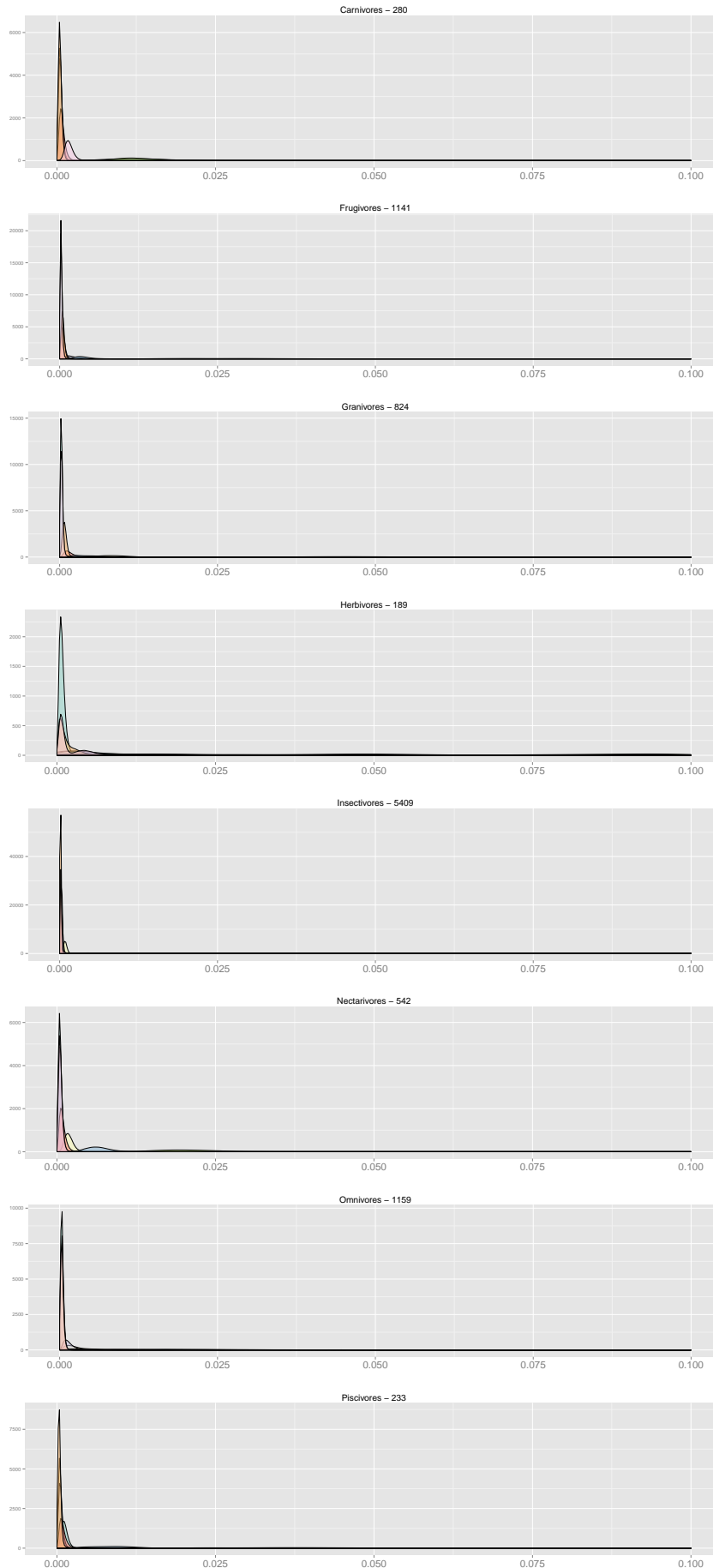
FIGURE A.12: Posterior distributions of transition rates from each one of the diets going into all other guilds. X-axis is truncated for better visualization.
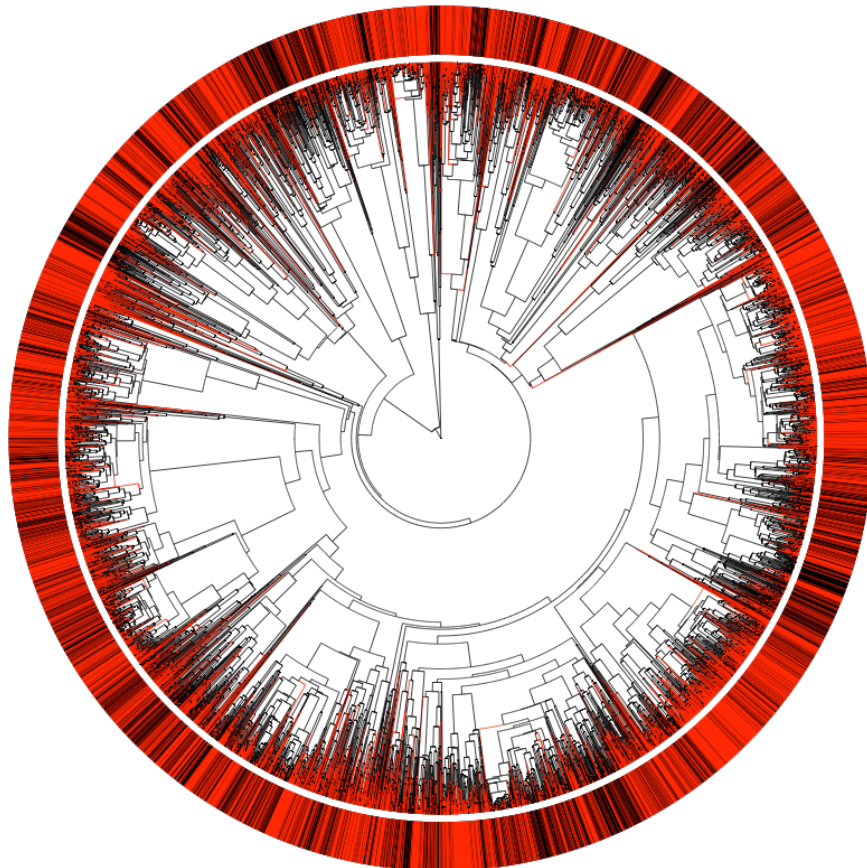
FIGURE A.13: Distribution of species without molecular data (3323 species, in black) and with molecular data (6670 species, red). The species without molecular data were inserted into the molecular phylogeny through a Yule process.
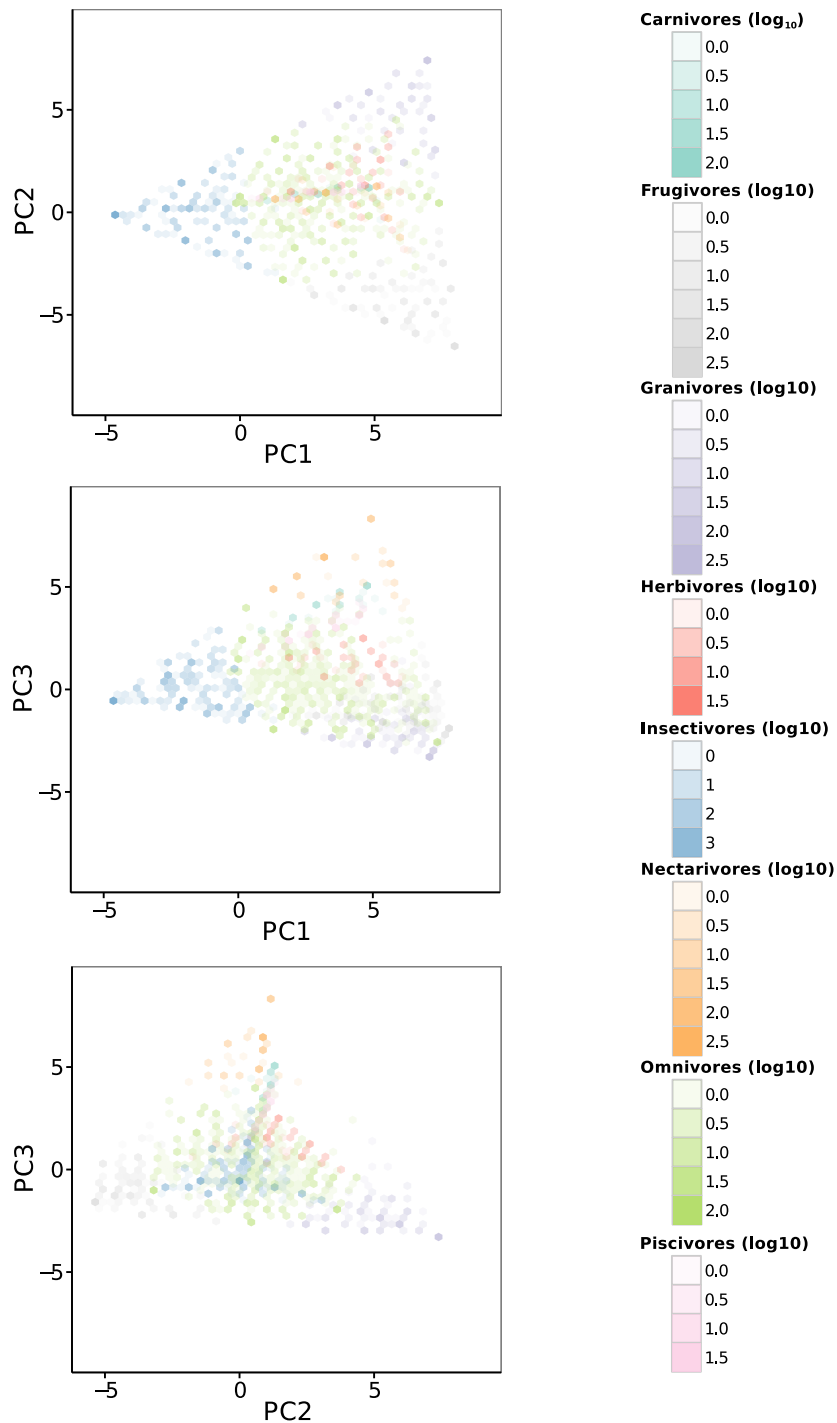
FIGURE A.14: First 3 principal components of PCA using the scores of each food item for omnivore species as variables plotted against one another. It is possible to see that herbivores and piscivores are similar to omnivores in all combinations, potentially reflecting the high transition rates from these two guilds into omnivores. Also possible to see that omnivory overlaps with more than 2 guilds in all axes.
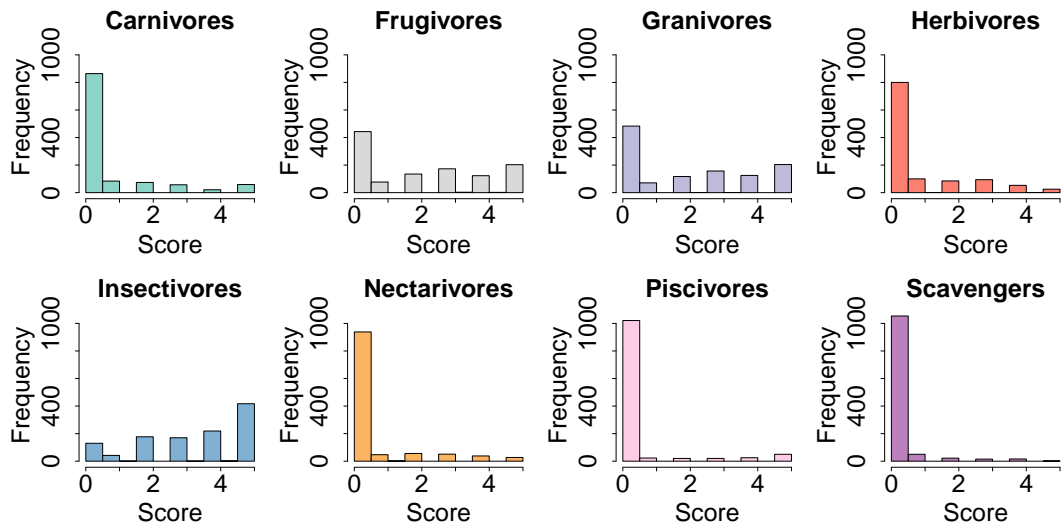
FIGURE A.15: Dietary composition of omnivorous birds (n = 1158 species). Frequency distribution of scores for each food item in the diet of all.
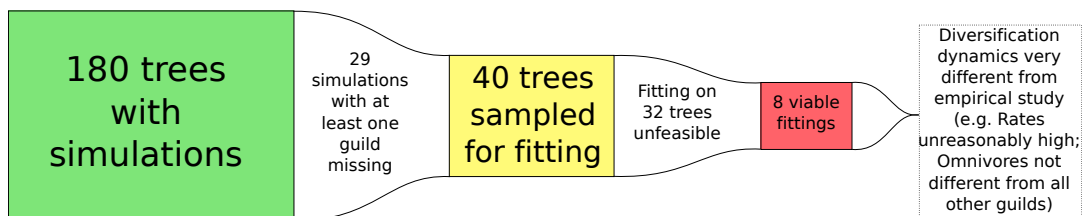


