



The phylogenetic signal of diversification rates

Fernanda S. Caron | Marcio R. Pie

Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil

Correspondence

Marcio R. Pie, Departamento de Zoologia, Universidade Federal do Paraná. C.P. 19020. 81531-990 Curitiba, PR, Brazil.
Email: marcio.pie@gmail.com

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Abstract

Hypotheses to explain the causes of diversity gradients have increasingly focused on the factors that actually change species numbers, namely speciation, extinction and dispersal. A common assumption of many of these hypotheses is that there should be phylogenetic signal in diversification rates, yet this assumption has rarely been tested explicitly. In this study, we compile a large data set including 328,219 species of plants, mammals, amphibians and squamates to assess the level of phylogenetic signal in their diversification rates. Significant phylogenetic signal was detected in all data sets, except for squamates, suggesting not only that closely related clades indeed might share similar diversification rates, but also that the level of phylogenetic signal might vary considerably between them. Moreover, there were intriguing differences among taxa in the rate of decay in phylogenetic autocorrelation over time, underscoring the existence of taxon-specific patterns of phylogenetic autocorrelation. These results have important implications for the development of more realistic models of species diversification.

KEY WORDS

diversity gradients, extinction, niche conservatism, speciation

1 | INTRODUCTION

A major property of life on Earth is its uneven distribution, both in space and among lineages. Geographically, species richness tends to be concentrated at lower latitudes (Hillebrand, 2004; Willig, Kaufmann, & Stevens, 2003), a trend that has been present during intervals of the Palaeozoic and over the past 30 million years (Mannion, Upchurch, Benson, & Goswami, 2014). Interestingly, substantial differences in species richness can occur in similar environments (also known as "diversity anomalies" sensu Ricklefs & Latham, 1993), such as the difference in species richness between mangrove communities in the Indo-West Pacific and the Atlantic/Caribbean regions (Ricklefs & Latham, 1993) and the greater diversity within disjunct genera of angiosperms in eastern Asia compared to eastern North America (Qian & Ricklefs, 2000). Taxonomically, some clades often account for a disproportionately large share of the species richness in any given taxon, such as Phyllostomidae among bats

(Jones, Bininda-Emonds, & Gittleman, 2005), beetles among insects (Farrell, 1998) and angiosperms among plants (Davies et al., 2004). On the other hand, some clades remain as ancient, species-poor relicts, such as *Amborella trichopoda* (Baill.), the sister group to all other flowering plants, and *Mastotermes darwiniensis* (Froggatt, 1897), the sister group to all other termites (Grandcolas, Nattier, & Trewick, 2014; see also Pie & Feitosa, 2016). Although understanding these discrepancies is a major theme in evolutionary biology, only recently have studies focused on hypotheses that are explicitly based on the mechanisms that actually change species numbers, namely speciation, extinction and dispersal (Ricklefs, 2006; Wiens, Graham, Moen, Smith, & Reeder, 2006).

A common approach to the study of lineage diversification is the use of equal rates Markov (ERM) models, under which instantaneous rates of diversification (speciation minus extinction) are equal for all lineages within an evolving clade (Heard & Mooers, 2002). Due to stochastic variation in realized diversification rates,

Contributing author: Fernanda S. Caron (fernandadesouzacaron@gmail.com)

ERM models can lead to trees of many shapes and sizes (Heard & Mooers, 2002), which emulate a variety of patterns found in real clades (Mooers & Heard, 1997). However, an important limitation of ERM models is that they show considerably less variation in richness among clades than what is found in real phylogenies (see Heard and Mooers (2002) and included references). Such discrepancy could be ameliorated by allowing for speciation rates to evolve over time and with the ensuing differences being inherited by the descending lineages (Heard, 1996), yet this mechanism has rarely been tested with real data sets. Harvey, Nee, Mooers, and Partridge (1991) first assessed this possibility by examining whether the shorter of two branches descended from a single common ancestor tends in turn to lead to shorter descendent branches ("branch-length heritability") and found significant evidence for this effect based on the avian phylogeny of Sibley and Ahlquist (1990). The only additional study to test for branch-length heritability was carried out by Savolainen, Heard, Powell, Davies, and Mooers (2002) and showed similar results for bacteria, fungi, orchids, monocots and angiosperms. Although these results are suggestive, they only take into account minimal information about the tree and ignore the species richness associated with each terminal in the studied phylogenies. In this study, the hypothesis of phylogenetic signal in diversification rates is tested using a rigorous, model-based method. Strong

evidence for phylogenetic signal was detected in all data sets, which could suggest that the inheritance of diversification rates might be a general phenomenon.

2 | MATERIALS AND METHODS

Information on phylogenetic relationships and species richness was compiled for seed plants, mammals, squamates and amphibians, with the combined analyses involving over 329,737 species. Relationships between plant families were obtained from Qian and Zhang (2014), which itself was based on previous efforts (Davies et al., 2004; Zanne et al., 2014), whereas species richness data were based on The Plant List (2013). There were slight inconsistencies between their respective taxonomies, but sensitivity analyses indicate that these differences would not affect our conclusions. Mammal phylogenetic relationships and species richness data were obtained from Bininda-Emonds et al. (2007). Amphibian phylogenetic relationships and species richness data were based on Jetz and Pyron (2018). Finally, phylogenetic relationships and species richness of squamate families were obtained from Tonini, Beard, Ferreira, Jetz, and Pyron (2016). Species richness data are provided in Data S1.