FIGURE A.16: Flowchart indicating the simulation protocol. Simulated scenarios where rates of diversification were not associated with trait states were unable to produce simulations that were similar to empirical data. Even with the 8 viable simulations for fitting, we could not observe any similarity between those fittings and the empirical results (posterior distributions do not show omnivores [or any other guild] as having negative net diversification rates, nor they show one guild with clearly distinct rates). The lack of viable simulations and differences in rate estimates and trait state distributions indicate that without an associated speciation and extinction dynamics the transition rates alone together with the empirical tree topologies cannot recover the observed empirical patterns.
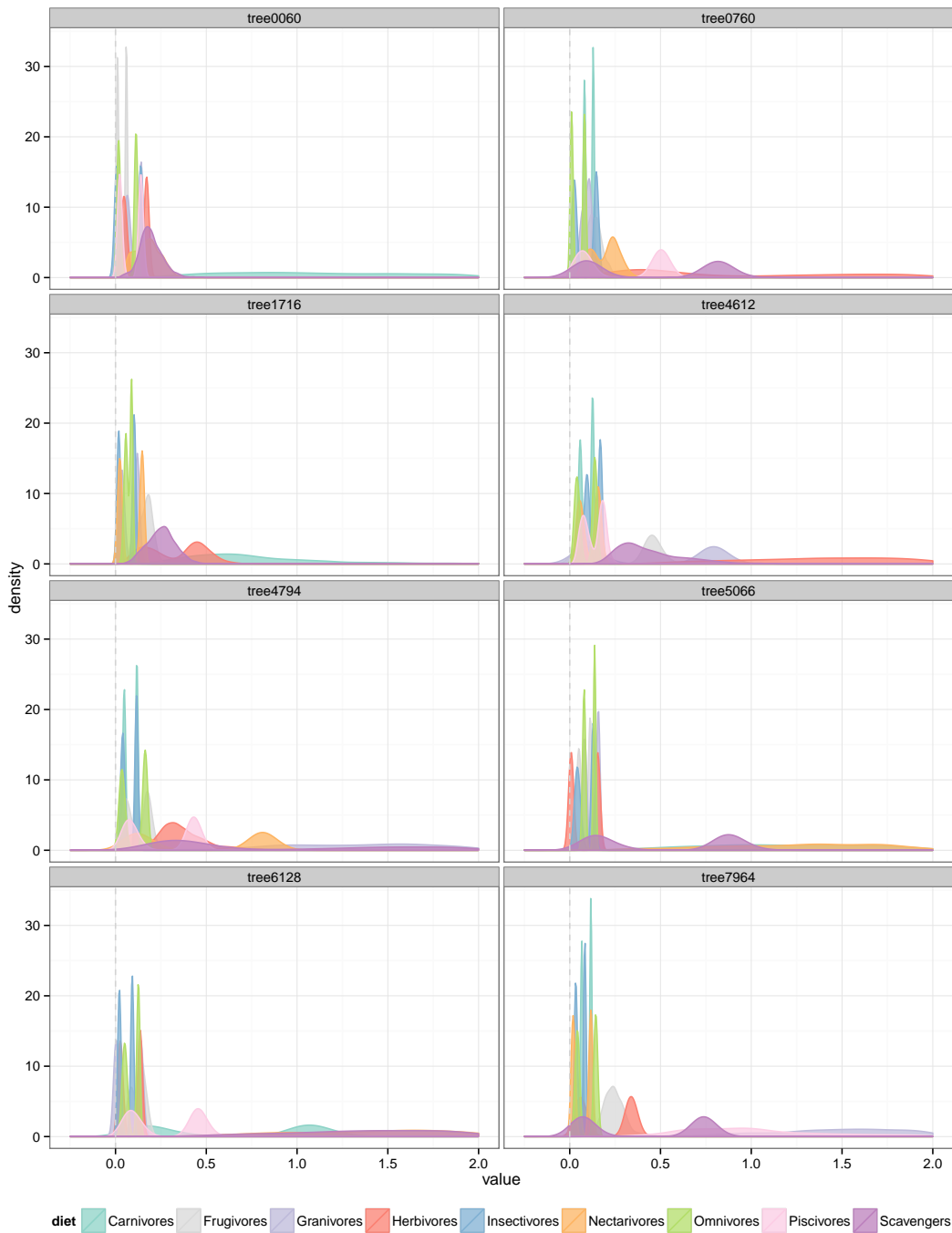
FIGURE A.17: Net diversification rates for all guilds in each of the 8 remaining simulations of character evolution using empirical transition rates. In none of the simulations it is possible to observe omnivores showing a distinct evolutionary dynamics in relation to all other guilds. Moreover, no dietary guild showed a predominantly negative net diversification as seen in the empirical data for omnivores.
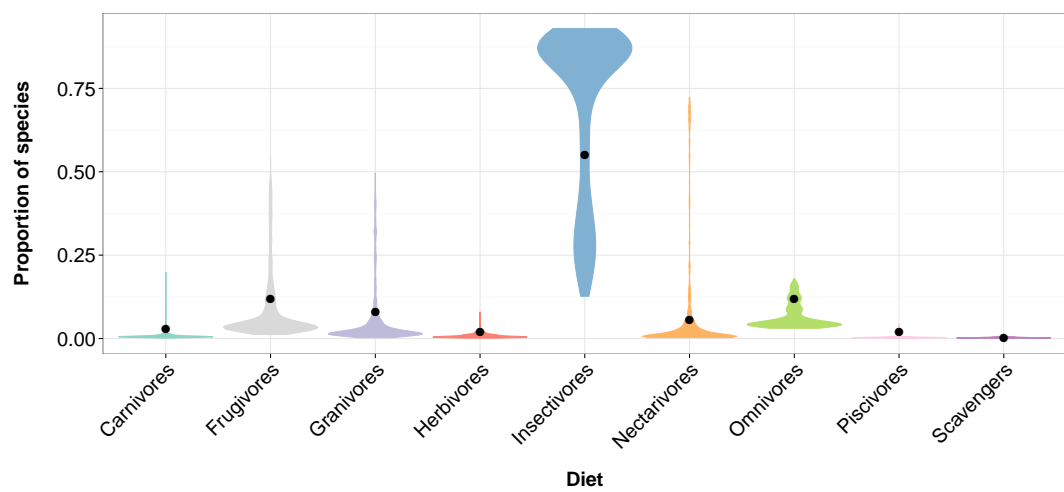
FIGURE A.18: Posterior predictive distributions for model adequacy. Distribution of proportions that each diet represents in the 1000 simulated trees using estimated empirical rates. The black dots represent the proportion of diets present on the data used in the study. Simulations produced proportions that encompass the empirical values. Although the figure scale is not adequate to see all the proportion distribution simultaneously, the empirical piscivores proportion is within the range, close to the upper limit of simulated proportions.
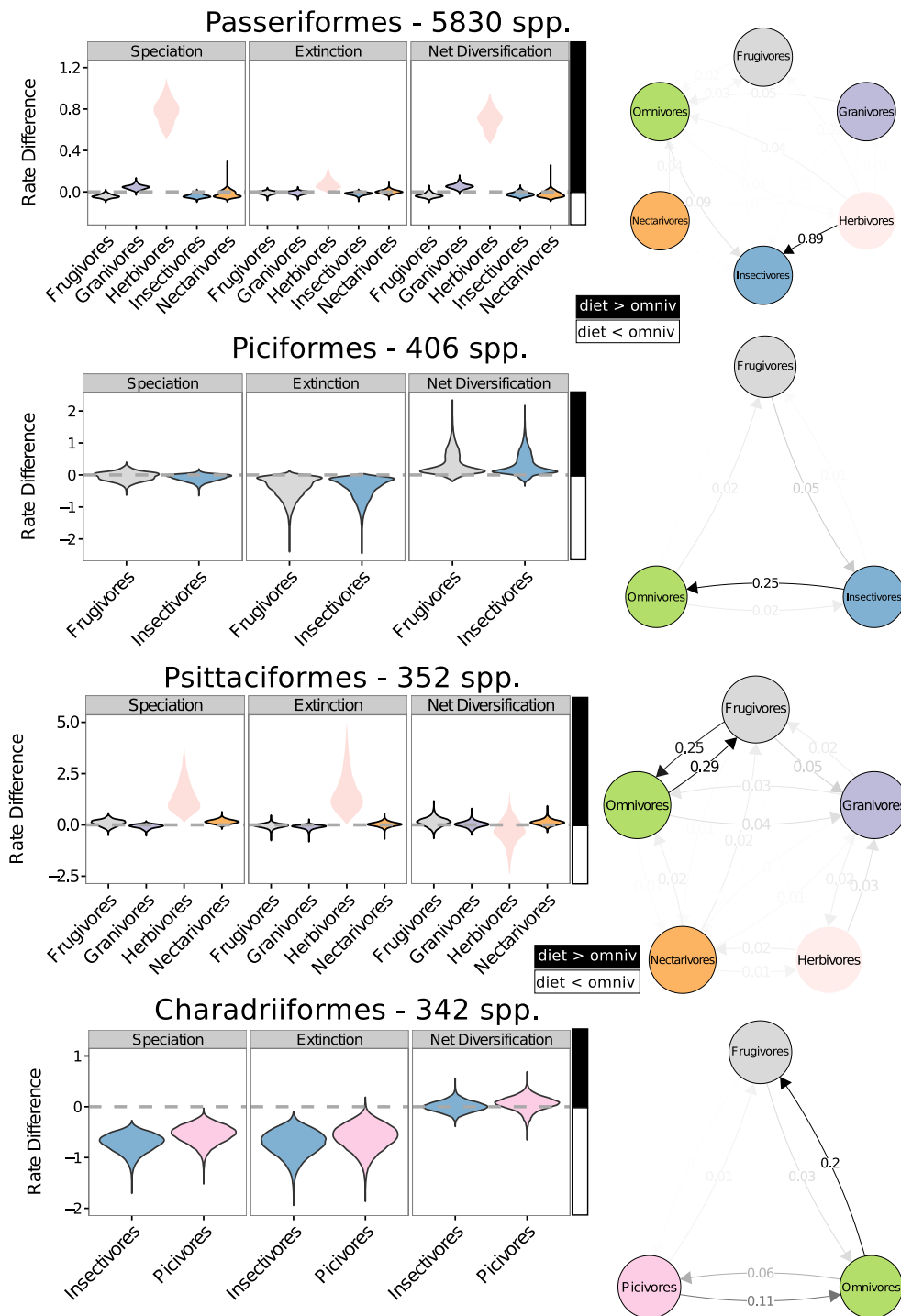
FIGURE A.19: Posterior distributions of speciation, extinction and net diversification rates (panels a, c, e, and g) and transition network (panels b, d, f, and h) for each of the 4 analyzed subclades: (a-b) Passeriformes; (c-d) Piciformes; (e-f) Psittaciformes; (g- h) Charadriiformes. Extinction rates show a similar trend to the main study, usually being higher in omnivores, whereas speciation and net diversification rates show inconclusive patterns. Transition networks for Charadriiformes (h) show a pattern similar to the whole tree, while the other three networks show different patterns.
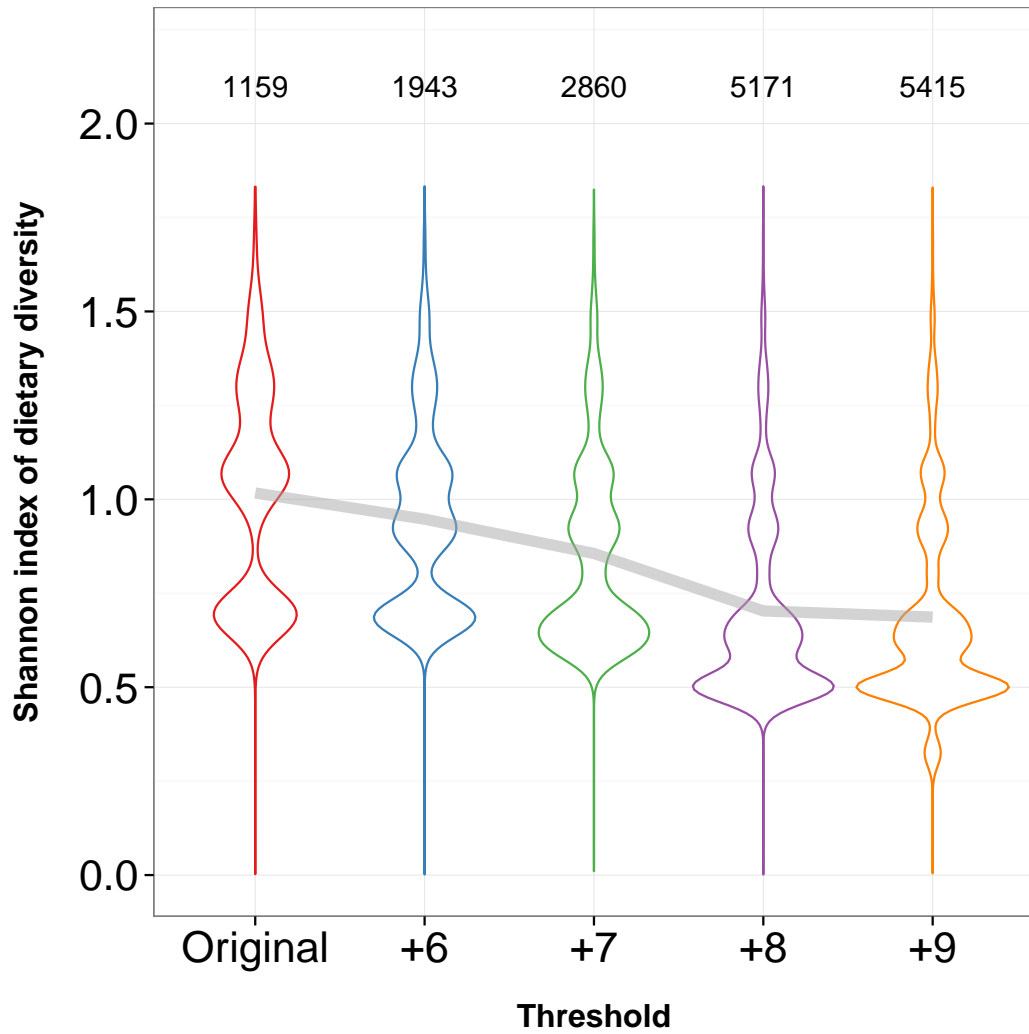
FIGURE A.20: Distribution of dietary diversity indexes for omnivores classified using different classification schemes. The number on the top represent the number of species classified as omnivores in each scheme. It is possible to see a steeper decrease in the average index when increasing the threshold from 70% to 80%. This reinforces our criterion in using 50% as an upper limit for a given item to be consumed in the diet of an omnivore species.
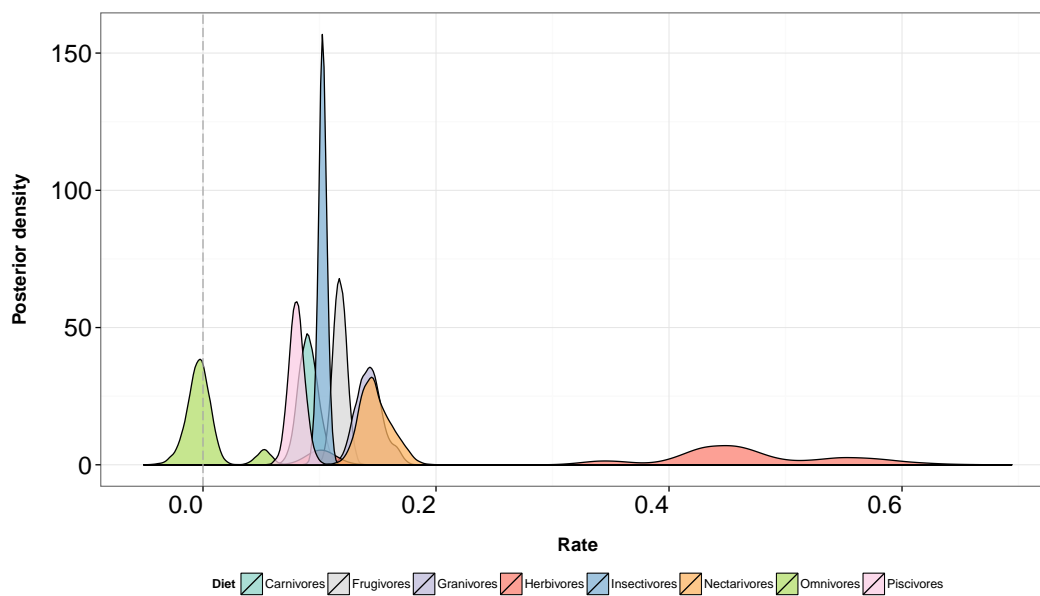
FIGURE A.21: Combined posterior distribution of net diversification rates for each dietary guild using the new classification scheme (70% threshold). Omnivores still have lower net diversification rates when compared to all other guilds.
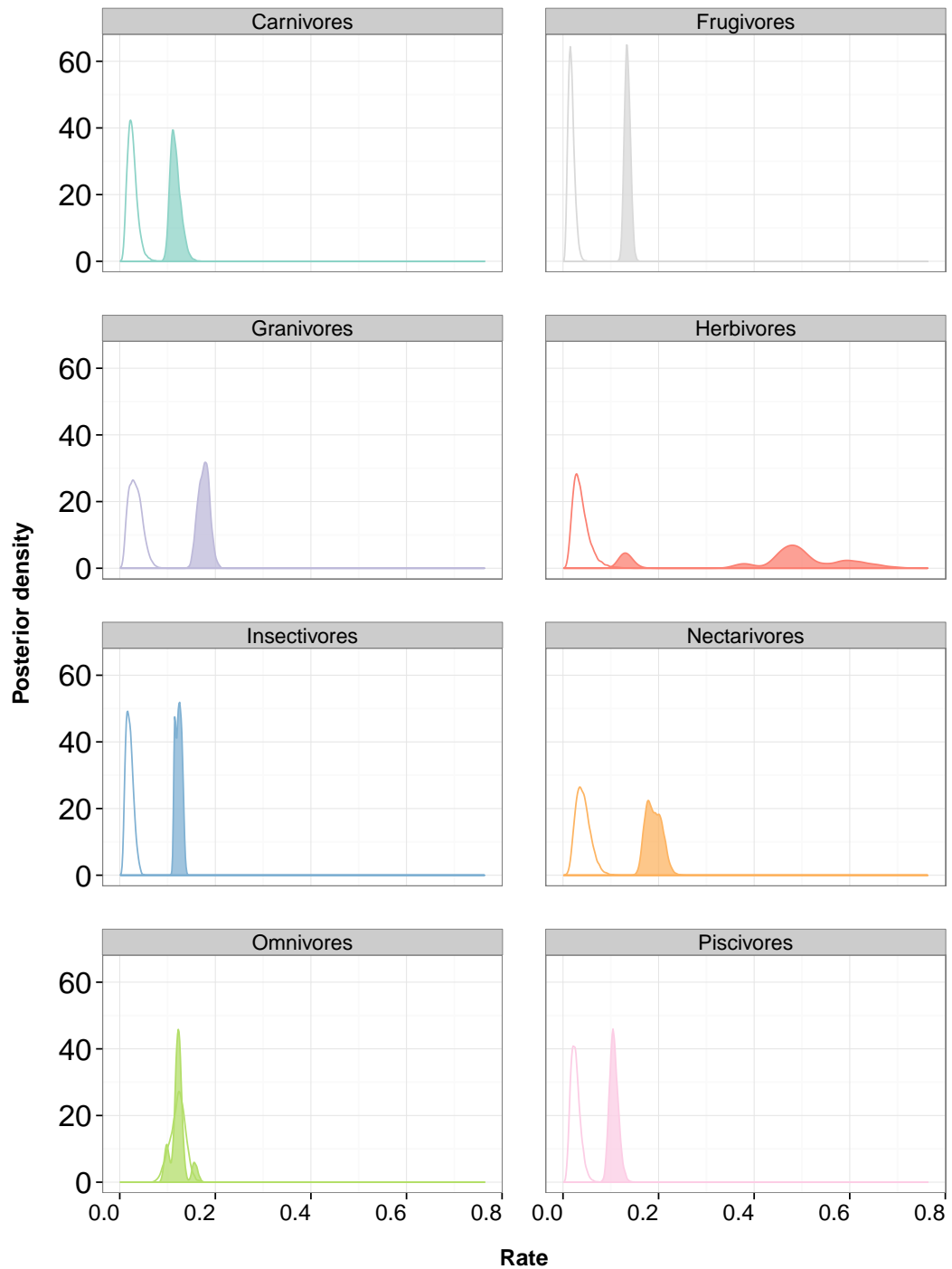
FIGURE A.22: Combined posterior distributions of speciation (filled curves) and extinction (hollow curves) rates for each guild using the new classification scheme (70% threshold). Omnivores is the only guild in which there is a almost complete overlap between the curves of the two rates.
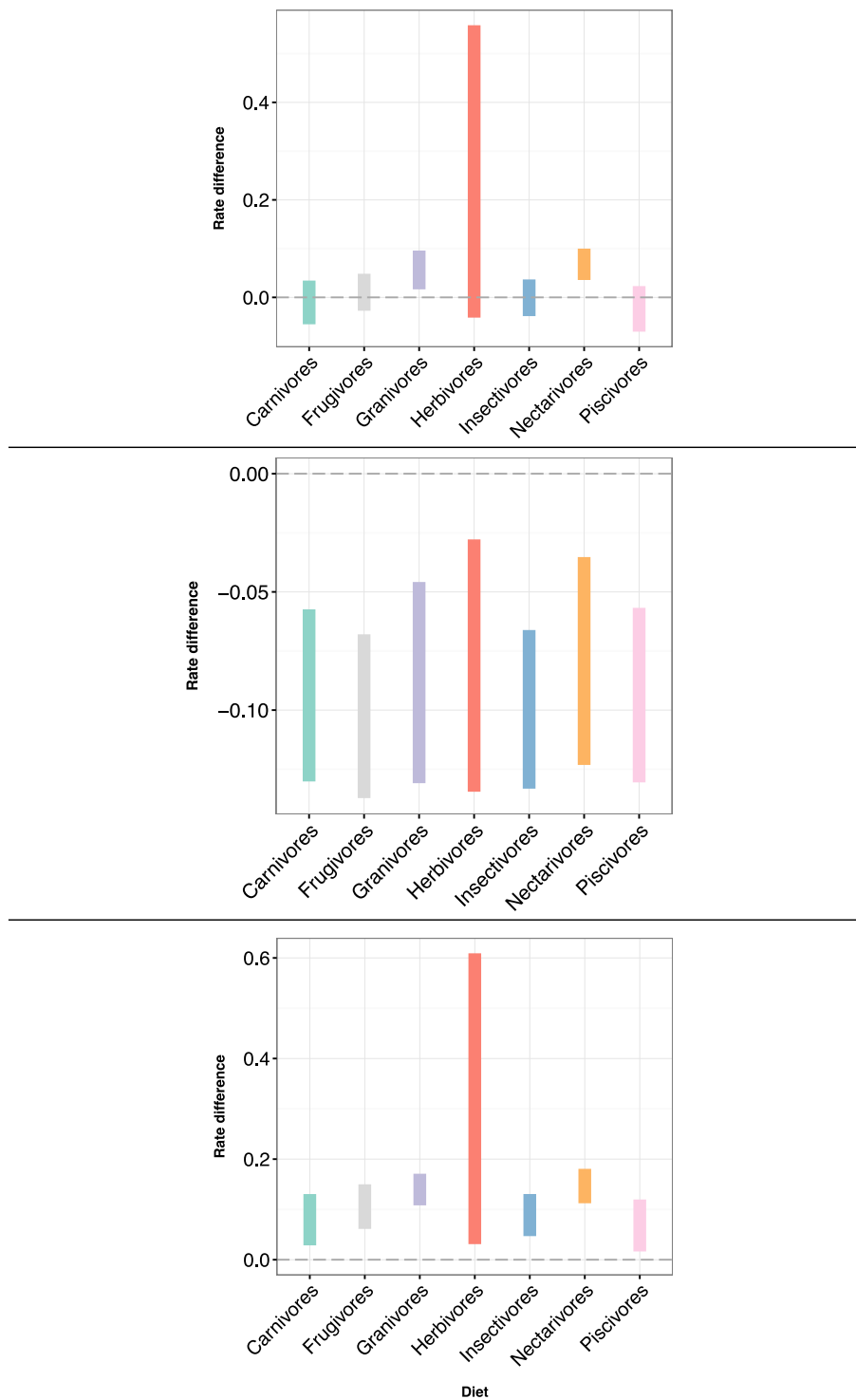
FIGURE A.23: 95% credibility intervals for the posterior distributions of differences between speciation (a), extinction (b) and net diversification (c) of all guilds in relation to omnivores using the new classification scheme (70% threshold). Omnivores still show either smaller speciation and/or greater extinction rates when compared to other guilds, which results in an overall low net diversification.
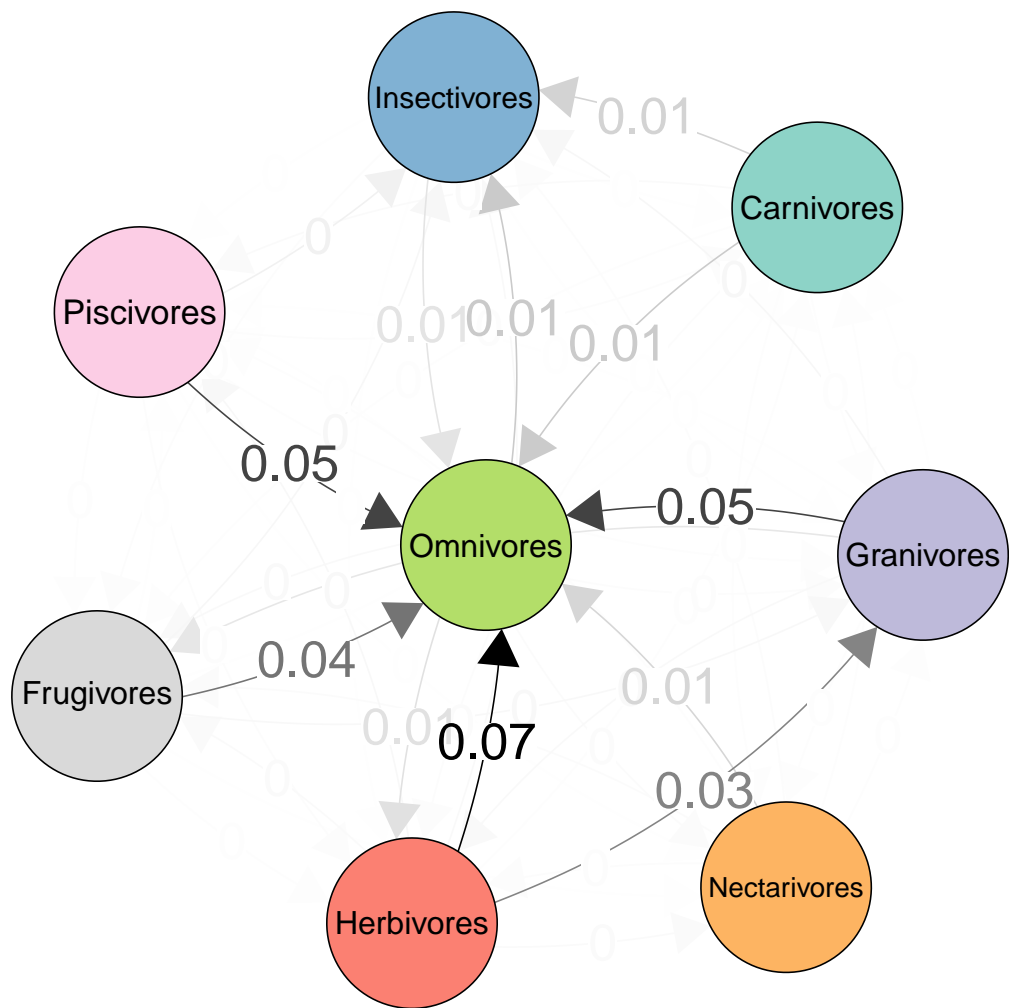
FIGURE A.24: Network of estimated transition rates between diets using the new classification scheme (70% threshold). Omnivores keep being the preferential target in transitions even in this new classification scheme, reinforcing their role as macroevolutionary sinks.
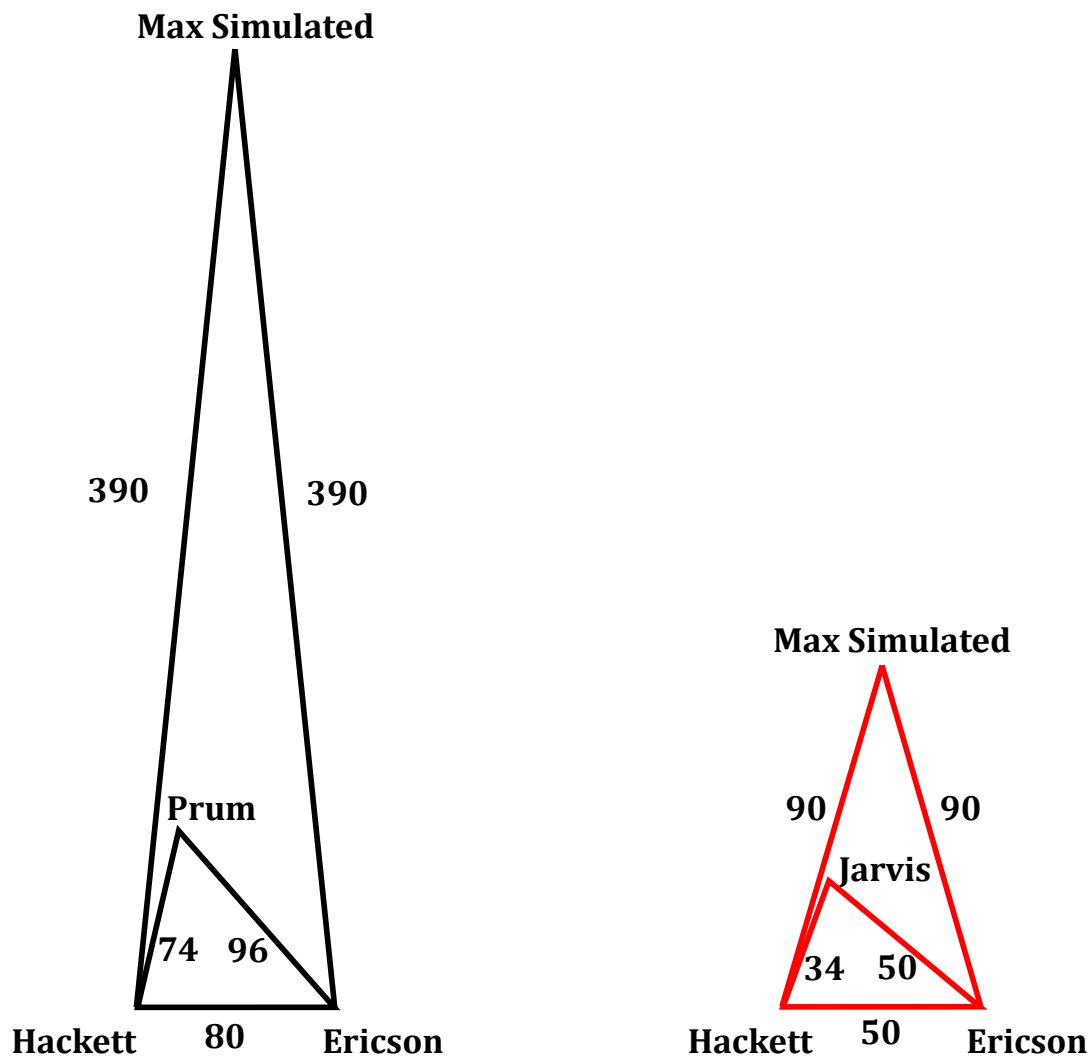
FIGURE A.25: Representation of the Robinson-Foulds distances between the two backbone trees (Hackett and Ericson, as used in our work) and two recently published high-order phylogenies (Prum, Javis) as well as simulated trees (Max Simulated). The distance values represent the number of permutations needed to transform one tree into another tree. The results show that the relative difference between the two backbones is similar to the difference between each backbone and either one of the two new phylogenetic hypotheses. This suggests that phylogenetic heterogeneity (or uncertainty) as incorporated in our analysis (the use of trees from both backbones) encapsulates an amount of phylogenetic dissimilarity that is comparable to the one captured when comparing the backbone trees with other phylogenetic hypothesis.

## A.2 Supplementary Table

TABLE A.1: Number of simulations with each ancestral state

| Diet | Number of Simulated Trees |
|---|---|
| Carnivores | 30 |
| Frugivores | 120 |
| Granivores | 80 |
| Herbivores | 20 |
| Insectivores | 550 |
| Nectarivore | 57 |
| Omnivores | 120 |
| Piscivores | 20 |
| Scavengers | 3 |

## A.3 Supplementary Notes

### A.3.1 Assessing xxSSE model limitations

**Assessing the coupling between speciation/ extinction and transition rates**

Our results indicate that 29 out of the 180 simulations had at least one guild missing. The considerable percentage of simulations with missing guilds (approximately 16%) is already indicative that transition dynamics alone (without a coupled speciation and extinction dynamics) rarely reproduce the empirical distribution of diets observed in extant species.

From the 40 randomly selected simulations that contained all guilds, our results showed that 32 out of those 40 simulations where we fitted MuSSE did not provide reliable results. The MCMC chains for those took as much as 20 times longer than the viable ones to reach the same number of iterations and showed no sign of convergence. This poor performance for those MCMC chains is caused by recurrent unrealistic estimated rate values such as speciation rates of $10^4$ species per lineage per million years. This is a reflection of underrepresentation of some guilds, which renders the estimate unreliable. Again, this lack of convergence can be interpreted as evidence that transition rates

alone are not capable to generate scenarios similar to the one seen in the empirical tree.

Taken together, those two previous results suggest that when simulations ignored the rates of speciation and extinction associated with trait states, the vast majority of these simulations resulted in scenarios, which differed from the empirical data either in relation to the proportion between guilds and/or from the perspective of rate estimates, to the point that those were not used or had to be discarded to the fitting exercise (Figure A.16).

The fitting of MuSSE was only possible on 8 simulations and in none of these remaining simulations we observe negative diversification rates for omnivores (Figure A.17). In fact, no trait state was estimated to be associated with negative net diversification rates on those 8 simulations, and the rate estimates were not even vaguely similar to the empirical estimates. With respect to our empirical case, these simulation results suggest that the transition dynamics (without changes in speciation and extinction due to trait states) and the specific tree topology alone are not capable of reproducing the empirical diversification dynamics (Figure A.17). Thus, we suggest that our results are unlikely to be caused by model misbehavior, but rather by an association between trait states (diets) and diversification rates.

**Posterior predictive simulations to test for model adequacy**

The results from the simulation that used the empirical rate estimates associated with different dietary guilds produced a distribution of proportions between guilds that lies around the proportions observed in the empirical data (Figure A.18). This indicates that the rates estimated by our analysis can generate plausible scenarios (Figure A.18). We interpret this result as evidence that the models used to characterize the diversification dynamics associated with the different dietary guilds are adequate.

**Model fitting in sub-clades**

The results from the sub-clades analyses showed a similar pattern for the extinction regimes associated with omnivory. Here, as in the main analysis of the whole tree, extinction rates associated with omnivory tended to be either indistinguishable from other guilds or higher than in other guilds (Figure A.19). The exceptions were the extinction rates of herbivores in both Passeriformes (Figure A.19a) and Psittaciformes (Figure A.19c). We suggest that these very high extinction rate estimates for herbivores result from the small number of herbivore species present in each of those orders (12 species in Passeriformes and 10 species in Psittaciformes) and therefore are in fact unreliable estimates.

Figure A.19 also shows that estimates of speciation rates of omnivores are either not significantly different or higher than the speciation rates of other guilds for all four orders (Figure A.19a,c,e,g). This is different from what we discovered in the main analysis, but we note that the transition dynamics between guilds are also different from the dynamics estimated for the whole tree with the exception of Piciformes, which show transitions towards omnivory. We suspect that using sub-clades will lead the models to preferentially assign the origin of new omnivore species to speciation rather than to transitions because fewer transitions remain at the sub-clade level.

Although these sub-clade results indicate some differences to the whole tree analysis, the direct interpretation of the sub-clade analysis in xxSSE models other than BiSSE may not be as straightforward as previously advocated for BiSSE (Rabosky and Goldberg, 2015). For a binary-state character all sub-clades of a given tree will have the same number of states (two) as the whole tree, but when working with multi-state characters this might not be necessarily true (for example the order Passeriformes comprise more than half of all bird species, but no carnivore, piscivore or scavenger species are present). Second, as previously mentioned, dividing a tree into sub-clades might obscure the dynamics of transitions, because a state that might

have had multiple origins in the whole tree might be perceived as having few transitions in a sub-clade that has, for example, just one or very few transitions. Finally, when looking at sub-clades some states may be very under-represented. According to (Rosenzweig, 1995), the low relative number of species in a given state leads BiSSE models to incorrectly estimate the parameters. This might be also the case in other xxSSE models, especially when the absolute number of species is low (for example the very low number of herbivore species in both Passeriformes and Psittaciformes, i.e. 12 and 10, respectively). Given those constraints, we do not expect that the sub-clade analysis always replicates the results from the whole tree analysis. Therefore, the results from this analysis should be taken with caution when using a MuSSE model.

**General conclusion on the use of MuSSE in our data**

To conclude, the first two sets of tests provided good evidence for the proper behavior of the model to estimate true state-dependent speciation, extinction and transition rates. The results from the sub-clade analysis were rather inconclusive, although some trends (e.g. extinction regimes) were similar to the whole tree analysis. We suggest that the overall signal from the sensitivity analyses provides evidence that the model is providing reliable results, and that the qualitative results and conclusions drawn from the whole tree analysis are robust.

## A.3.2   Sensitivity analysis for dietary classification

The results shown in figures A.20 - A.24 suggest that a more inclusive categorization of omnivory would result in the same patterns as observed in the main analysis. In this new classification scheme, omnivores also showed either lower speciation and/or higher extinction rates when compared to all other dietary guilds. This ultimately results in a lower (and again even negative) net diversification rate for this guild. Additionally, the observed transition rate patterns are similar to what we recover in our main analysis and support the scenario that poses

omnivory as a macroevolutionary sink. We therefore suggest that our main conclusions are independent to the classification scheme used.

### A.3.3 Comparison of backbone trees

It is possible to see that the two backbones used on our study show a level of phylogenetic dissimilarity that is comparable to the one captured when comparing those backbones to other recent phylogenetic hypothesis (figure A.25). This suggests that phylogenetic uncertainty incorporated in our analysis (the use of trees from both backbones) is comparable to the ones captured from the two other phylogenetic hypotheses.

## A.4 Supplementary methods

### A.4.1 Assessing xxSSE model limitations

We ran three sets of tests to evaluate to what extent the issues pointed out by Rabosky and Goldberg, 2015 might have affected our results and conclusions. These tests were suggested by those authors as a way of diagnosing possible biases on parameter estimation due to background rate heterogeneity in phylogenetic trees. For two sets of tests (A1 and A3) that require empirical trees, we used 10 randomly sampled trees (5 from each backbone) from the 200 trees used in the study. Since the second set of tests (A2) consists of simulated trees, it does not require the use of empirical trees.

**Assessing the coupling between speciation/ extinction and transition rates**

The recent study by Rabosky and Goldberg, 2015 criticizes the indiscriminate use of the xxSSE models for testing hypotheses about character state-dependent diversification rates. The main argument is that xxSSE models tend to exhibit high Type I error rates, i.e. detecting a character state-dependent diversification rate when there is no association between characters and rates

('false positives'). Given the clear relevance of such a potential problem, Rabosky and Goldberg, 2015 suggested to simulate "neutral characters" on empirical trees, with the aim to investigate if xxSSE models would attribute different diversification rates for different character states even in the absence of a direct association. As an example, Rabosky and Goldberg, 2015 simulated the evolution of a binary neutral character (without an influence on speciation or extinction) on a phylogeny of extant whales to quantify the Type I error rate using the BiSSE model. Their simulations involved only trait evolution (no birth-death process) and assumed symmetrical transition rates. We suggest that this way of implementation is inappropriate for testing Type I error rates in xxSSE models.

In the case of the xxSSE models, to properly test for a Type I error, the null model should be constructed with the premise that the tree itself was generated by a constant-rate birth-death process. If this is ignored, a potential false association between a simulated neutral character and rates of diversification (referred to as Type I error rates by Rabosky and Goldberg, 2015) could be either the result of model misbehavior (suggested by Rabosky and Goldberg, 2015) or result from violating the constant-rate birth-death process. The empirical trees used in our work, like most phylogenies for species-rich clades, are clearly subject to rate heterogeneity (Jetz et al., 2012, Huang and Rabosky, 2014) and hence deviate from the null scenario of constant-rate birth-death process. However, developing a null model that incorporates the rate heterogeneity as commonly seen in empirical trees to verify a potentially spurious association is not an easy task. Hence, rather than trying to develop a test to detect Type I errors, we think it is more appropriate to evaluate the reliability of empirical results by firstly decoupling the transition dynamics from the speciation/extinction dynamics and secondly testing whether similar associations between trait states and speciation and extinction rates can be recovered. The latter ones are ultimately the processes that determine rate heterogeneity seen in empirical trees.

We therefore propose a small modification to Rabosky and

Goldberg, 2015's protocol to assess the reliability of xxSSE models when dealing with specific empirical trees. Given the intricate roles of diversification and transition rates on generating the empirical distribution of trait states on the tips, which will eventually be used to test the reliability of the xxSSE models, we suggest to control for the effect of asymmetric transition rates. This can be done by simply using the empirical transition rates instead of symmetrical transition rates when simulating trait evolution. This gives a more reliable assessment of the risk of detecting a spurious association between diversification rates and given trait states. Note that this, as in the case of Rabosky and Goldberg, 2015, is not a test of Type I error in a purely statistical sense, but rather a test if the empirical pattern can be generated by a lack of association between trait states and speciation and extinction rates simulated via trait evolution on empirical trees. In the case of decoupled dynamics described above, if an association between speciation/extinction rate and trait state similar to the empirical ones is recovered then the there is weak support for the inferences derived from the use of xxSSE models to our empirical data. On the other hand, if the decoupled dynamics simulations produce a scenario very different then the ones recovered in the empirical analysis the empirical heterogeneity in the trees should not affect the performance of xxSSE models and our empirical analysis can be considered robust and reliable.

To test for spurious association between diversification rates and trait states when using MuSSE models in our empirical data we thus simulated the evolution of a nine-state trait (i.e. dietary guilds) evolving in 180 randomly selected trees from the 200 trees used in the main paper (90 from each backbone resulting in equal number of trees, twenty, for each of the nine possible ancestral state). In these simulations, we used the transition rates as estimated from MuSSE rather than symmetric transition rates. The ancestral states for each of the simulations were equally distributed among the nine states (20 simulations with each state as ancestral state). From the simulations containing all guilds (n = 151; see below), we randomly sampled 40 simulations (20 from each backbone, due to computational constraints)

and ran the same procedure as in the main paper to estimate speciation, extinction, and transition rates. We then counted how many simulations would show a similar dynamics to our empirical results that would have arisen from a scenario where rates of diversification were not associated with trait states.

**Posterior predictive simulations to test for model adequacy**

For the second set of tests, we simulated 1000 trees using the tree.musse function from the diversitree package. These trees were simulated using the mode of the empirical posterior distributions of all rates. This simulation function requires an ancestral state to be given to each simulation. Hence, following Price et al. 2012 SI, we have used the proportions of all 9 diets seen on extant species as ancestral states (table A.1). We then calculated the proportion of each diet in each simulated tree, and checked whether the proportion between diets created by the simulations lies around the proportion found in extant species as a way of checking for the adequacy of the estimated parameters.

**Model fitting in sub-clades**

According to Rabosky and Goldberg, 2015, if the macroevolutionary patterns we observe in a given tree are created by spurious association between trait states and diversification, the chances of observing the same macroevolutionary pattern in both the whole tree and in sub-clades of the same tree are quite low. Therefore in the last set of tests, we selected 4 of the 5 major bird orders (namely Passeriformes, Piciformes, Psittaciformes and Charadriiformes) as in Rolland et al., 2014. We did not use the order Apodiformes because it is predominantly composed by either insectivorous or nectarivorous species, with very few exceptions. Hence, testing for associations between traits and diversification in Apodiformes would (a) not include the dietary guild of omnivores, and (b) require the BiSSE model (which has been shown to have serious biases and hence was not used in our analysis).

For each one of the 4 selected sub-clades we used the same 10 randomly selected trees mentioned above, and the same protocol used to analyze the whole tree. Hence, we ran each MCMC chain for 2000000 generations, sampling every 1000th iteration. The combined posterior distribution of all rates (speciation, extinction, net diversification rates) and also the posterior distribution of the differences between the rates in each present diet in relation to omnivores in each of the 4 sub-clades were then analyzed to check whether or not different diversification regimes are associated with omnivory as apparent for the whole tree.

## A.4.2 Sensitivity analysis for dietary classification

To verify if our results are robust to different dietary classifications (especially concerning omnivorous species), we performed the same analysis as in our main analysis, but using a new threshold for assigning a species as an omnivore. Before running this sensitivity analysis, we investigated the effect of different dietary classifications on the average diversity of the omnivore diet, to characterize how different classification schemes would change the level of "generalization" for the omnivore diet and see which new schemes would consist on scenarios worth investigating in further detail. We used the original dataset (scores greater than 5) and created four other datasets (main diet scores greater than 6, 7, 8 and 9), representing different degrees of restriction to the "omnivore" guild. In the five datasets we characterized the degree of diet diversity for the omnivore dietary guild by calculating the Shannon index using the scores of all food items for each omnivore species (note that the definition of omnivory and hence the number of omnivore species changes among different datasets). We then compared the distribution of Shannon indexes of omnivorous species in the five datasets to identify the best schemes to perform a sensitivity analysis. Results showed that for the first three thresholds the average dietary diversity of omnivores decreased gently (Supplementary Figure 20), but a steeper change in the average diet diversity was apparent when using scores of 8 or 9 as a threshold (highly specialized species). Given this result we

focused our sensitivity analysis on the other lower categories (6 and 7). Due to computational limitations, we used only the dataset with score 7 as a threshold for the sensitivity analysis because this provided the highest sensible option. We should also note that the threshold value used in our main analysis (50%) maximizes the average diet diversity among omnivorous species (Figure A.20).

For the sensitivity analysis, we ran the MuSSE analysis for the 10 randomly selected trees using this new dietary classification. To evaluate the results we combined the posterior distributions of all rates (speciation, extinction, net diversification and transition rates) and also the posterior distribution of the differences between speciation, extinction and net diversification rates of each guild in relation to omnivores, to check for significant differences in these rates. As in the main analysis, the results for scavengers are not included due to the small number of species and the small statistical power to reliably estimate the rates. The results for the sensitivity analysis are shown in figures A.20, A.21, A.22, A.23 and A.24.

### A.4.3   Comparison of backbone trees

Two new high-order phylogenies were recently published aiming to resolve the deep-time phylogenetic relationships in birds (Jarvis et al., 2014, Prum et al., 2015). To examine how different the two backbones (Hackett, Ericson) used by Jetz et al., 2012 (both used in our work) are to these new trees, we selected two random trees from each backbone (note that all trees within the same backbone will have the identical higher-level organization) and then pruned those trees down to a tree that contained the same species of both new trees: 1- Jarvis et al., 2014 with 48 terminals; 2- Prum et al., 2015 with 198 terminals. The trees were then used to calculate the Robinson-Foulds distance between all three pairwise combinations within each tree size class (Robinson and Foulds, 1981). This distance represents differences in topology between two trees, and is calculated by counting the number of permutation operations that need to be performed to transform one tree into the other (Robinson and Foulds, 1981).

Since the difference between trees is expected to grow with tree size, these distances cannot be compared between different tree-size classes (i.e. here the trees with 48 and 198 terminals, respectively). Moreover, these Robinson-Foulds distances cannot be easily interpreted without a reference scenario. We therefore simulated 1000 random topologies for each tree size (48 and 198 terminals) using a constant-rate birth-death model, and later calculated the distances between each of the three empirical trees in each size class (Ericson, Hackett and Jarvis for the 48 terminals class, and Ericson, Hackett and Prum for the 198 terminals class), using all 1000 simulated trees from the respective size. This was done to provide a maximum expected value of distances for each size class, so that the absolute distance values could be better compared (Figure A.25).

# Appendix B

# Supplementary Material - Chapter 2

## B.1   Supplementary Figures
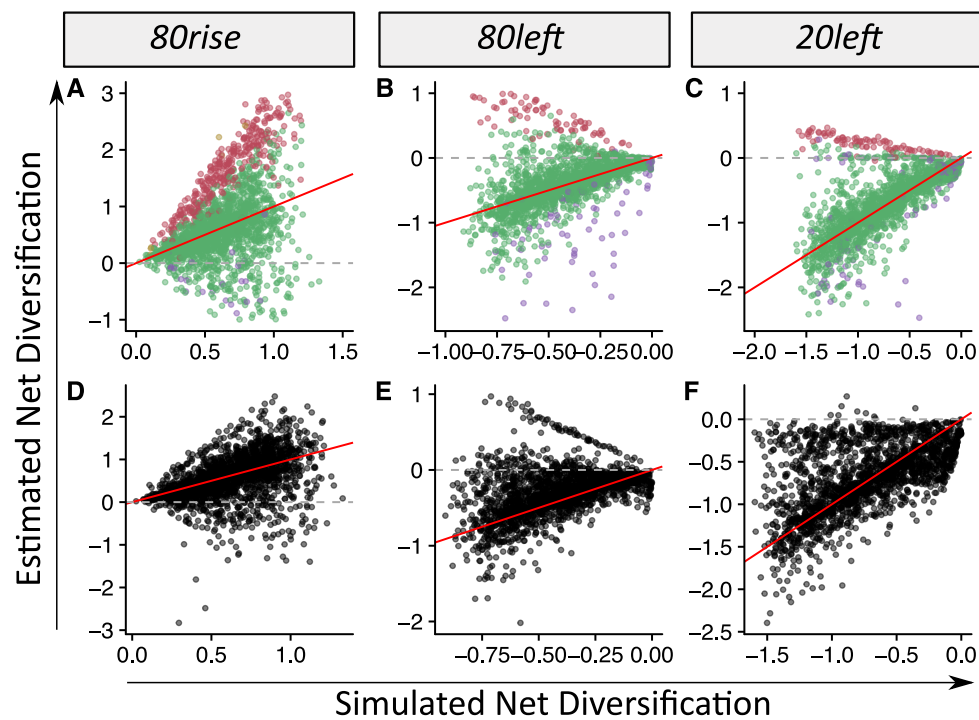
FIGURE B.1: Estimated versus simulated net diversification rates at present for the SP*var* scenario for RPANDA (panels a, b, and c) and BAMM (panels d, e, and f).  Estimates are for the 80rise time slice (left column), 80left time slice (middle column), and 20left time slice (right column).  For all RPANDA panels (a, b, c, g, h, and i), colors denote the best model selected, and in all panels the red line denotes the 'perfect fit' (estimated rate equal to the simulated rate).
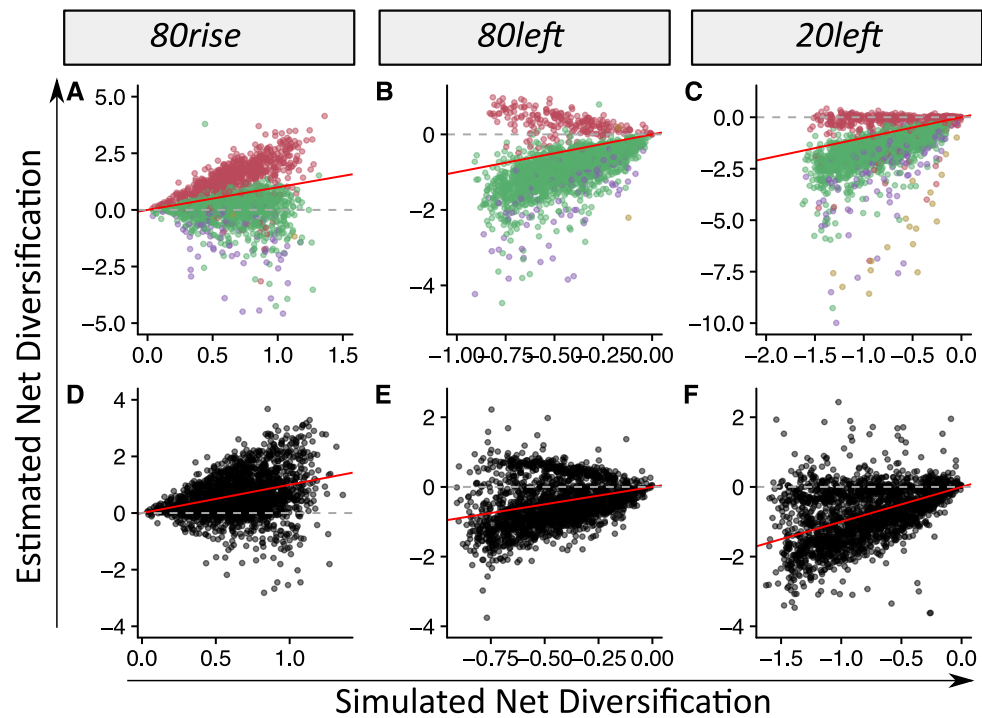
FIGURE B.2: Estimated versus simulated net diversification rates at present for the EX*var* scenario for RPANDA (panels a, b, and c) and BAMM (panels d, e, and f). Estimates are for the 80rise time slice (left column), 80left time slice (middle column), and 20left time slice (right column). For all RPANDA panels (a, b, c, g, h, and i), colors denote the best model selected, and in all panels the red line denotes the 'perfect fit' (estimated rate equal to the simulated rate).

FIGURE B.3:   Distribution of standardized ([estimated - simu-
lated]/simulated) speciation rate differences for RPANDA at the 80
left (panels A-D) and 20left (panels E-H) time slices in SP*var* scenario.

FIGURE B.4: Distribution of standardized ([estimated - simulated]/simulated) extinction rate differences for RPANDA at the 80 left (panels A-D) and 20left (panels E-H) time slices in SP*var* scenario.

FIGURE B.5: Distribution of standardized ([estimated - simulated]/simulated) net diversification rate differences for RPANDA at the 80 left (panels A-D) and 20left (panels E-H) time slices in SP*var* scenario.
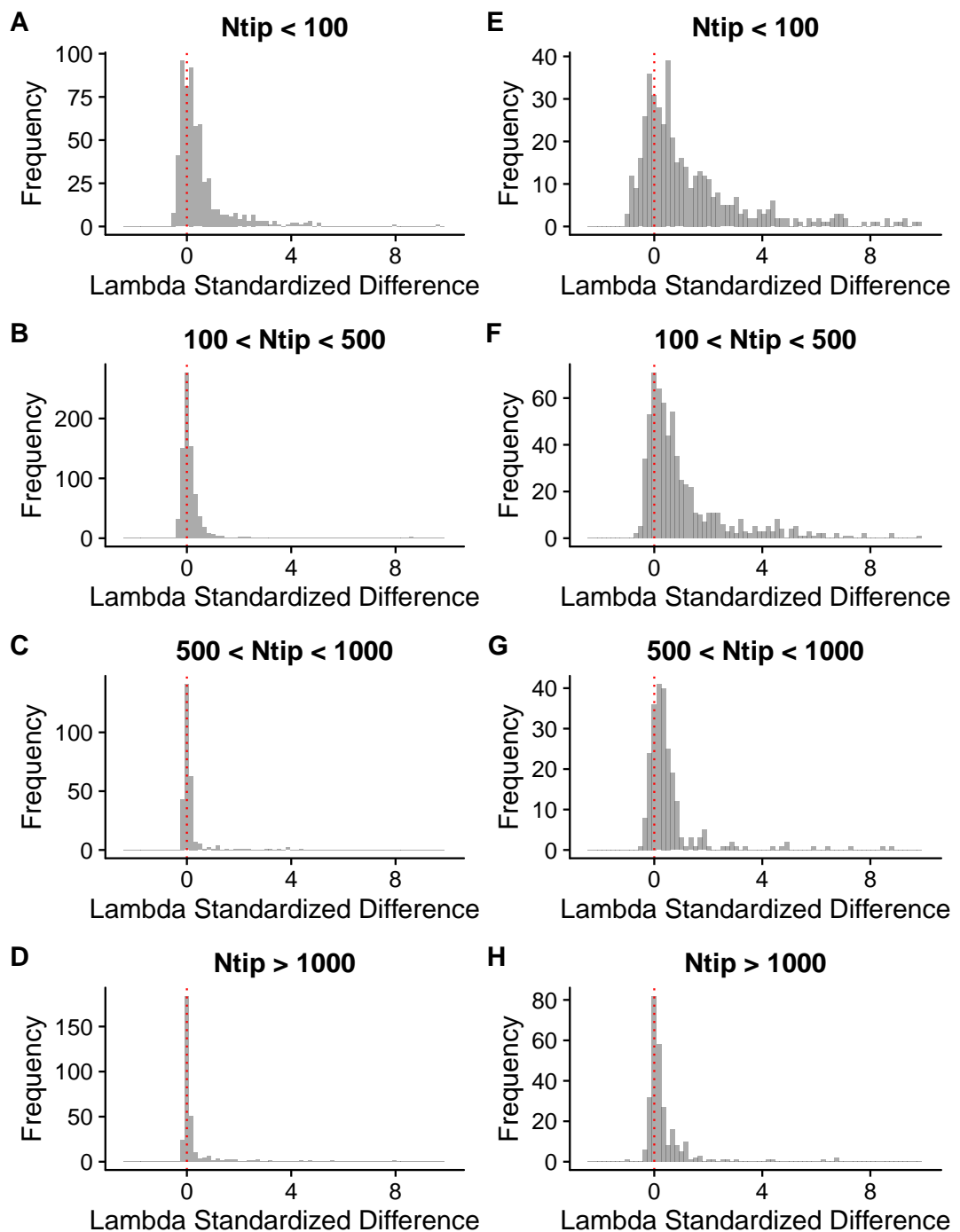
FIGURE B.6: Distribution of standardized ([estimated - simulated]/simulated) speciation rate differences for BAMM at the 80 left (panels A-D) and 20left (panels E-H) time slices in SP*var* scenario