FIGURE 1 Phylogenetic distribution of diversification rates in plants, mammals, squamates and amphibians. Rates were rescaled to a maximum of 1 to facilitate visualization. Tree tips correspond to families, and bars to the right represent diversification rates

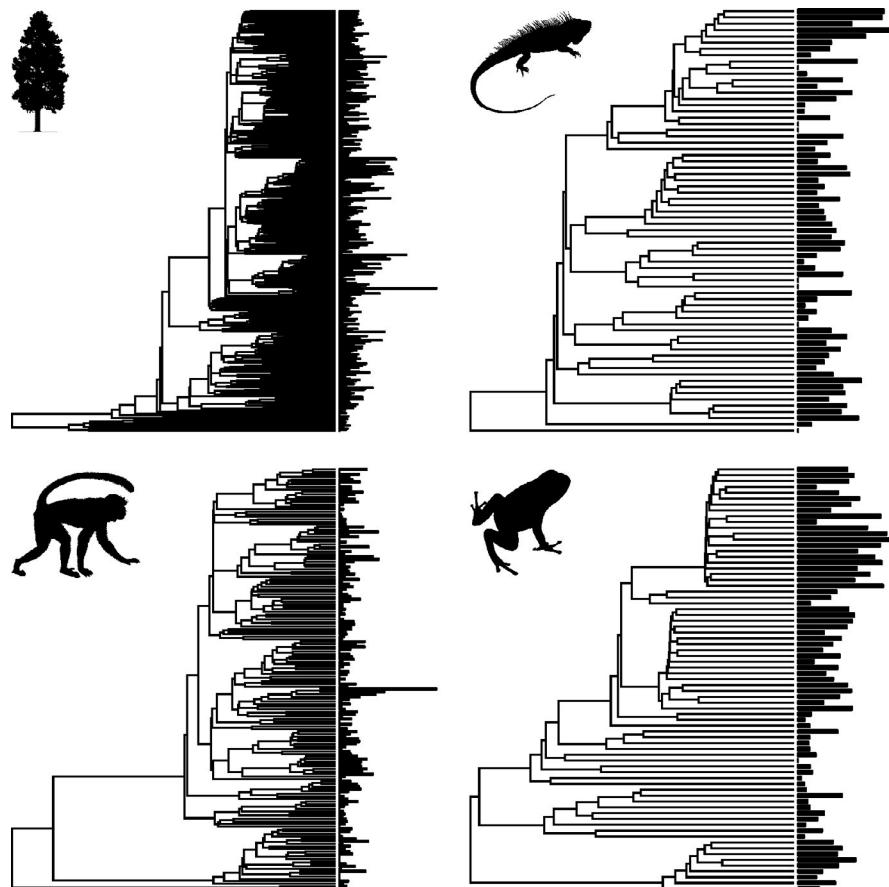


TABLE 1 Estimates of phylogenetic signal of diversification rates based on Pagel's λ

Taxon	Total number of species	λ	logL0	logL
Amphibia	7,238	0.61 (0.53–0.70)	179.5505 (172.3845/187.4458)	186.197 (179.4412/193.1349)
Mammalia	5,832	0.52 (0.43–0.60)	191.6083 (136.1059/217.8352)	196.0943 (141.5353/221.7816)
Tracheophytes	305,394	0.47 (0.48–0.46)	646.8349 (633.0166/660.6532)	674.8261 (660.309/689.3432)
Squamata	9,755	0.01 (0.0001–0.20)	146.0269 (136.9104/155.6151)	146.024 (136.9094/155.6143)

Note: In the case of mammals, estimates were repeated for each of 1,000 post-burnin topologies and parameter estimates and likelihoods are provided as means, followed by 95% credibility intervals in parentheses.