FIGURE B.7:  Distribution of standardized ([estimated - simulated]/simulated) extinction rate differences for BAMM at the 80 left (panels A-D) and 20left (panels E-H) time slices in SP*var* scenario.
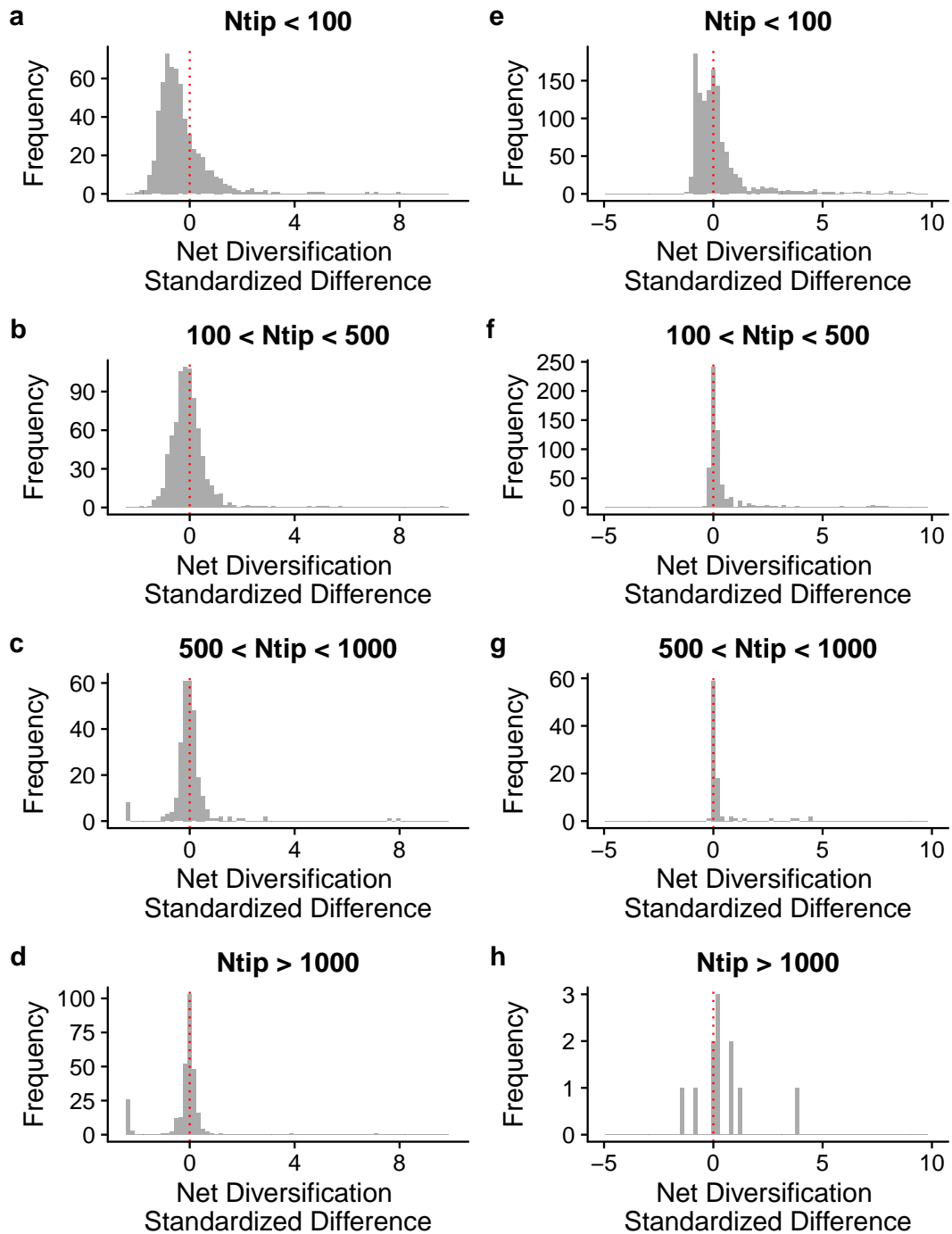
FIGURE B.8: Distribution of standardized ([estimated - simulated]/simulated) net diversification rate differences for BAMM at the 80 left (panels A-D) and 20left (panels E-H) time slices in SP*var* scenario.
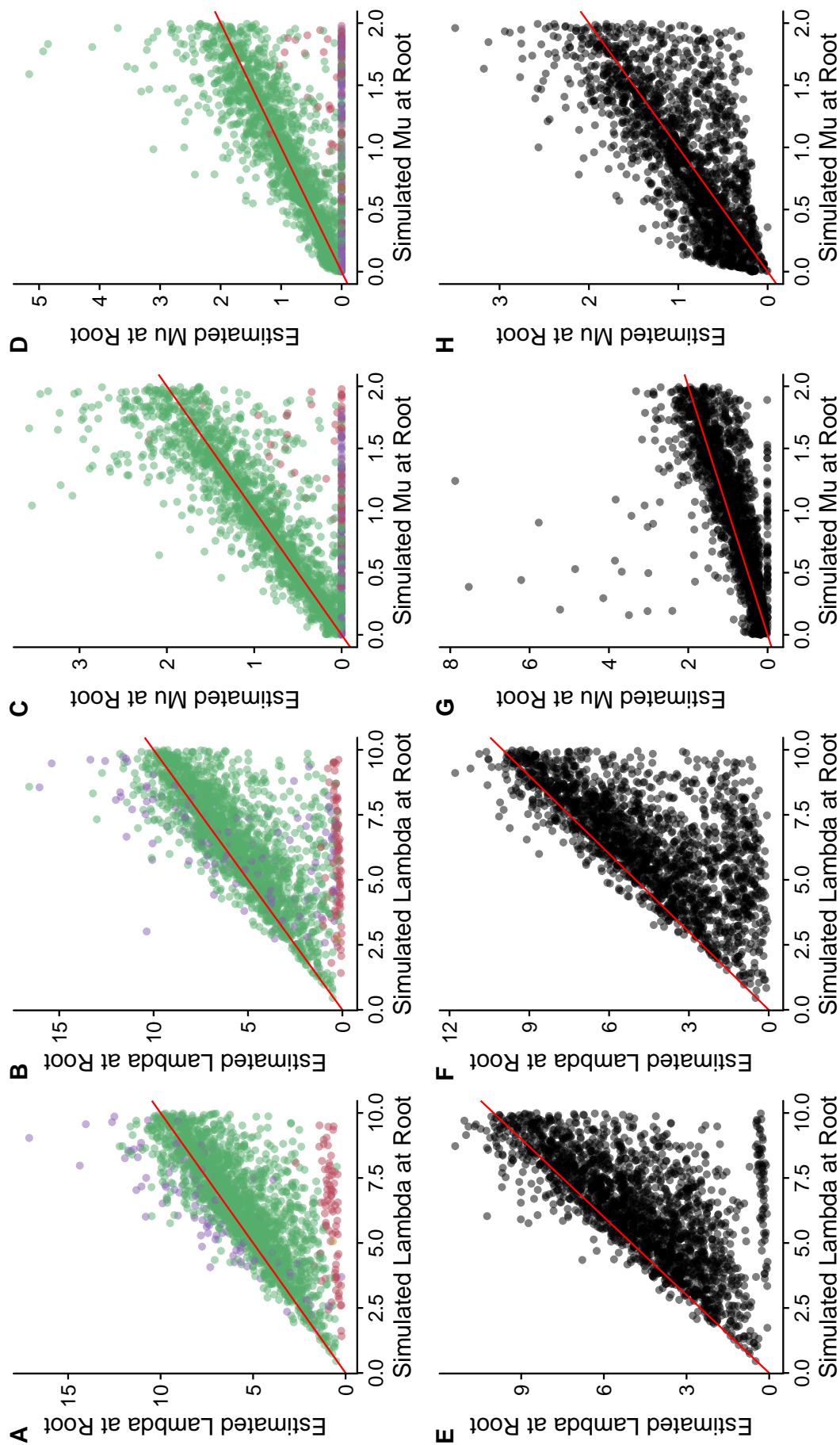
FIGURE B.9: Estimates of speciation (panels A, B, E, and F) and extinction (panels C, D, G, and H) at the root for RPANDA (upper panels) and BAMM (lower panels) for the 80left (panels A, E, C and G) and 20left (panels B, F, D and H) time slices in the SP*var* scenario.
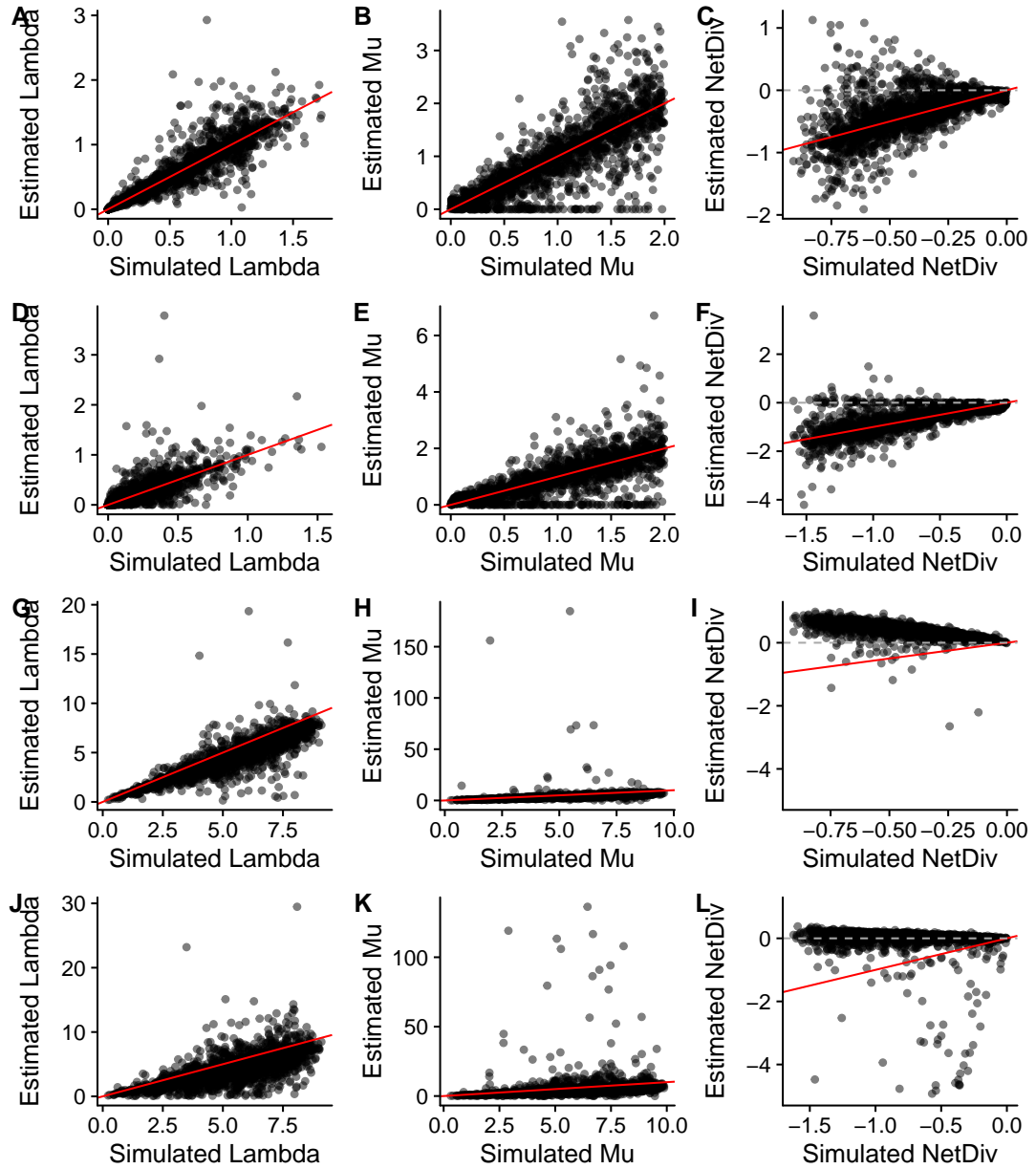
FIGURE B.10: Estimated versus simulated speciation (panels A, D, G and J), extinction (panels B, E, H and K) and net diversification (panels C, F, I, and L) for the true (simulated) model for RPANDA in the 80left (panels A-C and G-I) and 20left (panels D-F and J-L) at the SP*var* (panels A-F) and EX*var* (panels G-L) scenario.
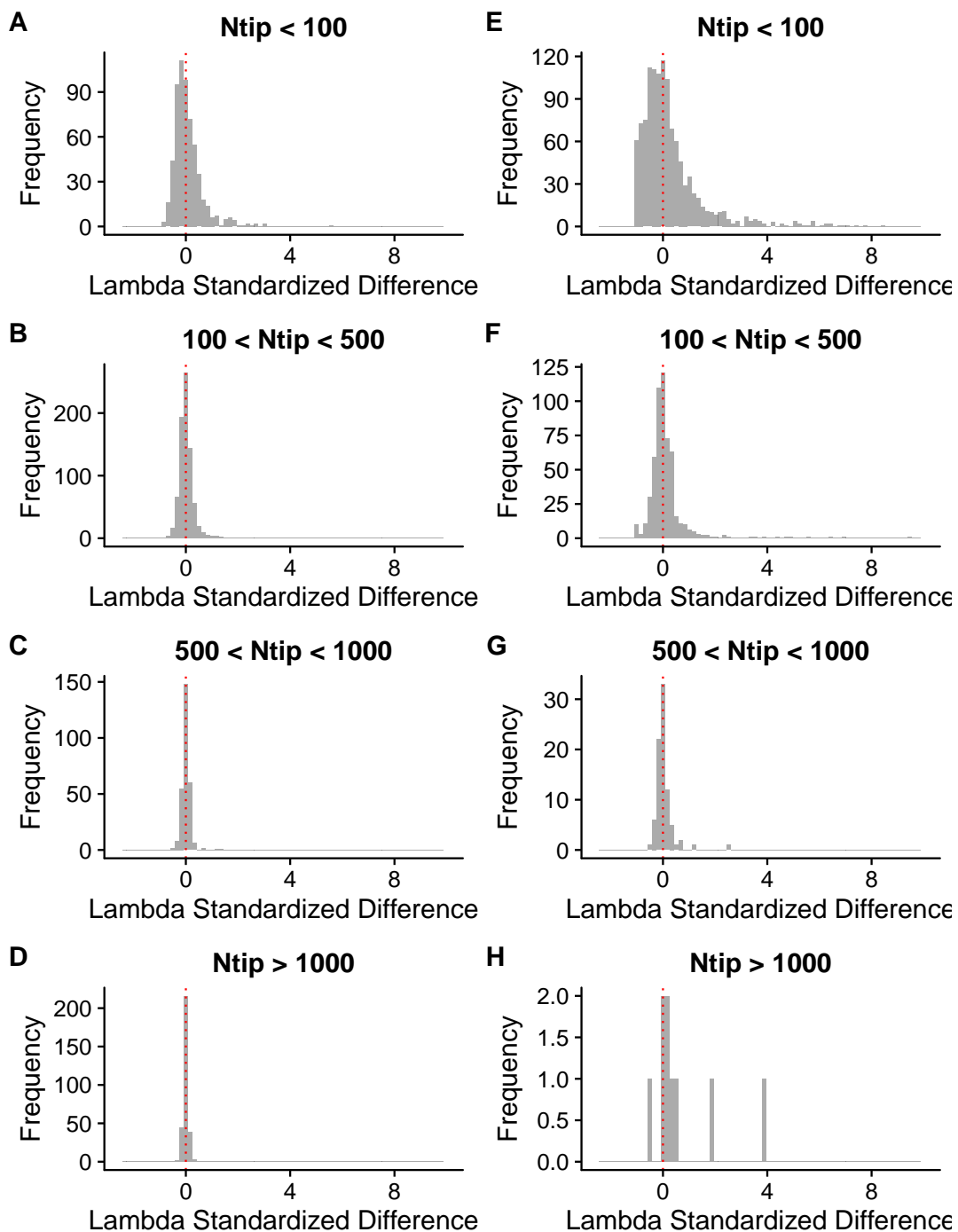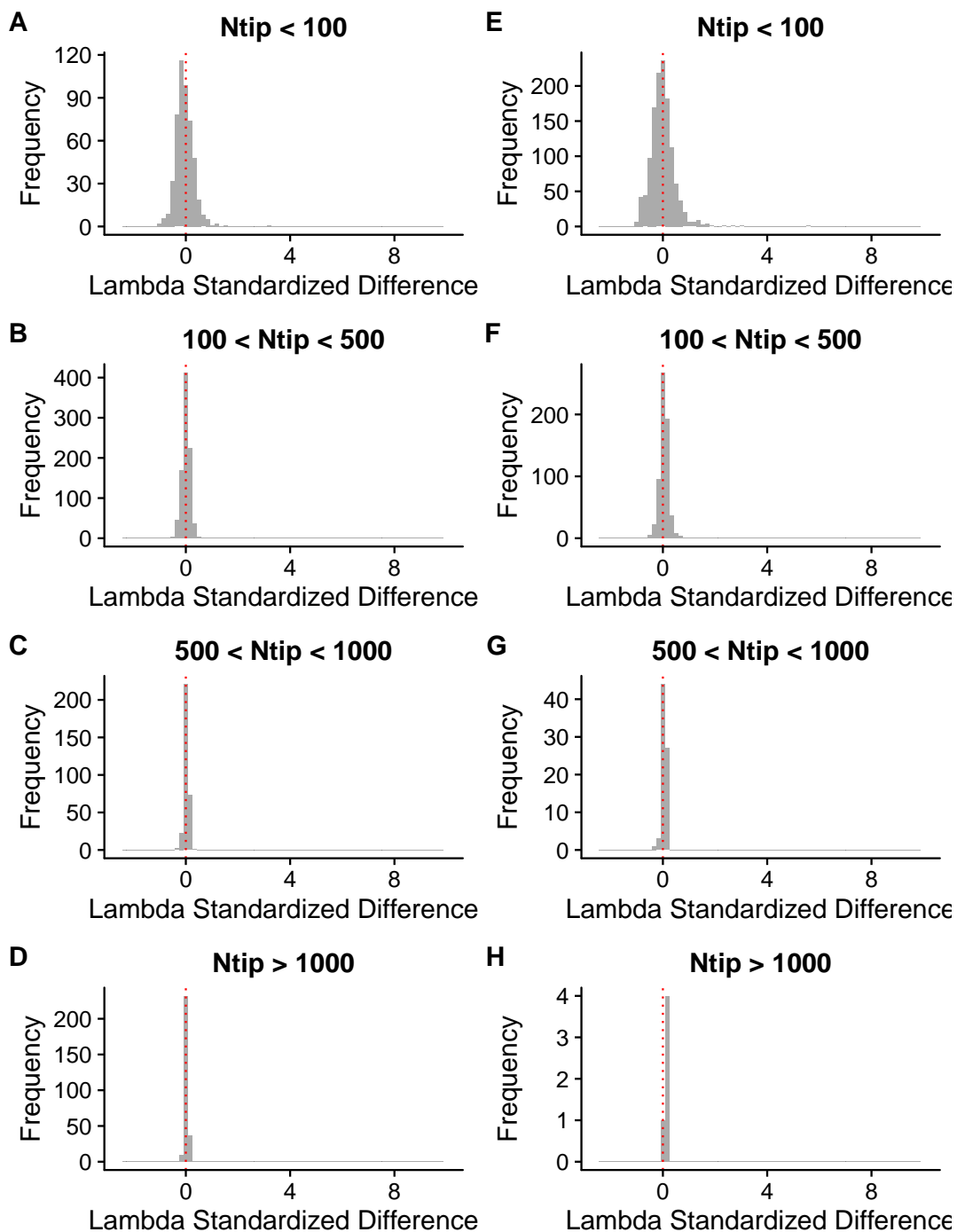
FIGURE B.11: Distribution of standardized ([estimated - simulated]/simulated) speciation rate differences for RPANDA at the 80 left (panels A-D) and 20left (panels E-H) time slices in EX*var* scenario.
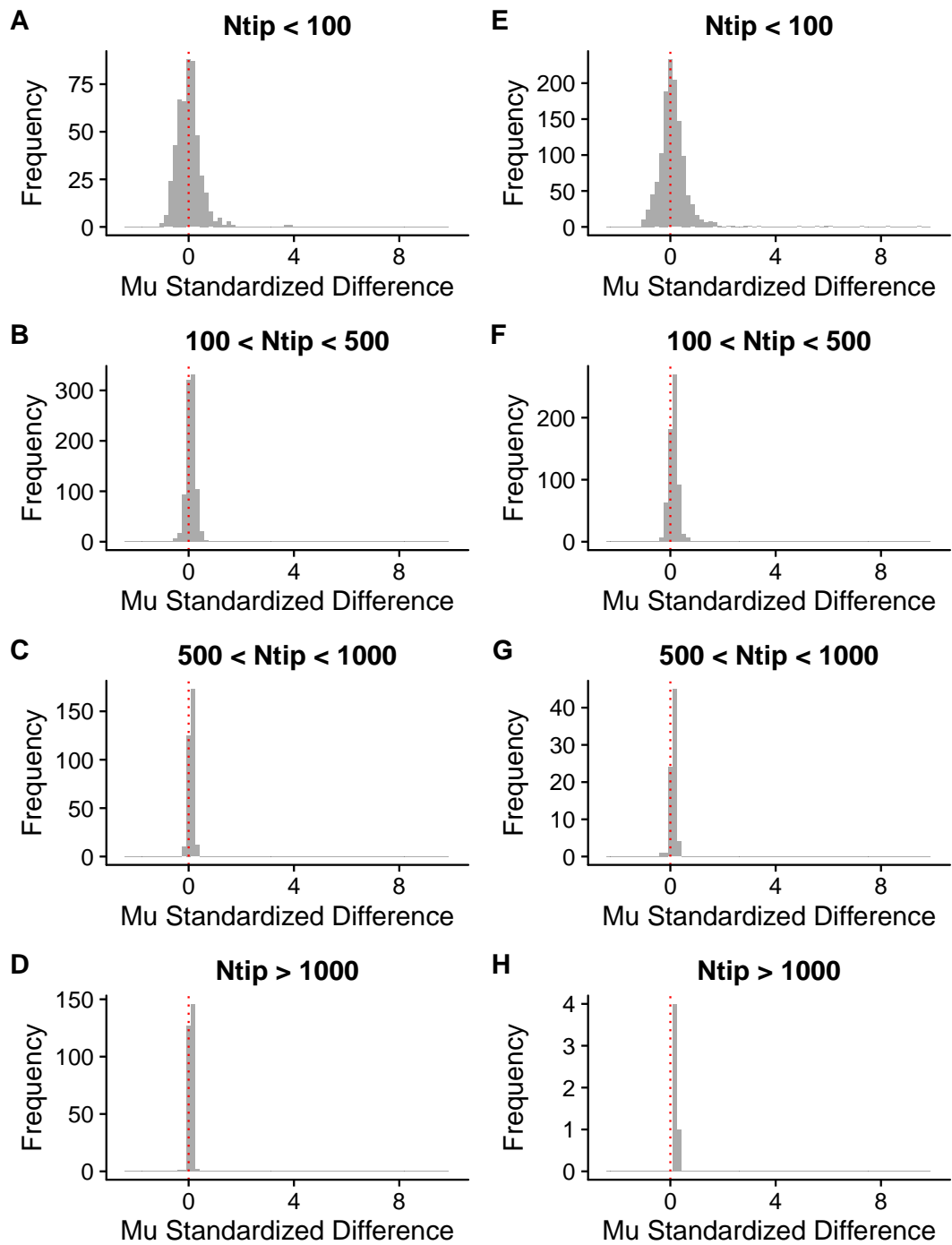
FIGURE B.12: Distribution of standardized ([estimated - simulated]/simulated) extinction rate differences for RPANDA at the 80 left (panels A-D) and 20left (panels E-H) time slices in EX*var* scenario.
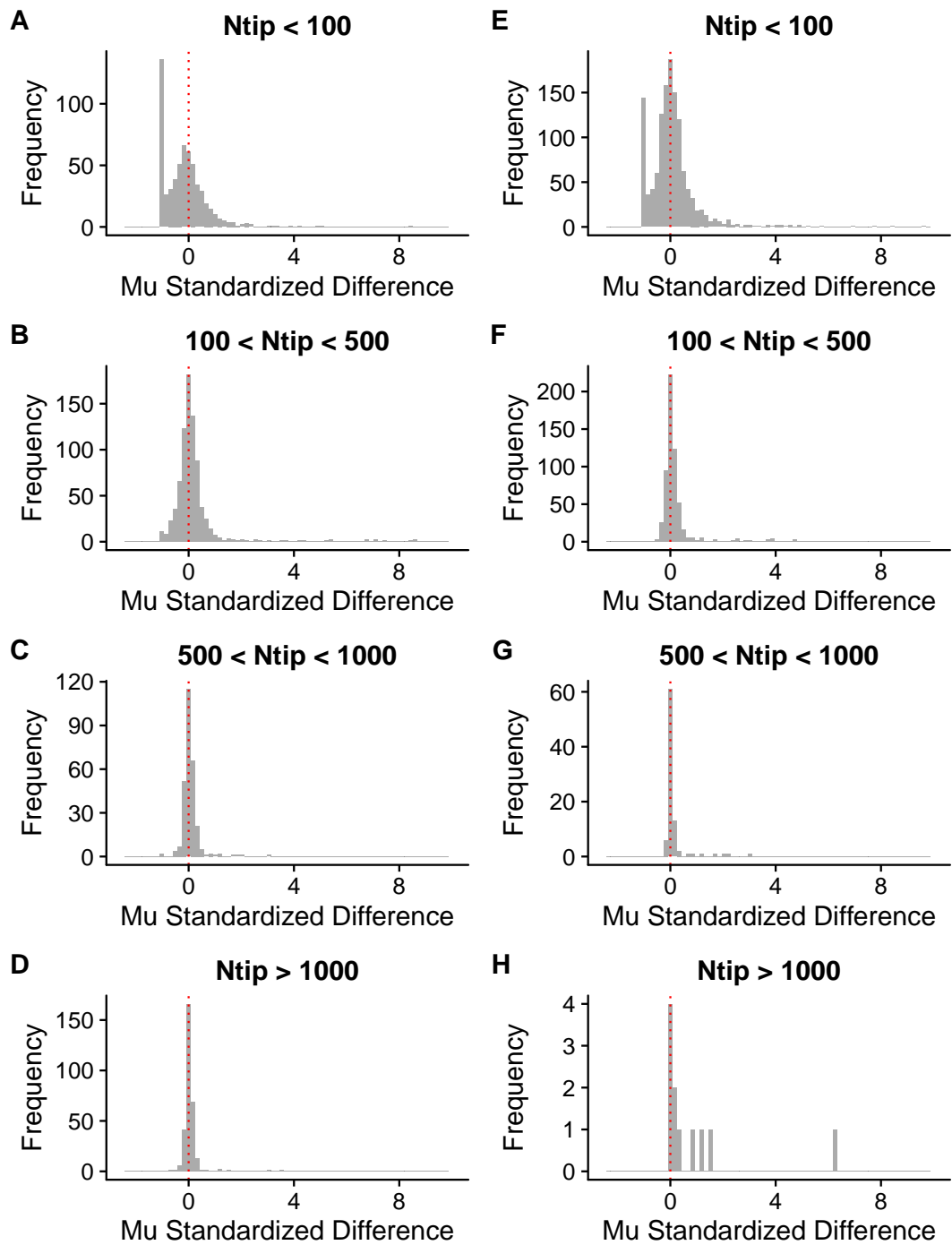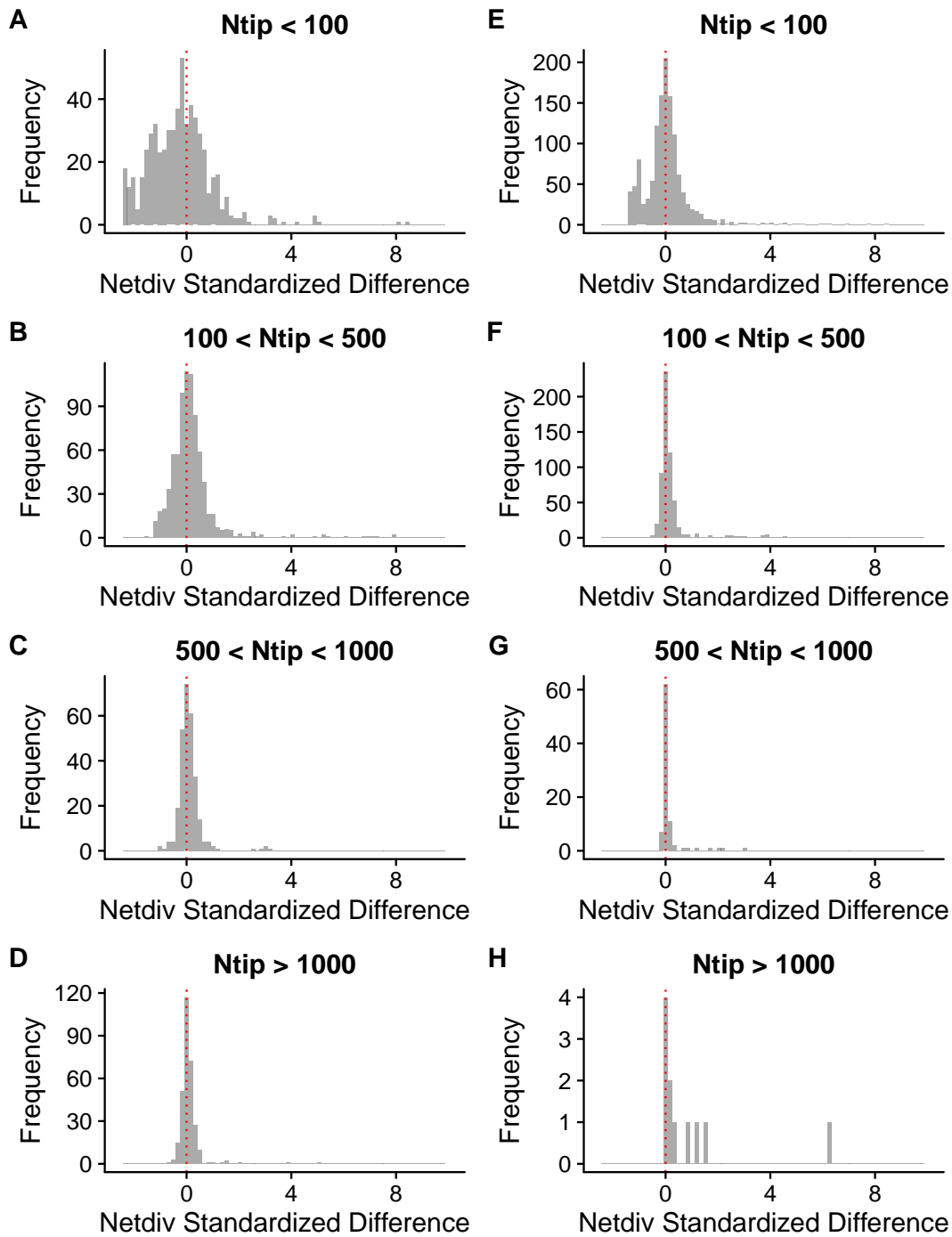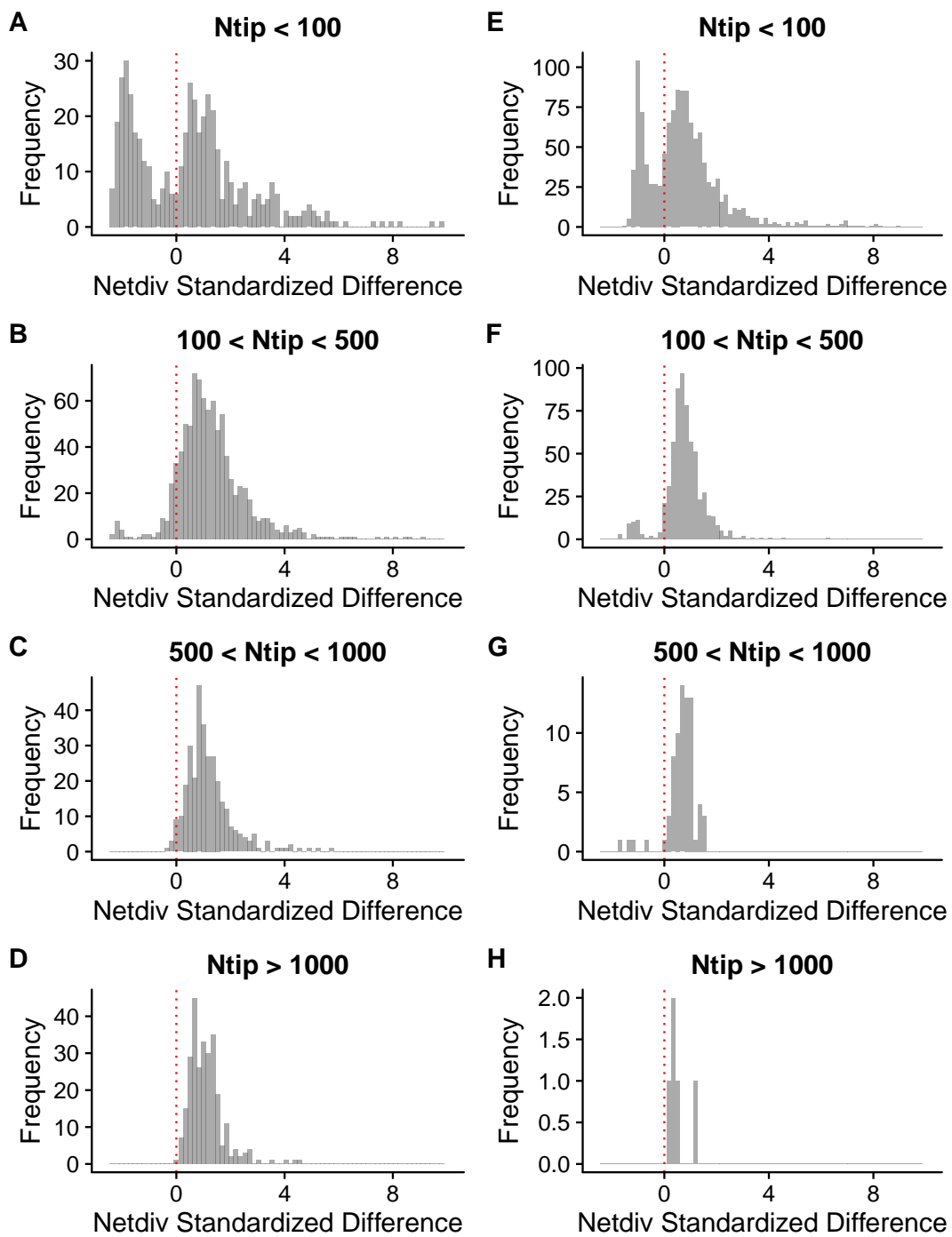
FIGURE B.13: Distribution of standardized ([estimated - simulated]/simulated) net diversification rate differences for RPANDA at the 80 left (panels A-D) and 20left (panels E-H) time slices in EX*var* scenario.
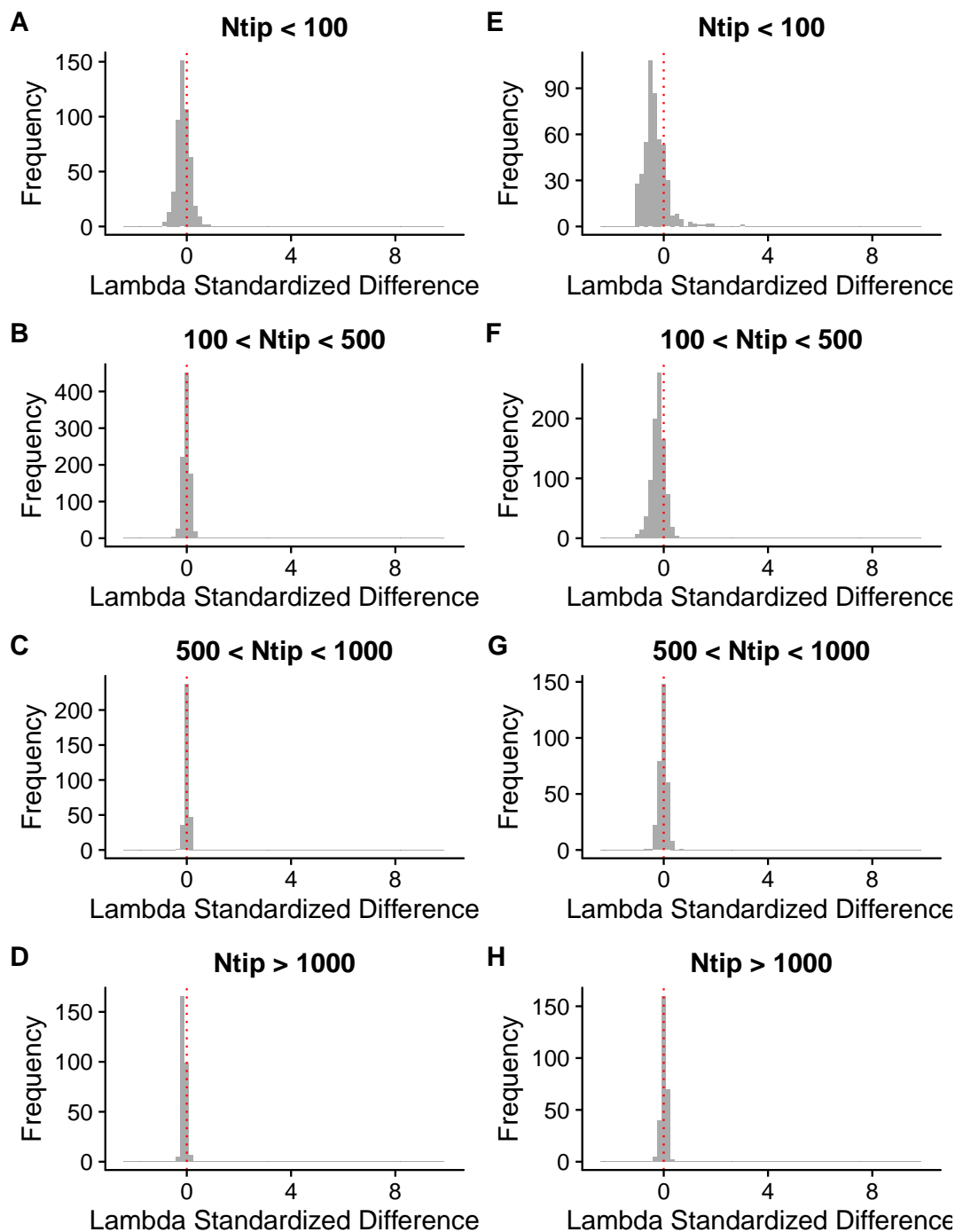
FIGURE B.14: Distribution of standardized ([estimated - simulated]/simulated) speciation rate differences for BAMM at the 80 left (panels A-D) and 20left (panels E-H) time slices in EX*var* scenario.
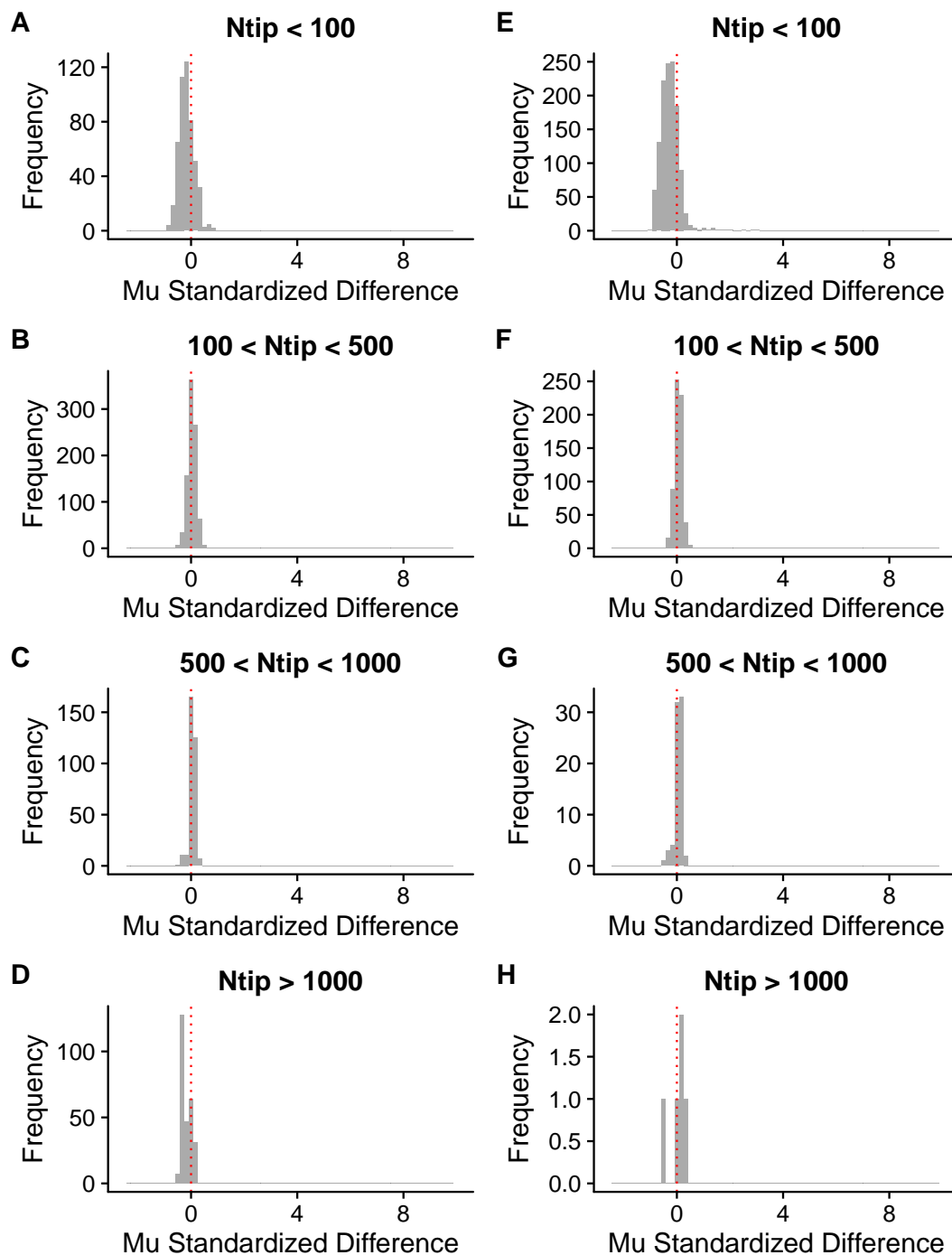
FIGURE B.15: Distribution of standardized ([estimated - simulated]/simulated) extinction rate differences for BAMM at the 80 left (panels A-D) and 20left (panels E-H) time slices in E*Xvar* scenario.
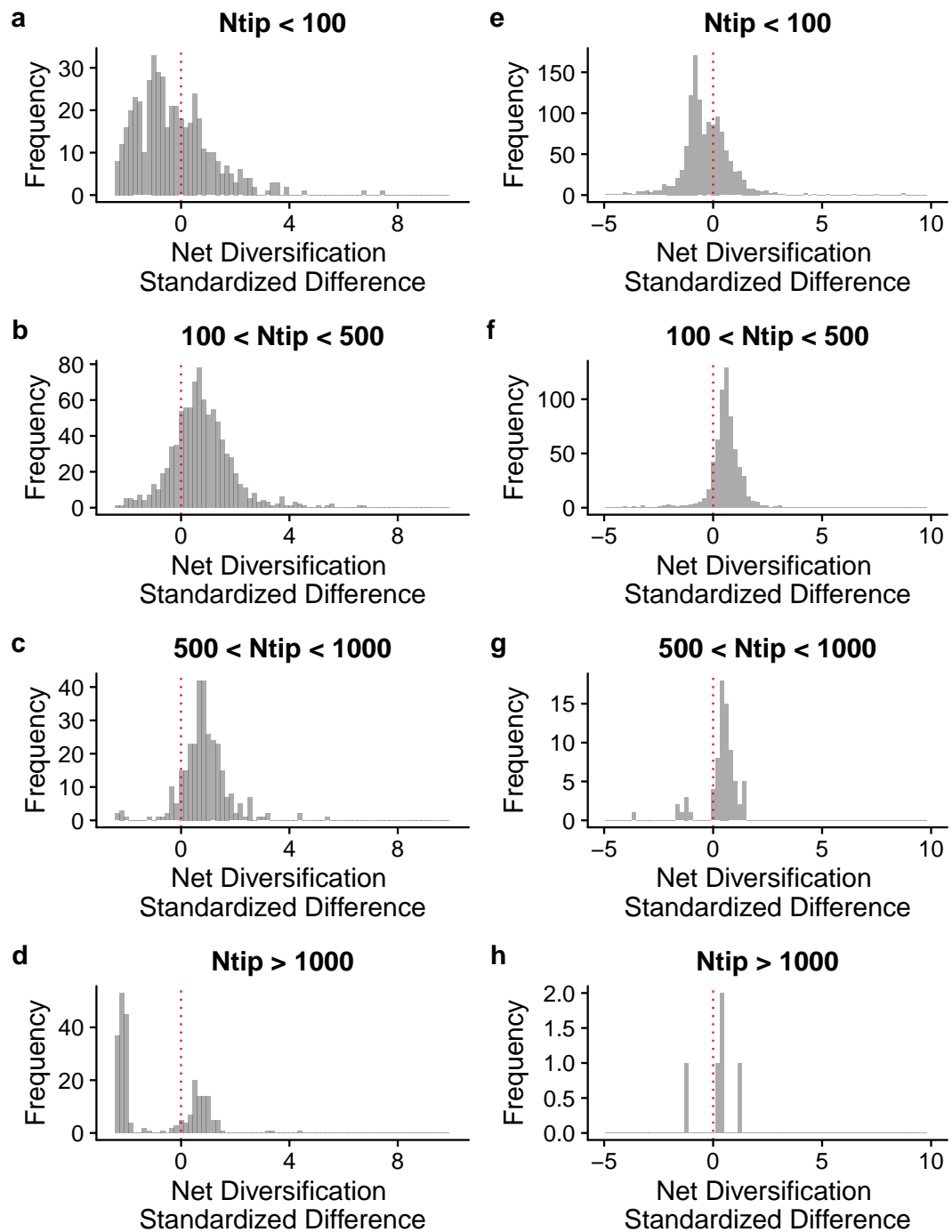
FIGURE B.16: Distribution of standardized ([estimated - simulated]/simulated) net diversification rate differences for BAMM at the 80 left (panels A-D) and 20left (panels E-H) time slices in EX*var* scenario.
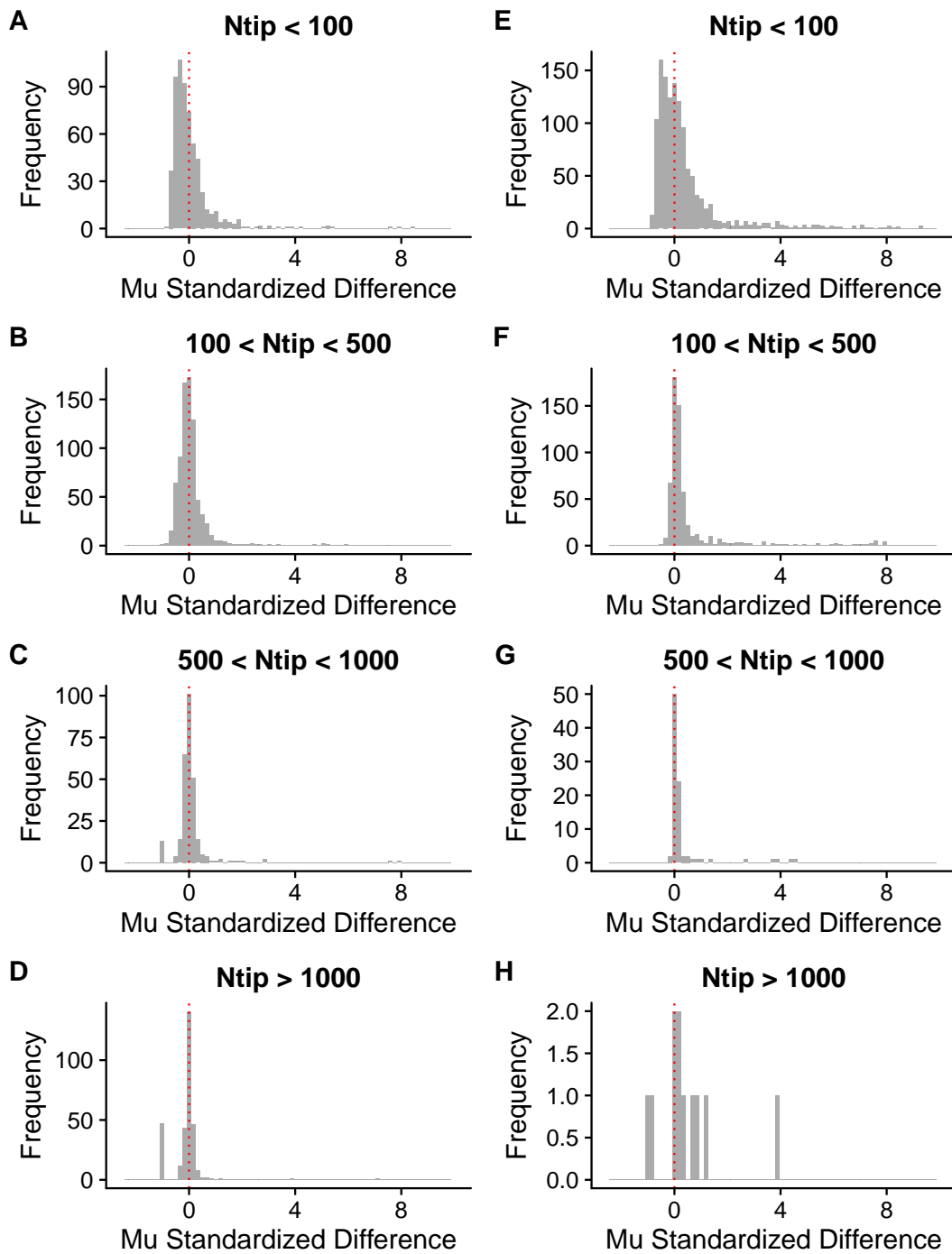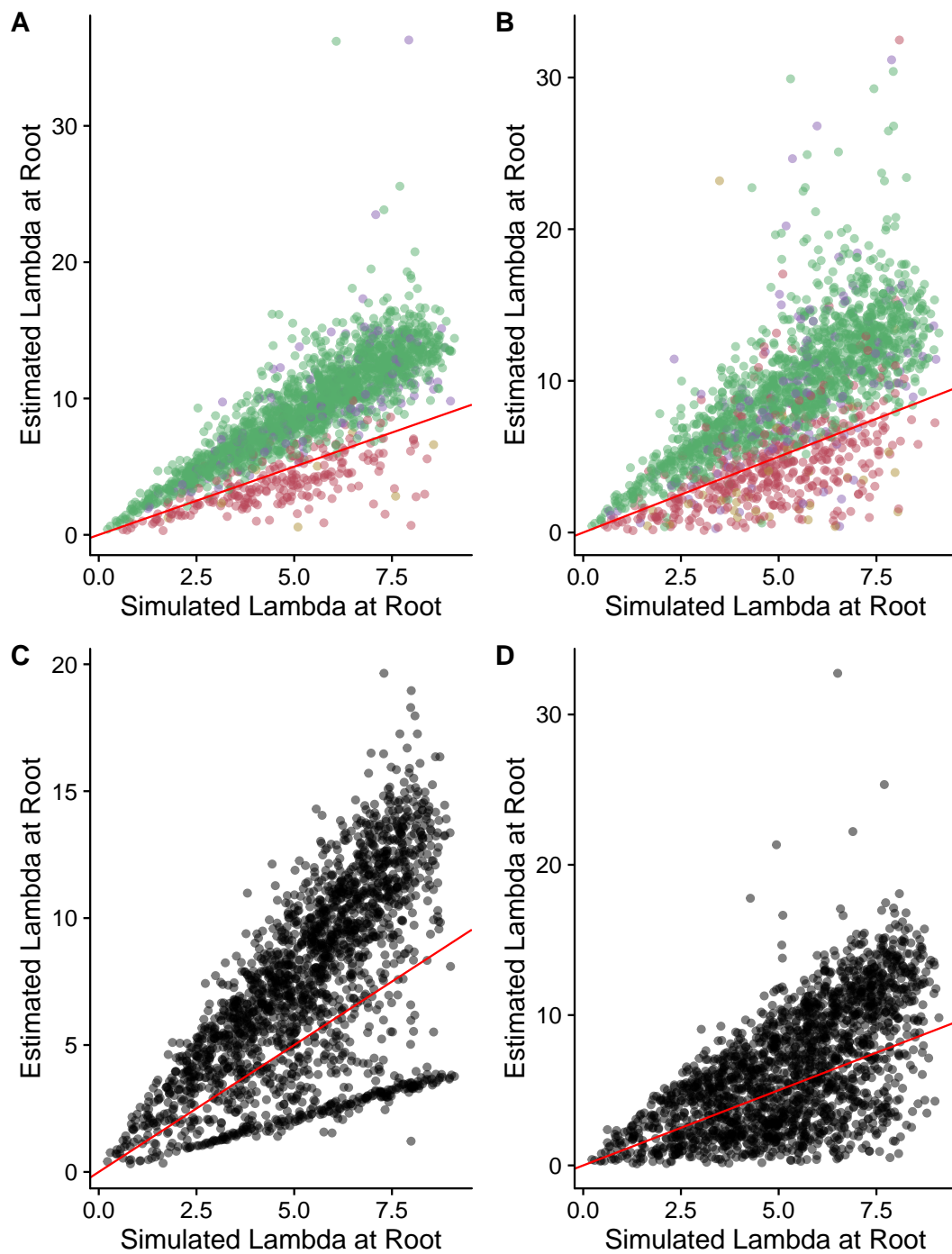
FIGURE B.17: Estimates of speciation rates at the root for RPANDA (upper panels) and BAMM (lower panels) for the 80left (panels A, E, C and G) and 20left (panels B, F, D and H) time slices in the SPvar scenario.
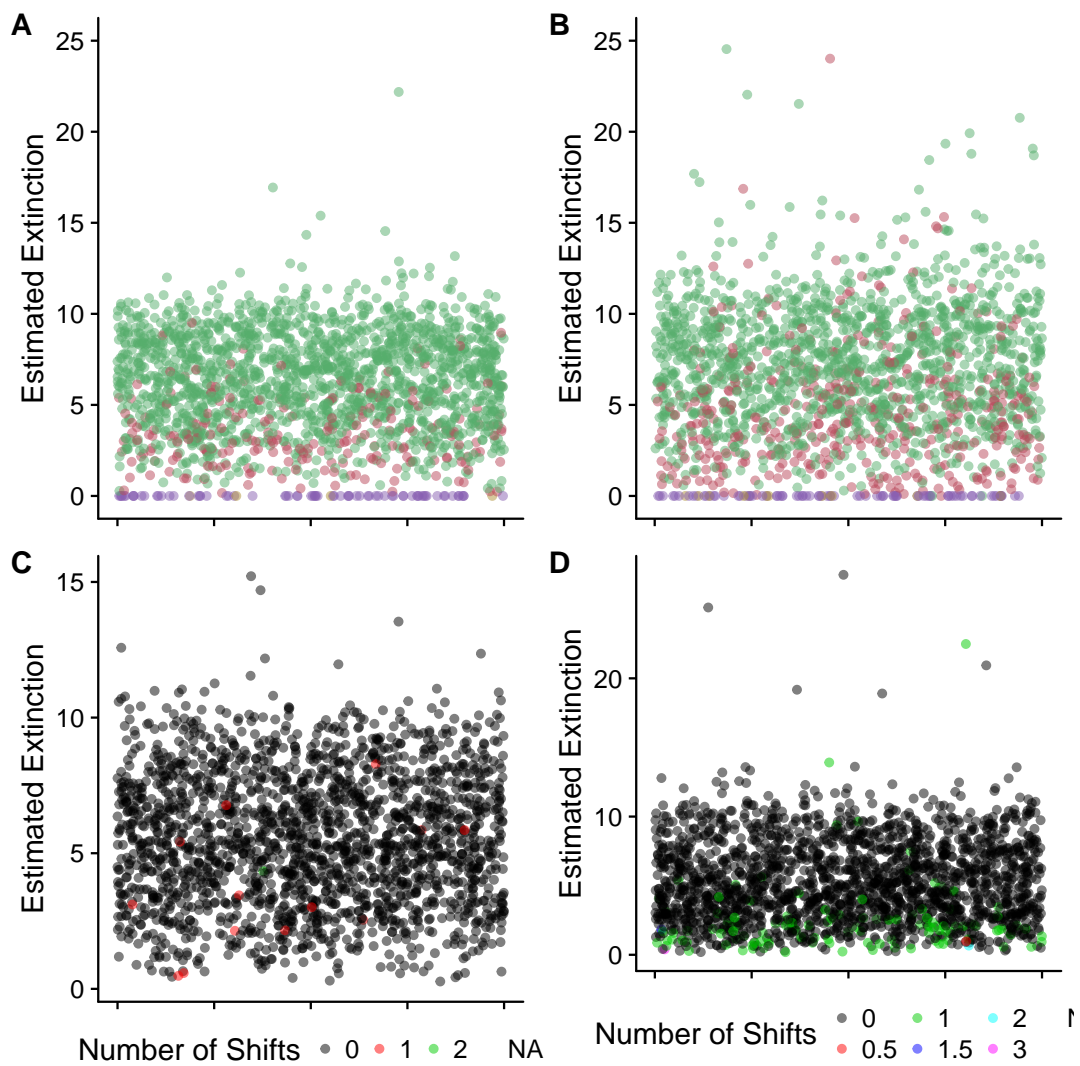
FIGURE B.18: Distribution of estimated extinction rates at the root for RPANDA (upper panels) and BAMM (bottom panels) for the 80left (left) and 20left (right) time slices in the EXvar scenario.
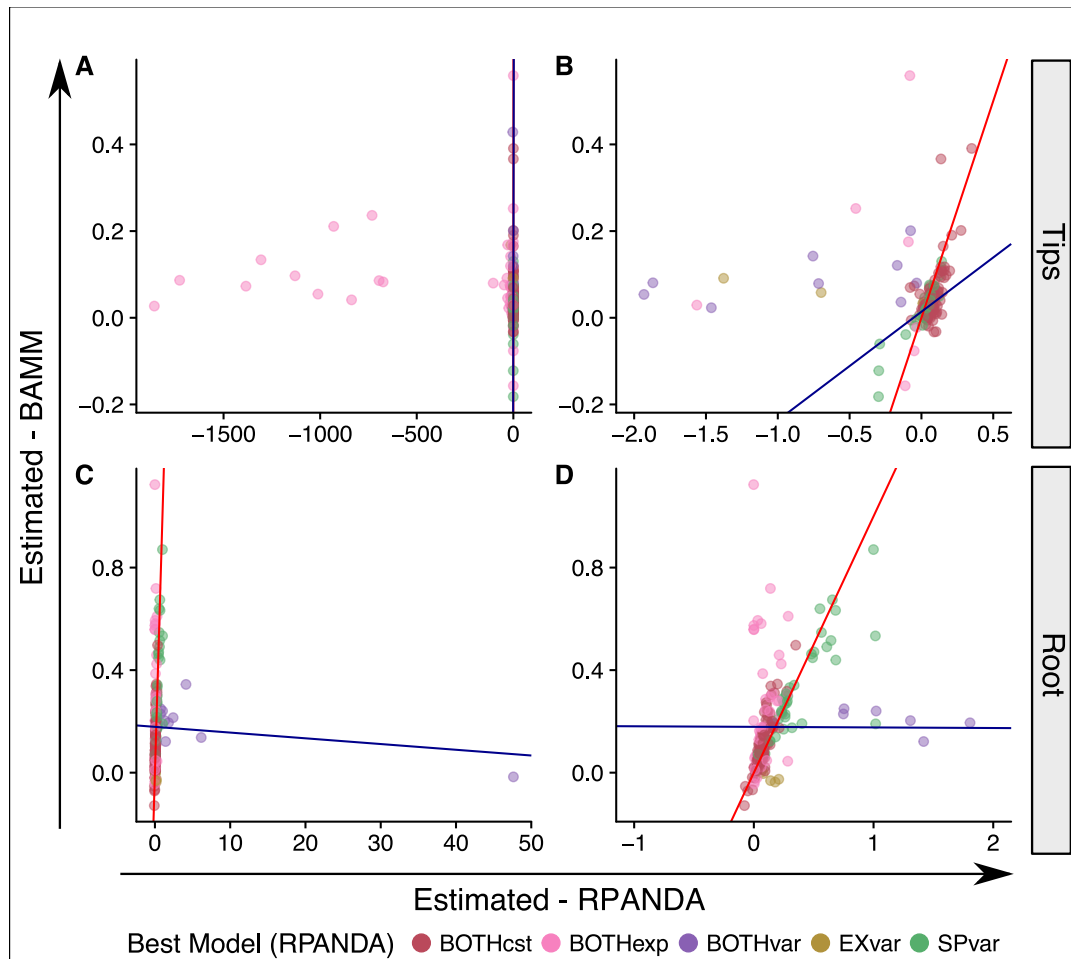
FIGURE B.19: Estimated rates for BAMM (y axis) and RPANDA (x axis) for (A - B) Net diversification at the tips, (C - D) net diversification rates at the root (original in C). Panels A and C are the full plot, whereas panels B and D show detailed views of the other panels. The red line represents the perfect association (estimates from BAMM and RPANDA are equal), and the blue line represents a linear fit between the two variables. $R^2$ values are shown in supplementary table 1.
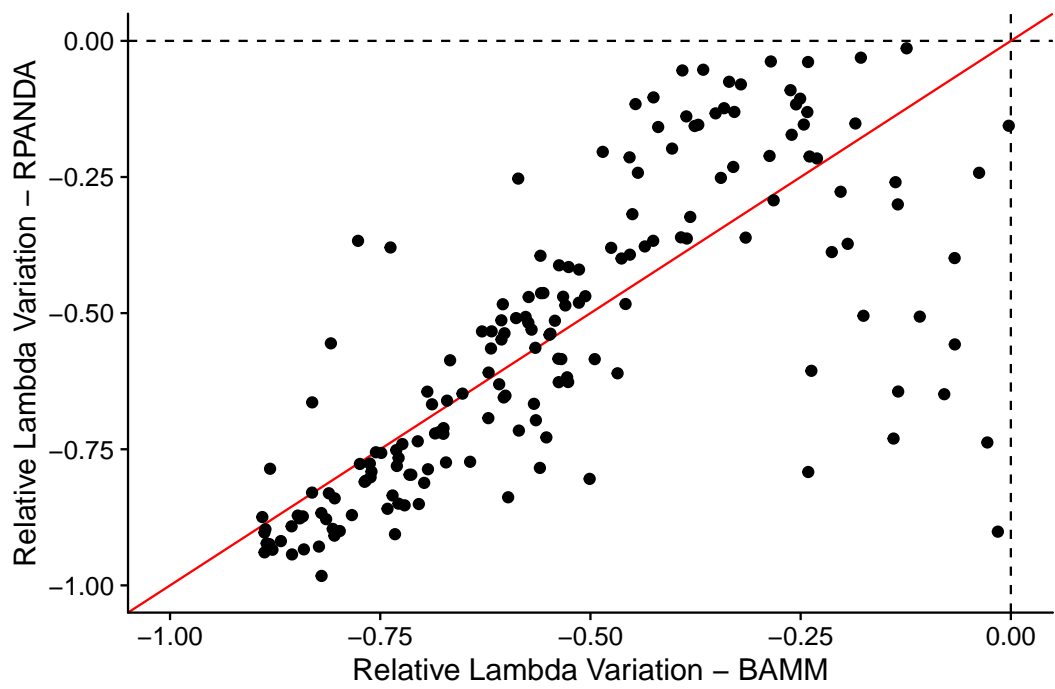
FIGURE B.20: Relative speciation rate variation ([lambda at tips - lambda at root]/max(lambda at tips, lambda at root)) of RPANDA using estimates of the SP*var* model (regardless of being the best model) as a function of the same index for BAMM.
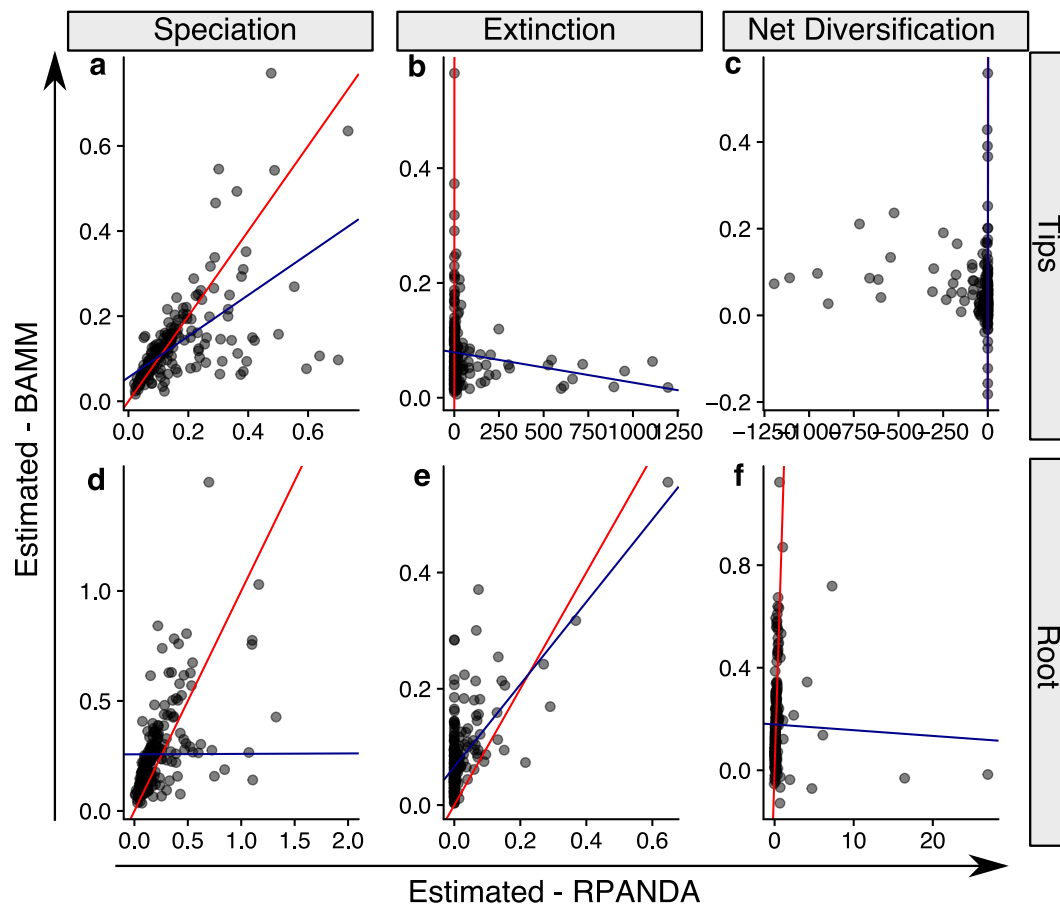
FIGURE B.21: Estimated rates for BAMM (y axis) and RPANDA (x axis) for (a and d) speciation rates at the tips and root, respectively; (b and e) extinction rates at the tips and root, respectively; and (c and f) net diversification at the tips and root, respectively. The red line represents the perfect correlation (estimates from BAMM and RPANDA are equal), and the blue line represents a linear fit between the two variables.
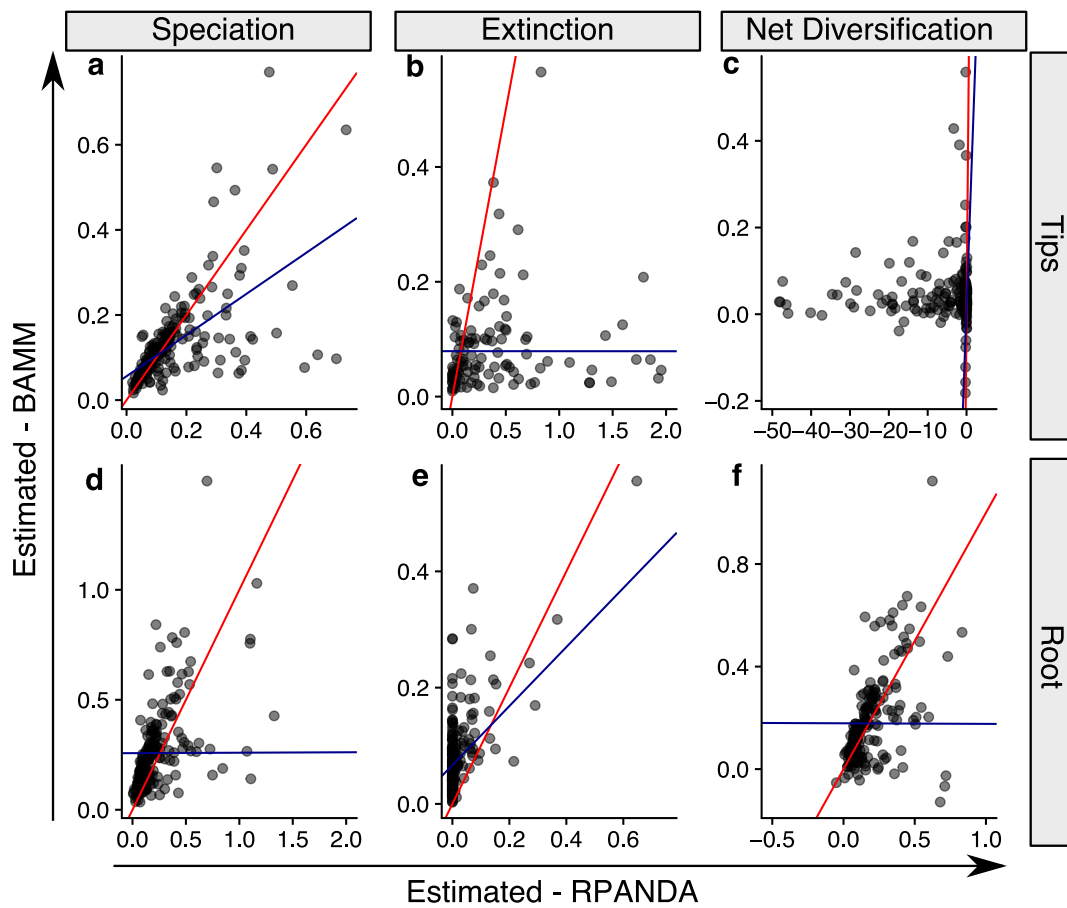
FIGURE B.22: Details (different scale for better visualization) of estimated rates for BAMM (y axis) and RPANDA (x axis) for (a and d) speciation rates at the tips and root, respectively; (b and e) extinction rates at the tips and root, respectively; and (c and f) net diversification at the tips and root, respectively. The red line represents the perfect correlation (estimates from BAMM and RPANDA are equal), and the blue line represents a linear fit between the two variables.