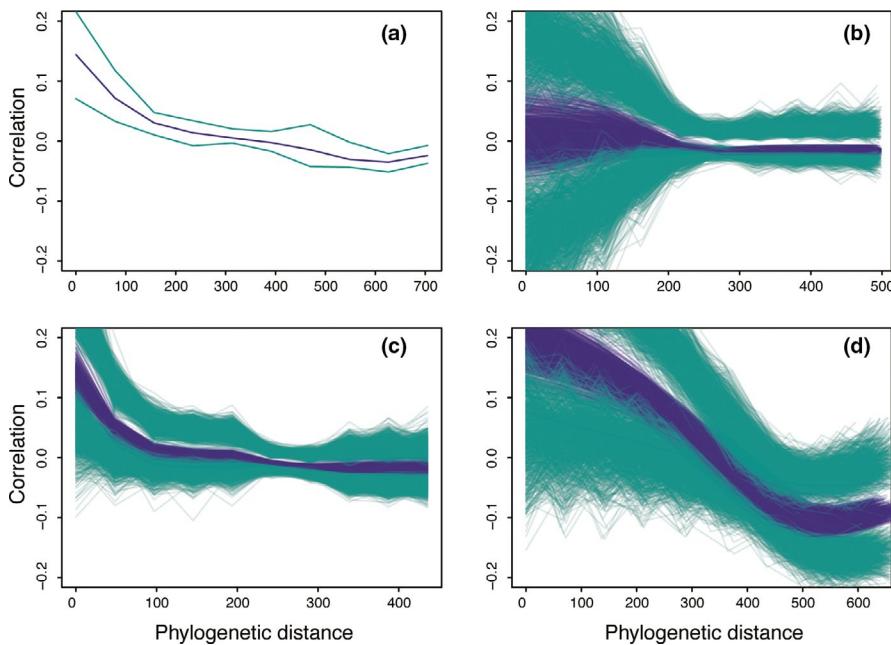


FIGURE 2 Correlograms indicating the level of phylogenetic autocorrelation of diversification rates in plants (a), mammals (b), squamates (c) and amphibians (d). Blue lines correspond to the estimated autocorrelation, whereas green lines indicate upper and lower confidence intervals. Different lines indicate estimates based on alternative underlying topologies. See text for details

In each data set, the tree was pruned so that only one representative of each family was present. The corresponding diversification rate was estimated by the natural logarithm of the current number of species in each taxon, divided by its respective stem age (Magallon & Sanderson, 2001; Raup, 1985). This procedure assumes that the extinction rate is zero, which is definitely not true, yet it should provide a reasonable first approximation, particularly given the inherent difficulties in estimating extinction rates. The extent of phylogenetic signal in the data set was assessed using the λ parameter of Pagel (1999) and tested using likelihood ratio tests using the PHYTOOLS 0.6-60 package (Revell, 2012) in R 3.5.3 (R Core Team, 2019). In addition, we calculated how phylogenetic autocorrelation varied over evolutionary time in the studied taxa by computing correlograms based on Moran's I , as implemented in the phyloCorrelogram function in the PHYLOSIGNAL 1.3 package (Keck, Rimet, Bouchez & franc, 2016) in R 3.5.3 (R Core Team, 2019). Given that a larger sample of possible topologies were available in the case of mammals, squamates and amphibians, the entire process was repeated for each of 1,000 trees in each analysis. It is important to note that each estimate of net diversification rate is not instantaneous but rather an average across the whole terminal branch. Although violation of this assumption might potentially

lead loss of accuracy in our estimates, the resulting effects are unlikely to change our conclusions.

3 | RESULTS AND DISCUSSION

There was considerable variation in diversification rates among lineages (Figure 1), with statistically significant support for phylogenetic signal in diversification rates in all data sets, except for Squamata (Table 1). The highest value for λ was found in amphibians ($\lambda = 0.61$), whereas the lowest was found in squamates ($\lambda = 0.01$; Table 1). Similar patterns were detected in the estimated correlograms, despite variation depending between topologies (Figure 2). These results are largely consistent with those by Harvey et al. (1991) for birds and Savolainen et al. (2002) for angiosperms, even though they used a completely different approach. Given that these results seem robust, one must wonder why lineages show phylogenetically autocorrelated diversification rates. Savolainen et al. (2002) provided two classes of possible explanation. The first involves biogeographical factors: if long-distance dispersal is rare, habitat is generally heritable and may include conditions that might differentially promote diversification.

Alternatively, diversification rates might be influenced by traits in the species themselves, such as mutation rates (Lanfear, Ho, Love, & Bromham, 2010) and range sizes (Waldron, 2007). Discriminating the relative contributions of these two classes of mechanism is challenging, particularly given that the analytical tools to carry out this kind of task have only become available recently (e.g. Freckleton & Jetz, 2009). In addition, it is important to note that phylogenetically patterned extinction might also contribute to the observed patterns. For instance, current extinction risk has been recently demonstrated to be influenced by phylogenetic history in amphibians (Corey & Waite, 2008) and birds (Thomas, 2008, but see Jetz et al. 2014), but not in felids (Diniz-Filho, 2004). These alternative mechanisms are particularly relevant given the considerable variation in phylogenetic signal between taxa (Figures 1 and 2). Discriminating "intrinsic" and "extrinsic" explanations for phylogenetic autocorrelation in speciation and extinction rates is certainly a major challenge for future studies.

An important implication for the results of the present study is related to the possibility of species sorting or clade-level selection (Eldredge, 1989; Stanley, 1975; Vrba, 1984; See Rabosky and McCune (2010) for a review). In particular, differences among clades in their propensity to speciate or go extinct are a prerequisite for evolution above the species level (Williams, 1992). As new and more comprehensive phylogenies become increasingly available, it will be possible to investigate the temporal scale in which phylogenetic autocorrelation in diversification is detected, as well as to develop more mechanistic models of lineage diversification.

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ORCID

Fernanda S. Caron  <https://orcid.org/0000-0002-1884-6157>
 Marcio R. Pie  <https://orcid.org/0000-0002-2949-4871>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Species richness of clades within each studied taxon.

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