FIGURE B.23: Rate through time plots of all empirical trees (black lines: speciation rates, red lines: extinction rates)

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FIGURE B.23: Rate through time plots of all empirical trees (black lines: speciation rates, red lines: extinction rates)

FIGURE B.24: Distribution of standardized gamma values for empirical trees with or without decline for both RPANDA (a) and BAMM (b).

## B.2 Supplementary Tables

TABLE B.1: Number of trees for which the true model was between the two equally likely models.

|  | *20left* | *50left* | *80left* | *80rise* |
|---|---|---|---|---|
| SPvar | 1935 | 1987 | 1987 | 1808 |
| EXvar | 99 | 48 | 32 | 108 |

TABLE B.2: Number of trees for which RPANDA detected each tested model as the best model, separated by whether the tree was inferred to be in decline or not.

|  |  | Decline | No Decline | Total |
|---|---|---|---|---|
|  | BOTHcst | 5 | 113 | 118 |
|  | EXvar | 3 | 2 | 5 |
| RPANDA | SPvar | 6 | 30 | 36 |
|  | BOTHvar | 10 | 2 | 12 |
|  | BOTHexp | 43 | 0 | 43 |
|  | Total | 67 | 147 | 214 |

TABLE B.3: $R^2$ values for the linear models between rate estimates of BAMM and model-averaged rates of RPANDA. Values in bold are significant ($p < 0.05$).

|  | Lambda | | Mu | | Net Diversification | |
|---|---|---|---|---|---|---|
|  | Tip | Root | Tip | Root | Tip | Root |
| Full Dataset | **0.374** | -0.004 | 0.014 | **0.433** | **0.293** | -0.004 |
| Without BOTHexp | **0.759** | -0.006 | 0.0004 | **0.608** | **0.334** | 0.003 |
| Without varying extinction | **0.727** | 0.092 | 0.0002 | **0.671** | **0.259** | 0.012 |
| Only varying extinction | **0.549** | **0.627** | -0.023 | **0.437** | **0.456** | **0.513** |

TABLE B.4: Percentage of empirical trees with gamma values that are significantly negative. Numbers in parenthesis represent the absolute number of trees.

| | Total trees | Decline RPANDA | Decline BAMM | Decreasing speciation RPANDA | Decreasing speciation BAMM |
|---|---|---|---|---|---|
| Gamma value significantly negative | 40.60% (87 out of 214) | 59.70% (40 out of 67) | 61.40% (8 out of 13) | 81.25% (39 out of 48) | 48% (83 out of 173) |
| Percentage of each scenario with negative Gamma | 100% (87 out of 87) | 46% (40 out of 87) | 9.20% (8 out of 87) | 44.80% (39 out of 87) | 95.40% (83 out of 87) |

# Appendix C

# Supplementary Material - Chapter 3

## C.1 Supplementary Figures
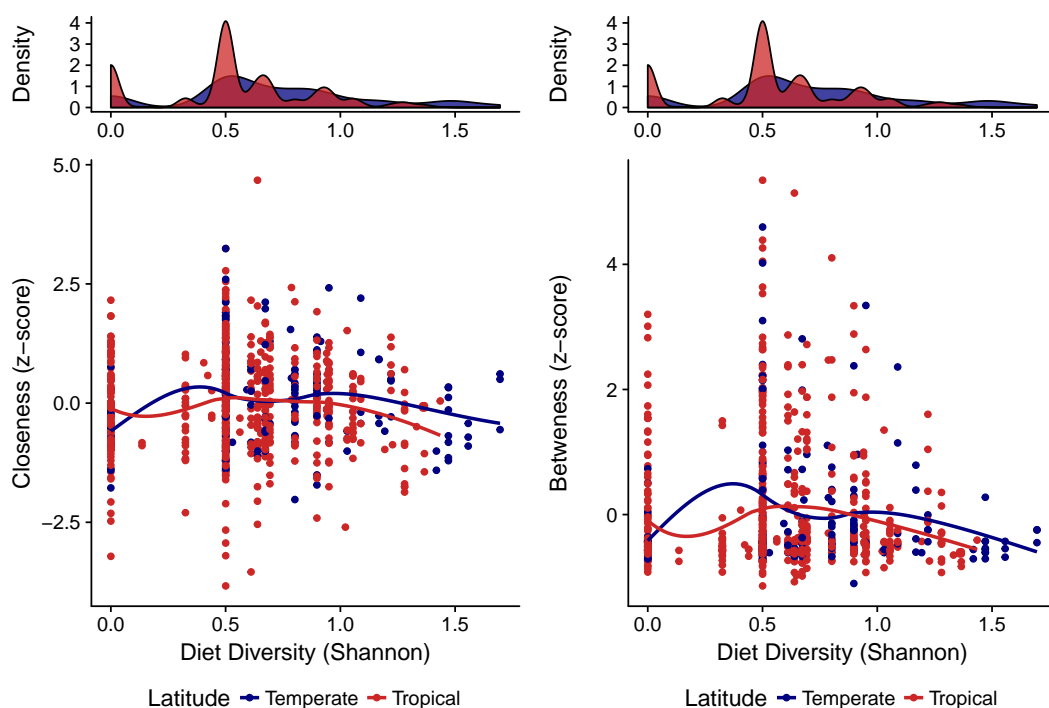


FIGURE C.1: Distribution of z-score values of a) betweenness and b) closeness centrality according to the dietary diversity of species. The indices of dietary diversity consist in the Shannon diversity index calculated using the dietary vectors of each species according to the database used in the first chapter. The histograms on the upper row represent the distribution of dietary diversity indexes.
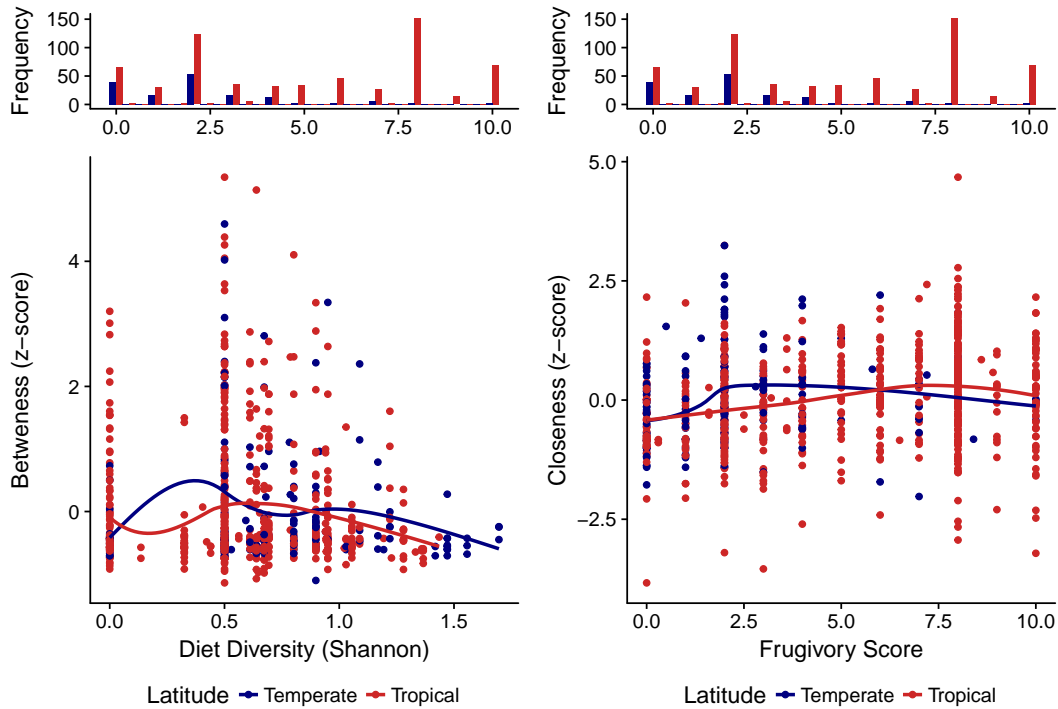
FIGURE C.2: Distribution of z-score values of a) betweenness and b) closeness centrality according to the frugivory degree of species. The indices of dietary diversity consist in the Shannon diversity index calculated using the dietary vectors of each species according to the database used in the first chapter. The histograms on the upper row represent the distribution of frugivory degree.

## C.2   Supplementary Table

TABLE C.1: Information about the networks used in the study, with nestedness and modularity values (raw and z-scores). (Modified from Pigot et al., 2016).

| Network | Bird Species | Plant Species | Number of observed individual Interactions | Network Type | Location | Latitude (binary) | Latitude (degrees) | Hemisphere | Longitude (degrees) | Hemisphere | Nestedness | Nestedness (z-score) | Modularity | Modularity (z-score) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BAIR | 21 | 7 | 655 | Quantitative | Princeton, USA | Temperate | 40.33 | N | 74.67 | W | 50.98 | 2.81 | 0.31 | -0.76 |
| BEEH | 9 | 31 | 1189 | Quantitative | Mount Missim, New Guinea | Tropical | 7.27 | S | 146.7 | E | 67.66 | 6.61 | 0.21 | -1.73 |
| CACG | 15 | 25 | 230 | Quantitative | Caguana, Puerto Rico | Tropical | 18.3 | N | 66.78 | W | 44.82 | 5.67 | 0.39 | -1.47 |
| CACI | 20 | 34 | 478 | Quantitative | Cialitos, Puerto Rico | Tropical | 18.34 | N | 66.47 | W | 43.38 | 7.93 | 0.39 | -2.51 |
| CACO | 13 | 25 | 122 | Quantitative | Cordillera, Puerto Rico | Tropical | 18.34 | N | 66.47 | W | 29.69 | 3.96 | 0.53 | 0.19 |
| CAFR | 15 | 21 | 118 | Quantitative | Fronton, Puerto Rico | Tropical | 18.34 | N | 66.47 | W | 34.17 | 4.22 | 0.47 | -0.58 |
| CROM | 7 | 72 | 143 | Binary | Queensland | Tropical | 17.85 | S | 146.08 | E | 51.67 | 8.89 | 0.31 | -2.44 |
| DOWS | 15 | 120 | 333 | Binary | Highlands, Malawi | Tropical | 10.8 | S | 33.8 | E | 35.12 | 9.1 | 0.39 | 1.61 |
| FROS | 9 | 16 | 3267 | Quantitative | Mtunzini, South Africa | Temperate | 28.96 | S | 31.75 | E | 80.71 | 2.66 | 0.12 | -0.93 |
| GEN1 | 18 | 7 | 150 | Quantitative | Santa Genebra Reserve T1, Brazil | Tropical | 22.82 | S | 47.11 | W | 34.24 | -0.04 | 0.39 | 0.06 |
| GEN2 | 29 | 35 | 397 | Quantitative | Santa Genebra Reserve T2, Brazil | Tropical | 22.82 | S | 47.11 | W | 35.49 | 8.19 | 0.37 | -1.92 |
| GORCH | 7 | 37 | 29 | Quantitative | Loreto, Peru | Tropical | 4.92 | S | 73.75 | W | 43.78 | 3.86 | 0.37 | -0.52 |
| GORCH2 | 6 | 6 | 200 | Quantitative | Loreto, Peru | Tropical | 4.92 | S | 73.75 | W | 71.39 | 1.3 | 0.24 | -0.48 |
| HAMM | 16 | 29 | 175 | Binary | North Negros, Philippines | Tropical | 10.68 | N | 123.18 | E | 49.65 | 2.47 | 0.32 | 4.89 |
| HRAT | 17 | 16 | 34044 | Quantitative | Hato Ratón, Spain | Temperate | 37.15 | N | 2.65 | W | 78.76 | 6.85 | 0.22 | 0.12 |
| KANT | 25 | 5 | 80 | Binary | Campeche state, Mexico | Tropical | 18.51 | N | 89.39 | W | 69.42 | 1.51 | 0.17 | 0.04 |
| KITA | 22 | 12 | 73 | Binary | Khao Yai, Thailand | Tropical | 14.17 | N | 101.38 | E | 35.91 | 0.71 | 0.35 | 0.1 |
| LAMB | 60 | 25 | 504 | Binary | Krau Game Reserve, Malaysia | Tropical | 3.72 | N | 102.28 | E | 58.94 | 11.04 | 0.21 | 0.07 |
| MACK | 29 | 28 | 58 | Binary | Crater Mountain, New Guinea | Tropical | 6.72 | S | 145.09 | E | 11.03 | 2.45 | 0.66 | 0.04 |
| MONT | 40 | 169 | 666 | Binary | Monteverde, Costa Rica | Tropical | 10.3 | N | 84.8 | W | 32.87 | 18.59 | 0.4 | 3.58 |
| NCOR | 33 | 25 | 7010 | Quantitative | Nava Correhuelas, Spain | Temperate | 38.16 | N | 2.74 | W | 58.98 | 12.39 | 0.31 | -2.31 |
| NNOG | 28 | 18 | 129 | Binary | Nava Noguera, Spain | Temperate | 38.16 | N | 2.74 | W | 61.52 | 9.88 | 0.28 | -2.24 |

TABLE C.1: Information about the networks used in the study, with nestedness and modularity values (raw and z-scores). (Modified from Pigot et al., 2016).

| Network | Bird Species | Plant Species | Number of observed individual Interactions | Network Type | Location | Latitude (binary) | Latitude (degrees) | Hemisphere | Longitude (degrees) | Hemisphere | Nestedness | Nestedness (z-score) | Modularity | Modularity (z-score) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| POULI | 19 | 4 | 292 | Quantitative | Panama | Tropical | 8.97 | N | 79.53 | W | 48.29 | 1.48 | 0.33 | -1.55 |
| POULI2 | 11 | 13 | 1415 | Quantitative | Panama | Tropical | 8.97 | N | 79.53 | W | 73.9 | 4.75 | 0.25 | 0.27 |
| SAAV1 | 36 | 34 | 354 | Quantitative | Andes, Bolivia | Tropical | 16.41 | S | 67.53 | W | 26.09 | 9.5 | 0.46 | -1.8 |
| SAAV2 | 21 | 20 | 145 | Quantitative | Andes, Bolivia | Tropical | 16.41 | S | 67.53 | W | 22.43 | 3.73 | 0.57 | -0.11 |
| SAPF | 8 | 15 | 60 | Quantitative | Yakushima Island, Japan | Temperate | 30.34 | N | 130.51 | E | 66.8 | 4.45 | 0.32 | -0.87 |
| SARM | 8 | 28 | 41 | Binary | Atlantic forest, Brazil | Tropical | 8.97 | S | 36.05 | W | 21.07 | 1.5 | 0.54 | 0.55 |
| SCHLE | 83 | 32 | 154 | Quantitative | Kakamega Forest, Kenya | Tropical | 0.28 | N | 34.78 | E | 33.15 | 13.32 | 0.3 | -4.23 |
| SOREN | 14 | 11 | 2745 | Quantitative | Wytham Woods, UK | Temperate | 51.78 | N | 1.31 | W | 45.41 | 1.6 | 0.34 | -0.28 |
| STEIB | 31 | 31 | 844 | Quantitative | Hesse, Germany | Temperate | 50.65 | N | 9.16 | E | 53.85 | 11.73 | 0.29 | -3.24 |
| VELHO | 29 | 6 | 626 | Quantitative | Arunchal Pradesh, India | Tropical | 27 | N | 92.77 | E | 50.16 | 2.9 | 0.37 | 0.52 |
| VELHO2 | 23 | 6 | 700 | Quantitative | Arunchal Pradesh, India | Tropical | 27.02 | N | 92.55 | E | 48.8 | 2.14 | 0.39 | -0.2 |
| WES | 81 | 178 | 975 | Binary | Intervales and Saibadela, Brazil | Tropical | 14.27 | S | 48.41 | W | 22.3 | 25.48 | 0.33 | -2.23 |

# Bibliography

Abrahamczyk, Stefan and Michael Kessler (2014). "Morphological and behavioural adaptations to feed on nectar: how the feeding ecology determines the diversity and composition of hummingbird assemblages". In: *Journal of Ornithology*, pp. 1–15. ISSN: 2193-7192.

Afik, Daniel and William H Karasov (1995). "The trade-offs between digestion rate and efficiency in warblers and their ecological implications". In: *Ecology* 76.7, pp. 2247–2257. ISSN: 00129658.

Alencar, Laura R V, Tiago B Quental, Felipe G Grazziotin, Michael L Alfaro, Marcio Martins, Mericien Venzon, and Hussam Zaher (2016). "Diversification in vipers: Phylogenetic relationships, time of divergence and shifts in speciation rates." In: *Mol Phylogenet Evol* 105, pp. 50–62.

Alroy, John (1996). "Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals". In: *Palaeogeography, Palaeoclimatology, Palaeoecology* 127.1-4, pp. 285–311. ISSN: 00310182.

Alroy, John et al. (2010). "Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates". In: *Quantitative methods in paleobiology. Paleontological Society Papers* 16, pp. 55–80.

Analytics, Revolution and Steve Weston (2015a). *doMC: Foreach Parallel Adaptor for 'parallel'*. R package version 1.3.4.

– (2015b). *foreach: Provides Foreach Looping Construct for R*. R package version 1.4.3.

Ballabeni, P and M Rahier (2000). "A quantitative genetic analysis of leaf beetle larval performance on two natural host: incluiding a mixed diet". In: *Journal of Evolutionary Biology* 13.2000, pp. 98–106.

Bapst, David W (2012). "paleotree : an R package for paleontological and phylogenetic analyses of evolution". In: *Methods in Ecology and Evolution* 3.5, pp. 803–807. ISSN: 2041210X.

Barnagaud, Jean-Yves, W Daniel Kissling, Brody Sandel, Wolf L Eiserhardt, Çağan H. Şekercioğlu, Brian J Enquist, Constantinos Tsirogiannis, Jens-Christian Svenning, Cağan H Sekercioğlu, Brian J Enquist, Constantinos Tsirogiannis, and Jens-Christian Svenning (2014). "Ecological traits influence the phylogenetic structure of bird species co-occurrences worldwide." In: *Ecology Letters* 17.7. Ed. by David Mouillot, pp. 811–20. ISSN: 1461-0248.

Barraclough, Timothy G and Sean Nee (2001). "Phylogenetics and speciation". In: *Trends in Ecology & Evolution* 16.7, pp. 391–399.

Bascompte, Jordi, Pedro Jordano, Carlos J Melián, and Jens M Olesen (2003). "The nested assembly of plant–animal mutualistic networks". In: *Proceedings of the National Academy of Sciences* 100.16, pp. 9383–9387.

Bavelas, Alex (1950). "Communication patterns in task-oriented groups". In: *The Journal of the Acoustical Society of America* 22.6, pp. 725–730.

Beaulieu, Jeremy M. and Brian C. O'Meara (2015). "Extinction can be estimated from moderately sized molecular phylogenies." In: *Evolution* 69.4, pp. 1036–1043. ISSN: 00143820.

Benton, Michael J (2009). "The Red Queen and the Court Jester: Species Diversity and the Role of Biotic and Abiotic Factors Through Time". In: *Science* 323.5915, pp. 728–732. ISSN: 0036-8075.

Blüthgen, Nico, Jochen Fründ, Diego P Vázquez, and Florian Menzel (2008). "What do interaction network metrics tell us about specialization and biological traits". In: *Ecology* 89.12, pp. 3387–3399.

Bonacich, Phillip (1972). "Factoring and weighting approaches to status scores and clique identification". In: *Journal of Mathematical Sociology* 2.1, pp. 113–120.

Bonner, John Tyler (2011). *Why size matters: from bacteria to blue whales*. Princeton University Press.

Bréda, Nathalie, Roland Huc, André Granier, and Erwin Dreyer (2006). "Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences". In: *Annals of Forest Science* 63.6, pp. 625–644.

Brown, William L and Edward O Wilson (1956). "Character displacement". In: *Systematic zoology* 5.2, pp. 49–64.

Büchi, Lucie and Séverine Vuilleumier (2014). "Coexistence of specialist and generalist species is shaped by dispersal and environmental factors." In: *The American Naturalist* 183.5, pp. 612–24. ISSN: 1537-5323.

Burin, Gustavo, W. Daniel Kissling, Paulo R. Guimarães, Çağan H. Şekercioğlu, and Tiago B. Quental (2016). "Omnivory in birds is a macroevolutionary sink". In: *Nature Communications* 7, p. 11250. ISSN: 2041-1723.

Cantalapiedra, Juan L, Richard G Fitzjohn, Tyler S Kuhn, Manuel Hernández Fernández, Daniel Demiguel, Beatriz Azanza, Jorge Morales, and Arne Ø Mooers (2014). "Dietary innovations spurred the diversification of ruminants during the Caenozoic." In: *Proceedings of the Royal Society B: Biological Sciences* 281.1776, p. 20132746. ISSN: 1471-2954.

Carnicer, Jofre, Pedro Jordano, and Carlos J Melián (2009). "The temporal dynamics of resource use by frugivorous birds: a network approach". In: *Ecology* 90.7, pp. 1958–1970.

Condamine, Fabien L., Jonathan Rolland, and Hélène Morlon (2013). "Macroevolutionary perspectives to environmental change". In: *Ecology Letters* 16, pp. 72–85. ISSN: 1461-0248.

Cooper, W (2002). "Convergent evolution of plant chemical discrimination by omnivorous and herbivorous scleroglossan lizards". In: *Journal of Zoology* 257.1, pp. 53–66. ISSN: 09528369.

Coyne, J.A. and H.A. Orr (2006). *Speciation*. Sinauer. ISBN: 9780878930890.

Currie, David J, Gary G Mittelbach, Howard V Cornell, Richard Field, Jean-Francois Guégan, Bradford A Hawkins, Dawn M Kaufman, Jeremy T Kerr, Thierry Oberdorff, Eileen O'Brien, et al. (2004). "Predictions and tests of

climate-based hypotheses of broad-scale variation in taxonomic richness". In: *Ecology letters* 7.12, pp. 1121–1134.

Davis, Naomi E, Dennis J O'Dowd, Ralph Mac Nally, and Peter T Green (2009). "Invasive ants disrupt frugivory by endemic island birds". In: *Biology Letters*, rsbl20090655.

De León, Luis Fernando, Gregor Rolshausen, Eldredge Bermingham, Jeffrey Podos, and Andrew P Hendry (2012). "Individual specialization and the seeds of adaptive radiation in Darwin's finches". In: *Evolutionary Ecology Research* 14.4, pp. 365–380.

Díaz-Castelazo, Cecilia, Paulo R Guimarães, Pedro Jordano, John N Thompson, Robert J Marquis, and Víctor Rico-Gray (2010). "Changes of a mutualistic network over time: reanalysis over a 10-year period". In: *Ecology* 91.3, pp. 793–801.

Dormann, Carsten F, Jochen Fründ, Nico Blüthgen, and Bernd Gruber (2009). "Indices, graphs and null models: analyzing bipartite ecological networks". In: *The Open Ecology Journal* 2, pp. 7–24.

Dunne, Jennifer A, Richard J Williams, Neo D Martinez, Rachel A Wood, and Douglas H Erwin (2008). "Compilation and network analyses of Cambrian food webs". In: *PLoS biology* 6.4, e102.

Ehrlich, Paul R and Peter H Raven (1964). "Butterflies and plants: a study in coevolution". In: *Evolution* 18.4, pp. 586–608.

Fick, Stephen E and Robert J Hijmans (2017). "WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas". In: *International Journal of Climatology*.

Field, Richard, Eileen M O'Brien, and Robert J Whittaker (2005). "Global models for predicting woody plant richness from climate: development and evaluation". In: *Ecology* 86.9, pp. 2263–2277.

FitzJohn, Richard G (2010). "Quantitative traits and diversification". In: *Systematic biology* 59.6, pp. 619–633.

FitzJohn, Richard G. (2012). "Diversitree : comparative phylogenetic analyses of diversification in R". In: *Methods in Ecology and Evolution* 3.6, pp. 1084–1092. ISSN: 2041210X.

FitzJohn, Richard G, Wayne P Maddison, and Sarah P Otto (2009). "Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies". In: *Systematic biology* 58.6, pp. 595–611.

Fleming, Theodore H and Nathan Muchhala (2008). "Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems". In: *Journal of Biogeography* 35.5, pp. 764–780.

Foote, Michael (2007). "Symmetric waxing and waning of marine invertebrate genera". In: *Paleobiology* 33.4, pp. 517–529. ISSN: 0094-8373.

Futuyma, D. (2009). *Evolution*. Sinauer. ISBN: 0878931880.

Futuyma, Douglas J and Anurag A Agrawal (2009). "Macroevolution and the biological diversity of plants and herbivores". In: *Proceedings of the National Academy of Sciences* 106.43, pp. 18054–18061.

Gaekde, Ursula, Silke Hochstädter, and Dietmar Straile (2002). "Erratum: Interplay between Energy Limitation and Nutritional Deficiency: Empirical

Data and Food-Web Models". In: *Ecological Monographs* 72.4, pp. 251–270. ISSN: 00129615.

Garcia-R, Juan C, Gillian C Gibb, and Steve a Trewick (2014). "Deep global evolutionary radiation in birds: Diversification and trait evolution in the cosmopolitan bird family Rallidae." In: *Molecular Phylogenetics and Evolution* 81C, pp. 96–108. ISSN: 1095-9513.

Gilinsky, Norman (1994). "Volatility and the Phanerozoic decline of background extinction intensity". In: *Paleobiology* 20.4, pp. 445–458. ISSN: 0036-8075.

Gilinsky, Norman L and Richard K Bambach (1987). "Asymmetrical pattrns of origination and extinction in higher taxa". In: *Paleobiology* 13.May 2013, pp. 427–445.

Godoy, Oscar, Nathan J. B. Kraft, and Jonathan M. Levine (2014). "Phylogenetic relatedness and the determinants of competitive outcomes". In: *Ecology Letters* 17.7. Ed. by Jerome Chave, pp. 836–844. ISSN: 1461023X.

Goldberg, Emma E, Joshua R Kohn, Russell Lande, Kelly a Robertson, Stephen a Smith, and Boris Igić (2010). "Species selection maintains self-incompatibility." In: *Science* 330.6003, pp. 493–5. ISSN: 1095-9203.

Gómez, José M. and Miguel Verdú (2012). "Mutualism with plants drives primate diversification." In: *Systematic Biology* 61.4, pp. 567–77. ISSN: 1076-836X.

Grant, Peter Rosemary and B Rosemary Grant (2006). "Evolution of character displacement in Darwin's finches." In: *Science* 313.5784, pp. 224–6. ISSN: 1095-9203.

Grant, P.R. and B.R. Grant (2011). *How and Why Species Multiply: The Radiation of Darwin's Finches*. Princeton Series in Evolutionary Biology. Princeton University Press. ISBN: 9780691149998.

Guimarães, Paulo R, Victor Rico-Gray, Sergio Furtado Dos Reis, and John N Thompson (2006). "Asymmetries in specialization in ant–plant mutualistic networks". In: *Proceedings of the Royal Society of London B: Biological Sciences* 273.1597, pp. 2041–2047.

Guimarães Jr, Paulo R, Pedro Jordano, and John N Thompson (2011). "Evolution and coevolution in mutualistic networks". In: *Ecology letters* 14.9, pp. 877–885.

Hardin, G (1960). "The competitive exclusion principle." In: *Science* 131, pp. 1292–1297. ISSN: 0036-8075.

Harmon, Luke J and Susan Harrison (2015). "Species diversity is dynamic and unbounded at local and continental scales". In: *The American Naturalist* 185.5, pp. 584–593.

Harvey, Paul H, Robert M May, and Sean Nee (1994). "Phylogenies without fossils". In: *Evolution* 48.3, pp. 523–529.

Heil, Martin, Marcia González-Teuber, Lars W Clement, Stefanie Kautz, Manfred Verhaagh, and Juan Carlos Silva Bueno (2009). "Divergent investment strategies of Acacia myrmecophytes and the coexistence of mutualists and exploiters". In: *Proceedings of the National Academy of Sciences* 106.43, pp. 18091–18096.

Hendry, Andrew P, Sarah K Huber, Luis F De Leon, Anthony Herrel, and Jeffrey Podos (2009). "Disruptive selection in a bimodal population of Darwin's finches". In: *Proceedings of the Royal Society of London B: Biological Sciences* 276.1657, pp. 753–759.

Hillebrand, Helmut (2004). "On the generality of the latitudinal diversity gradient". In: *The American Naturalist* 163.2, pp. 192–211.

Hoyo, Josep del, Andrew Elliot, Jordi Sargatal, and David Christie (2013). *Handbook of the Birds of the World: Special Volume: New Species and Global Index*. Lynx Edicions.

Huang, Huateng and Daniel L. Rabosky (2014). "Sexual Selection and Diversification: Reexamining the Correlation between Dichromatism and Speciation Rate in Birds". In: *The American Naturalist* 184.5, E101–E114. ISSN: 00030147.

Hurlbert, Allen H and John P Haskell (2002). "The effect of energy and seasonality on avian species richness and community composition". In: *The American Naturalist* 161.1, pp. 83–97.

Jablonski, David (2008). "Biotic interactions and macroevolution: extensions and mismatches across scales and levels." In: *Evolution* 62.4, pp. 715–39. ISSN: 0014-3820.

Jarvis, Erich D, Siavash Mirarab, Andre J Aberer, Bo Li, Peter Houde, Cai Li, Simon YW Ho, Brant C Faircloth, Benoit Nabholz, Jason T Howard, et al. (2014). "Whole-genome analyses resolve early branches in the tree of life of modern birds". In: *Science* 346.6215, pp. 1320–1331.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers (2012). "The global diversity of birds in space and time." In: *Nature* 491.7424, pp. 444–8. ISSN: 1476-4687.

Jordano, P. (1992). *Seeds: The Ecology of Regeneration in Plant Communities*. Ed. by M. Fenner. CABI Publishing Series. CABI Pub. ISBN: 9780851986777.

Karr, James R (1976). "Within-and between-habitat avian diversity in African and Neotropical lowland habitats". In: *Ecological Monographs* 46.4, pp. 457–481.

Kissling, W D, Cagan H Sekercioglu, and Walter Jetz (2012a). "Bird dietary guild richness across latitudes, environments and biogeographic regions". In: *Global Ecology and Biogeography* 21.3, pp. 328–340. ISSN: 1466822X.

Kissling, W Daniel, Carsten Rahbek, and Katrin Böhning-Gaese (2007). "Food plant diversity as broad-scale determinant of avian frugivore richness". In: *Proceedings of the Royal Society of London B: Biological Sciences* 274.1611, pp. 799–808.

Kissling, W Daniel, Katrin Böhning-Gaese, and Walter Jetz (2009). "The global distribution of frugivory in birds". In: *Global Ecology and Biogeography* 18.2, pp. 150–162.

Kissling, W Daniel, Wolf L Eiserhardt, William J Baker, Finn Borchsenius, Thomas LP Couvreur, Henrik Balslev, and Jens-Christian Svenning (2012b). "Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide". In: *Proceedings of the National Academy of Sciences* 109.19, pp. 7379–7384.

Krishna, Abhay, Paulo R Guimaraes Jr, Pedro Jordano, and Jordi Bascompte (2008). "A neutral-niche theory of nestedness in mutualistic networks". In: *Oikos* 117.11, pp. 1609–1618.

Lartillot, Nicolas and Frédéric Delsuc (2012). "Joint reconstruction of divergence times and life-history evolution in placental mammals using a phylogenetic covariance model". In: *Evolution* 66.6, pp. 1773–1787.

Lavergne, Sébastien, Nicolas Mouquet, Wilfried Thuiller, and Ophélie Ronce (2010). "Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities". In: *Annual review of ecology, evolution, and systematics* 41, pp. 321–350.

Lefcheck, Jonathan S, Matthew A Whalen, Theresa M Davenport, Joshua P Stone, and J Emmett Duffy (2013). "Physiological effects of diet mixing on consumer fitness: a meta-analysis". In: *Ecology* 94.3, pp. 565–572.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez (2004). "The metacommunity concept: A framework for multi-scale community ecology". In: *Ecology Letters* 7.7, pp. 601–613. ISSN: 1461023X. arXiv: 2042.

Levin, S.A., S.R. Carpenter, H.C.J. Godfray, A.P. Kinzig, M. Loreau, J.B. Losos, B. Walker, and D.S. Wilcove (2009). *The Princeton Guide to Ecology*. Princeton University Press. ISBN: 9781400833023.

Lewitus, Eric and Helene Morlon (2016). "Characterizing and Comparing Phylogenies from their Laplacian Spectrum." In: *Syst Biol* 65.3, pp. 495–507.

Liow, Lee Hsiang and Nils Chr Stenseth (2007). "The rise and fall of species: implications for macroevolutionary and macroecological studies". In: *Proceedings of the Royal Society of London B: Biological Sciences* 274.1626, pp. 2745–2752. ISSN: 0962-8452. eprint: http : / / rspb . royalsocietypublishing.org/content/274/1626/2745.full. pdf.

Liow, Lee Hsiang, Tiago B Quental, and Charles R Marshall (2010). "When can decreasing diversification rates be detected with molecular phylogenies and the fossil record?" In: *Systematic Biology* 59.6, pp. 646–59. ISSN: 1076-836X.

Liow, Lee Hsiang, Trond Reitan, and Paul G. Harnik (2015). "Ecological interactions on macroevolutionary time scales: clams and brachiopods are more than ships that pass in the night". In: *Ecology Letters* 18.10, pp. 1030–1039. ISSN: 1461023X.

MacAarthur, R and R Levins (1964). "Competition, Habitat Selection, and Character Displacement in a Patchy Environment". In: *Proceedings of the National Academy of Sciences* 51, pp. 1207–1210. ISSN: 0027-8424.

Macarthur, Robert H and Richard Levins (1967). "The Limiting Similarity, Convergence, and Divergence of Coexisting Species". In: *The American Naturalist* 101.921, pp. 377–385. ISSN: 10773711.

MacArthur, Robert H and Eric R Pianka (1966). "On Optimal Use of a Patchy Environment". In: *The American Naturalist* 100.916, pp. 603–609.

Maddison, Wayne P. and Richard G. FitzJohn (2014). "The Unsolved Challenge to Phylogenetic Correlation Tests for Categorical Characters". In: *Systematic Biology* 64.1, pp. 127–136. ISSN: 1063-5157.

Maddison, Wayne P, Peter E Midford, and Sarah P Otto (2007). "Estimating a binary character's effect on speciation and extinction." In: *Systematic Biology* 56.5, pp. 701–10. ISSN: 1063-5157.

Marquitti, Flavia Maria Darcie, Paulo Roberto Guimarães, Mathias Mistretta Pires, and Luiz Fernando Bittencourt (2014). "MODULAR: software for the autonomous computation of modularity in large network sets". In: *Ecography* 37.3, pp. 221–224.

Marshall, Charles R (2007). "Explaining latitudinal diversity gradients". In: *Science* 317.5837, pp. 451–453.

Marshall, Charles R and Tiago B Quental (2016). "The uncertain role of diversity dependence in species diversification and the need to incorporate time-varying carrying capacities". In: *Phil. Trans. R. Soc. B* 371.1691, p. 20150217.

Martínez del Rio, C., H. G. Baker, and I Baker (1992). *Ecological and evolutionary implications of digestive processes: Bird preferences and the sugar constituents of floral nectar and fruit pulp*.

Martins, Emilia P and Thomas F Hansen (1997). "Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data". In: *The American Naturalist* 149.4, pp. 646–667.

McPeek, Mark A (2008). "The ecological dynamics of clade diversification and community assembly". In: *The American Naturalist* 172.6, E270–E284.

Melián, Carlos J, Jordi Bascompte, Pedro Jordano, and Vlastimil Krivan (2009). "Diversity in a complex ecological network with two interaction types". In: *Oikos* 118.1, pp. 122–130.

Mello, Marco Aurelio Ribeiro, Francisco Aparecido Rodrigues, Luciano da Fontoura Costa, W Daniel Kissling, Çağan H Şekercioğlu, Flavia Maria Darcie Marquitti, and Elisabeth Klara Viktoria Kalko (2015). "Keystone species in seed dispersal networks are mainly determined by dietary specialization". In: *Oikos* 124.8, pp. 1031–1039.

Mittelbach, Gary G, Douglas W Schemske, Howard V Cornell, Andrew P Allen, Jonathan M Brown, Mark B Bush, Susan P Harrison, Allen H Hurlbert, Nancy Knowlton, Harilaos A Lessios, et al. (2007). "Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography". In: *Ecology letters* 10.4, pp. 315–331.

Moore, Brian R, Sebastian Höhna, Michael R May, Bruce Rannala, and John P Huelsenbeck (2016). "Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures." In: *Proc Natl Acad Sci U S A* 113.34, pp. 9569–9574.

Morlon, H, E Lewitus, F L Condamine, M Manceau, J Clavel, and J Drury (2016). "RPANDA: an R package for macroevolutionary analyses on phylogenetic trees". In: *Methods Ecol Evol*, n/a–n/a. ISSN: 2041210X.

Morlon, Hélène (2014). "Phylogenetic approaches for studying diversification". In: *Ecology Letters* 17.4. Ed. by Arne Mooers, pp. 508–525. ISSN: 1461023X.

Morlon, Hélène, Matthew D Potts, and Joshua B Plotkin (2010). "Inferring the dynamics of diversification: a coalescent approach." In: *PLoS Biol* 8.9. ISSN: 1545-7885.

Morlon, Hélène, Todd L Parsons, and Joshua B Plotkin (2011). "Reconciling molecular phylogenies with the fossil record." In: *Proceedings of the National Academy of Sciences of the United States of America* 108.39, pp. 16327–16332. ISSN: 1091-6490.

Nee, S, R M May, and P H Harvey (1994). "The Reconstructed Evolutionary Process". In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 344.1309, pp. 305–311. ISSN: 0962-8436.

Nichols, James D and Kenneth H Pollock (1983). "Estimating taxonomic diversity, extinction rates, and speciation rates from fossil data using capture-recapture models". In: *Paleobiology*, pp. 150–163.

Noë, Ronald and Peter Hammerstein (1994). "Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating". In: *Behavioral ecology and sociobiology* 35.1, pp. 1–11.

Nosil, P. (2012). *Ecological Speciation*. Oxford Series in Ecology and Evolution. OUP Oxford. ISBN: 9780191628023.

Nuismer, Scott L, Pedro Jordano, and Jordi Bascompte (2013). "Coevolution and the architecture of mutualistic networks". In: *Evolution* 67.2, pp. 338–354.

O'Donnell, Sean, Corina J Logan, and Nicola S Clayton (2012). "Specializations of birds that attend army ant raids: An ecological approach to cognitive and behavioral studies". In: *Behavioural Processes* 91.3, pp. 267–274. ISSN: 03766357.

Olesen, Jens M, Jordi Bascompte, Yoko L Dupont, and Pedro Jordano (2007). "The modularity of pollination networks". In: *Proceedings of the National Academy of Sciences* 104.50, pp. 19891–19896.

Olesen, Jens M, Jordi Bascompte, Yoko L Dupont, Heidi Elberling, Claus Rasmussen, and Pedro Jordano (2010). "Missing and forbidden links in mutualistic networks". In: *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20101371.

Pagel, Mark (1999). "The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies". In: *Systematic biology* 48.3, pp. 612–622.

Paradis, Emmanuel (2005). "Statistical analysis of diversification with species traits". In: *Evolution* 59.1, pp. 1–12.

Peters, Shanan E (2005). "Geologic constraints on the macroevolutionary history of marine animals." In: *Proc Natl Acad Sci U S A* 102.35, pp. 12326–12331. ISSN: 0027-8424.

Phillimore, Albert B and Trevor D Price (2008). "Density-dependent cladogenesis in birds". In: *PLoS biology* 6.3, e71.

Pigot, Alexander L, Tom Bregman, Catherine Sheard, Benjamin Daly, Rampal S Etienne, and Joseph A Tobias (2016). "Quantifying species contributions

to ecosystem processes: a global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks". In: *Proc. R. Soc. B*. Vol. 283. 1844. The Royal Society, p. 20161597.

Price, Samantha A and Samantha S B Hopkins (2015). "The macroevolutionary relationship between diet and body mass across mammals". In: *Biological Journal of the Linnean Society*.

Price, Samantha A, Samantha S B Hopkins, Kathleen K Smith, and V Louise Roth (2012). "Tempo of trophic evolution and its impact on mammalian diversification." In: *Proceedings of the National Academy of Sciences* 109.18, pp. 7008–12. ISSN: 1091-6490.

Prum, Richard O, Jacob S Berv, Alex Dornburg, Daniel J Field, Jeffrey P Townsend, Emily Moriarty Lemmon, and Alan R Lemmon (2015). "A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing". In: *Nature*.

Pybus, O G and P H Harvey (2000). "Testing macro-evolutionary models using incomplete molecular phylogenies." In: *Proceedings of the Royal Society B: Biological Sciences* 267.1459, pp. 2267–72. ISSN: 0962-8452.

Pyron, R Alexander and Frank T Burbrink (2012). "Extinction, ecological opportunity, and the origins of global snake diversity". In: *Evolution* 66.1, pp. 163–178.

Quental, Tiago B and Charles R Marshall (2009). "Extinction during evolutionary radiations: reconciling the fossil record with molecular phylogenies." In: *Evolution* 63.12, pp. 3158–67. ISSN: 1558-5646.

– (2010). "Diversity dynamics: molecular phylogenies need the fossil record." In: *Trends Ecol Evol (Amst)* 25.8, pp. 434–441.

– (2011). "The molecular phylogenetic signature of clades in decline." In: *PLoS ONE* 6.10. Ed. by Carles Lalueza-Fox, e25780. ISSN: 1932-6203.

– (2013). "How the Red Queen drives terrestrial mammals to extinction." In: *Science* 341.6143, pp. 290–2. ISSN: 1095-9203.

R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria.

Rabosky, Daniel L. (2010). "Extinction rates should not be estimated from molecular phylogenies." In: *Evolution* 64.6, pp. 1816–1824. ISSN: 00143820.

Rabosky, Daniel L (2014). "Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees." In: *PLoS ONE* 9.2, e89543.

Rabosky, Daniel L (2016). "Challenges in the estimation of extinction from molecular phylogenies: A response to Beaulieu and O'Meara." In: *Evolution* 70.1, pp. 218–228.

Rabosky, Daniel L. and Emma E. Goldberg (2015). "Model Inadequacy and Mistaken Inferences of Trait-Dependent Speciation". In: *Systematic Biology* 64.2, pp. 340–355. ISSN: 1063-5157. arXiv: 1412.7082.

Rabosky, Daniel L and Allen H Hurlbert (2015). "Species richness at continental scales is dominated by ecological limits". In: *The American Naturalist* 185.5, pp. 572–583.

Rabosky, Daniel L and Irby J Lovette (2008). "Density-dependent diversification in North American wood warblers." In: *Proceedings of the Royal Society B: Biological Sciences* 275.1649, pp. 2363–71. ISSN: 0962-8452.

Rabosky, Daniel L and Amy R McCune (2010). "Reinventing species selection with molecular phylogenies". In: *Trends in Ecology & Evolution* 25.2, pp. 68–74.

Rabosky, Daniel L, Francesco Santini, Jonathan Eastman, Stephen a Smith, Brian Sidlauskas, Jonathan Chang, and Michael E Alfaro (2013). "Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation." In: *Nature Communications* 4, p. 1958. ISSN: 2041-1723.

Rabosky, Daniel L., Michael Grundler, Carlos Anderson, Pascal Title, Jeff J. Shi, Joseph W. Brown, Huateng Huang, and Joanna G. Larson (2014). "BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees". In: *Methods in Ecology and Evolution* 5.7, pp. 701–707. ISSN: 2041-210X.

Rabosky, Daniel L, Jonathan S Mitchell, and Jonathan Chang (2017). "Is BAMM flawed? Theoretical and practical concerns in the analysis of multirate diversification models." In: *Syst Biol*.

Raubenheimer, David, Steven J Simpson, and David Mayntz (2009). "Nutrition, ecology and nutritional ecology: toward an integrated framework". In: *Functional Ecology* 23.1, pp. 4–16.

Raup, D M (1986). "Biological extinction in earth history." In: *Science* 231, pp. 1528–1533.

Ricklefs, Robert E (2007). "Estimating diversification rates from phylogenetic information." In: *Trends Ecol Evol (Amst)* 22.11, pp. 601–610.

– (2011). "A biogeographical perspective on ecological systems: some personal reflections". In: *Journal of Biogeography* 38.11, pp. 2045–2056.

Ricklefs, Robert E and David G Jenkins (2011). "Biogeography and ecology: towards the integration of two disciplines". In: *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 366.1576, pp. 2438–2448.

Robinson, David F and Leslie R Foulds (1981). "Comparison of phylogenetic trees". In: *Mathematical biosciences* 53.1-2, pp. 131–147.

Roggenbuck, Michael, Ida Bærholm Schnell, Nikolaj Blom, Jacob Bælum, Mads Frost Bertelsen, Thomas Sicheritz-Pontén, Søren Johannes Sørensen, M Thomas P Gilbert, Gary R Graves, and Lars H Hansen (2014). "The microbiome of New World vultures". In: *Nature communications* 5.

Rojas, Danny, Angel Vale, Victoria Ferrero, and Luis Navarro (2012). "The role of frugivory in the diversification of bats in the Neotropics". In: *Journal of Biogeography* 39.11, pp. 1948–1960.

Rolland, Jonathan, Frédéric Jiguet, Knud Andreas Jønsson, Fabien L Condamine, and Hélène Morlon (2014). "Settling down of seasonal migrants promotes bird diversification". In: *Proc. R. Soc. B* 281.1784, p. 20140473.

Roopnarine, Peter D (2006). "Extinction cascades and catastrophe in ancient food webs". In: *Paleobiology* 32.1, pp. 1–19. ISSN: 0094-8373.

Roopnarine, Peter D. (2010). "Networks, Extinction and Paleocommunity Food Webs". In: *The Paleontological Society Papers* 16, 143–161.

Roopnarine, Peter D, Kenneth D Angielczyk, Steve C Wang, and Rachel Hertog (2007). "Trophic network models explain instability of Early Triassic terrestrial communities". In: *Proceedings of the Royal Society of London B: Biological Sciences* 274.1622, pp. 2077–2086.

Root, Richard B (1967). "The niche exploitation pattern of the blue-gray gnatcatcher". In: *Ecological monographs* 37.4, pp. 317–350.

Rosenblum, Erica Bree, Brice AJ Sarver, Joseph W Brown, Simone Des Roches, Kayla M Hardwick, Tyler D Hether, Jonathan M Eastman, Matthew W Pennell, and Luke J Harmon (2012). "Goldilocks meets Santa Rosalia: an ephemeral speciation model explains patterns of diversification across time scales". In: *Evolutionary Biology* 39.2, pp. 255–261.

Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press. ISBN: 9780521499521.

Roslin, Tomas, Bess Hardwick, Vojtech Novotny, William K Petry, Nigel R Andrew, Ashley Asmus, Isabel C Barrio, Yves Basset, Andrea Larissa Boesing, Timothy C Bonebrake, et al. (2017). "Higher predation risk for insect prey at low latitudes and elevations". In: *Science* 356.6339, pp. 742–744.

Sabidussi, Gert (1966). "The centrality index of a graph". In: *Psychometrika* 31.4, pp. 581–603.

Sakamoto, Manabu, Michael J Benton, and Chris Venditti (2016). "Dinosaurs in decline tens of millions of years before their final extinction." In: *Proc Natl Acad Sci U S A*. ISSN: 0027-8424.

Sazima, Cristina, Paulo R Guimarães, Sérgio F Dos Reis, and Ivan Sazima (2010). "What makes a species central in a cleaning mutualism network?" In: *Oikos* 119.8, pp. 1319–1325.

Schluter, Dolph (2000). "Ecological character displacement in adaptive radiation". In: *the american naturalist* 156.S4, S4–S16.

Sekercioglu, Cagan H (2011). "Functional extinctions of bird pollinators cause plant declines". In: *Science* 331.6020, pp. 1019–1020.

Şekercioğlu, Çağan H, Gretchen C Daily, and Paul R Ehrlich (2004). "Ecosystem consequences of bird declines". In: *Proceedings of the National Academy of Sciences* 101.52, pp. 18042–18047.

Silvestro, Daniele, Jan Schnitzler, Lee Hsiang Liow, Alexandre Antonelli, and Nicolas Salamin (2014a). "Bayesian estimation of speciation and extinction from incomplete fossil occurrence data." In: *Systematic Biology* 63.3, pp. 349–67. ISSN: 1076-836X.

Silvestro, Daniele, Georg Zizka, and Katharina Schulte (2014b). "Disentangling the effects of key innovations on the diversification of Bromelioideae (Bromeliaceae)". In: *Evolution* 68.1, pp. 163–175.

Silvestro, Daniele, Alexandre Antonelli, Nicolas Salamin, and Tiago B Quental (2015). "The role of clade competition in the diversification of North American canids." In: *Proceedings of the National Academy of Sciences* 112.28, pp. 8684–8689. ISSN: 1091-6490.

Snow, David W. (1981). "Tropical Frugivorous Birds and Their Food Plants: A World Survey". In: *Biotropica* 13.1, pp. 1–14. ISSN: 00063606, 17447429.

Soons, Joris, Anthony Herrel, Annelies Genbrugge, Peter Aerts, Jeffrey Podos, Dominique Adriaens, Yoni De Witte, Patric Jacobs, and Joris Dirckx

(2010). "Mechanical stress, fracture risk and beak evolution in Darwin's ground finches (Geospiza)". In: *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365.1543, pp. 1093–1098.

Spotswood, Erica N, Jean-Yves Meyer, and James W Bartolome (2012). "An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia". In: *Journal of Biogeography* 39.11, pp. 2007–2020.

Stadler, T (2013a). "Recovering speciation and extinction dynamics based on phylogenies". In: *Journal of evolutionary biology* 26.6, pp. 1203–1219.

Stadler, Tanja (2009). "On incomplete sampling under birth–death models and connections to the sampling-based coalescent". In: *Journal of theoretical biology* 261.1, pp. 58–66.

– (2013b). "How can we improve accuracy of macroevolutionary rate estimates?" In: *Systematic Biology* 62.2, pp. 321–9. ISSN: 1076-836X.

Stanley, Steven M (1990). "The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages". In: *Causes of evolution: a paleontological perspective.* Ed. by Robert M Ross and Warren D Almon. University of Chicago Press, Chicago, pp. 103–127.

– (2007). "An Analysis of the History of Marine Animal Diversity". In: *Paleobiology* 33.sp6, pp. 1–55. ISSN: 0094-8373.

Starrfelt, Jostein and Lee Hsiang Liow (2016). "How many dinosaur species were there? Fossil bias and true richness estimated using a Poisson sampling model." In: *Philos Trans R Soc Lond, B, Biol Sci* 371.1691, p. 20150219.

Straub, Cory S, Anthony R Ives, and Claudio Gratton (2011). "Evidence for a trade-off between host-range breadth and host-use efficiency in aphid parasitoids". In: *The American Naturalist* 177.3, pp. 389–395.

Switzer, William M, Marco Salemi, Vedapuri Shanmugam, Feng Gao, et al. (2005). "Ancient co-speciation of simian foamy viruses and primates". In: *Nature* 434.7031, p. 376.

Tange, O. (2011). "GNU Parallel - The Command-Line Power Tool". In: *;login: The USENIX Magazine* 36.1, pp. 42–47.

Thébault, Elisa and Colin Fontaine (2010). "Stability of ecological communities and the architecture of mutualistic and trophic networks". In: *Science* 329.5993, pp. 853–856.

Thompson, J.N. (2013). *Relentless Evolution.* EBSCOhost ebooks online. University of Chicago Press. ISBN: 9780226018898.

Thompson, John N (2005). *The geographic mosaic of coevolution.* University of Chicago Press.

Thompson, John N and Mary F Willson (1979). "Evolution of temperate fruit/bird interactions: phenological strategies". In: *Evolution* 33.3, pp. 973–982.

Traveset, Anna, Jens M Olesen, Manuel Nogales, Pablo Vargas, Patricia Jaramillo, Elena Antolín, María Mar Trigo, and Ruben Heleno (2015). "Bird–flower visitation networks in the Galápagos unveil a widespread interaction release". In: *Nature communications* 6.

Vamosi, Jana C, W Scott Armbruster, and Susanne S Renner (2014). "Evolutionary ecology of specialization: insights from phylogenetic analysis". In: *Proc. R. Soc. B* 281, p. 20142004.

Van Valen, Leigh M (1985). "A theory of origination and extinction". In: *Evolutionary Theory* 7.3, pp. 133–142.

Vermeij, Geerat J (1987). "The dispersal barrier in the tropical Pacific: implications for molluscan speciation and extinction". In: *Evolution*, pp. 1046–1058.

Vrba, Elisabeth S (1984). "What is species selection?" In: *Systematic Zoology* 33.3, pp. 318–328.

Waide, RB, MR Willig, CF Steiner, G Mittelbach, L Gough, SI Dodson, GP Juday, and R Parmenter (1999). "The relationship between productivity and species richness". In: *Annual Review of Ecology and Systematics* 30.1, pp. 257–300.

Weir, Jason T and Dolph Schluter (2007). "The latitudinal gradient in recent speciation and extinction rates of birds and mammals". In: *Science* 315.5818, pp. 1574–1576.

Wheelwright, Nathaniel T (1988). "Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone". In: *Trends in ecology & evolution* 3.10, pp. 270–274.

Wickham, Hadley and Romain Francois (2016). *dplyr: A Grammar of Data Manipulation*. R package version 0.5.0.

Wilson, David Sloan and Jin Yoshimura (1994). "On the coexistence of specialists and generalists". In: *The American Naturalist* 144.4, pp. 692–707.

# Abstract

To understand how diversity varies through time and/or space we need to understand speciation and extinction dynamics, and ultimately which factors (biotic or abiotic) affect such dynamics. It has been argued that biological interactions play an important role on the diversification of organisms, but macroevolutionary studies have usually adopted a simple characterization of species interactions. On the other hand ecological studies usually focus on well-characterized interactions of very few species. A network approach can augment our understanding of the ecological roles played by different species but it still lacks an evolutionary perspective preventing us to fully understand how ecological interactions are assembled. Using the available phylogeny, dietary data for virtually all bird species (approximately 9965 species) and a large collection of frugivory networks, we tested the effect of diet on the diversification of birds, and the relationship between ecological roles within interaction networks and diversification dynamics of frugivorous species. Lastly, using computational simulations, we assessed the performance of two state-of-the-art methods to estimate diversification rates using molecular phylogenies. We suggest that omnivory acts as macroevolutionary sink where its ephemeral nature is retrieved through transitions from other guilds rather than from omnivore speciation. We propose that these dynamics result from competition within and among dietary guilds, influenced by the deep-time availability and predictability of food resources. We also observed that in the temperate zone, lineages with high-paced evolutionary dynamics (e.g. higher turnover rates) typically do not occupy central roles in frugivory networks, and that these restrictions are modulated by water availability/predictability. Lastly, we found that the two state-of-the

art phylogenetic methods perform equally well in diversity decline scenarios when estimating current rates, but both fail to detect the true diversification trajectory when extinction rates vary in time. This dissertation contributes to the understanding of biotic and abiotic mechanisms driving both the diversification and the assembly of interaction networks, and also provides important information on the reliability of diversification rate estimates by current, widely used methods.

# Resumo

Para entendermos como a biodiversidade varia no tempo e/ou no espaço precisamos entender a dinâmcia de especiação e extinção, e quais fatores (bióticos ou abióticos) afetam essa dinâmica. Acredita-se que as interações biológicas desempenham um papel importante na diversificação de organismos, porém estudos macroevolutivos usualmente adotam caracterizações simples de interações entre espécies. Por outro lado, estudos ecológicos comumente focam na descrição detalhada de interações entre poucas espécies. Uma abordagem de redes pode aumentar a compreensão dos papéis ecológicos desempenhados por diferentes espécies, mas a pouca ênfase em abordagens evolutivas em estudos de redes biológicas nos impedem de compreender completamente como essas redes são montadas. Usando a filogenia e dados de dieta disponíveis para virtualmente todas as espécies de aves (aprox. 9965 espécies), e uma grande coleção de redes de frugivoria, investigamos o efeito da dieta na diversificação de aves, e testamos a relação entre papéis ecológicos em redes de interação e a dinâmica da diversificação de espécies frugívoras. Ainda, usando simulações computacionais, avaliamos a performance de dois métodos amplamente utilizados para estimar taxas de diversificação usando filogenias moleculares. Sugerimos que onivoria atua como um ralo macroevolutivo, onde sua natureza efêmera é recuperada através de transições de outras guildas de dieta ao invés de através da especiação de espécies onívoras. Nós sugerimos que essa dinâmica resulta da competição intra- e entre guildas, influenciada pela disponibilidade e previsibilidade de recursos em ampla escalas de tempo. Nós também observamos que em regiões temperadas, linhagens com uma dinâmica evolutiova mais rápida (maiores taxas de substituição de espécies) em geral

não ocupam papéis centrais em redes de frugivoria, e que essas restrições são principalmente modificadas por disponibilidade/previsibilidade hídricas. Por fim, observamos que ambos os métodos filogenéticos testados tem desempenho igualmente bom para estimar taxas atuais, porém ambos falham em detectar a trajetória da diversificação quando as taxas de extinção variam no tempo. Essa tese contribui para o conhecimento de mecanismos bióticos e abióticos que afetam tanto a diversificação quanto a montagem de redes de interação, e também provê informações importantes acerca da confiabilidade das estimativas de taxas de diversificação advindas dos métodos atuais amplamente utilizados.