Uncovering Higher-Taxon Diversification Dynamics from Clade Age and Species-Richness Data

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Abstract.—The relationship between clade age and species richness has been increasingly used in macroevolutionary studies as evidence for ecologically versus time-dependent diversification processes. However, theory suggests that phylogenetic structure, age type (crown or stem age), and taxonomic delimitation can affect estimates of the age–richness correlation (ARC) considerably. We currently lack an integrative understanding of how these different factors affect ARCs, which in turn, obscures further interpretations. To assess its informative breadth, we characterize ARC behavior with simulated and empirical phylogenies, considering phylogenetic structure and both crown and stem ages. First, we develop a two-state birth–death model to simulate phylogenies including the origin of higher taxa and a hierarchical taxonomy to determine ARC expectations under ecologically and time-dependent diversification processes. Then, we estimate ARCs across various taxonomic ranks of extant amphibians, squamate reptiles, mammals, birds, and flowering plants. We find that our model reproduces the general ARC trends of a wide range of biological systems despite the particularities of taxonomic practice within each, suggesting that the model is adequate to establish a framework of ARC null expectations for different diversification processes when taxa are defined with a hierarchical taxonomy. ARCs estimated with crown ages were positive in all the scenarios we studied, including ecologically dependent processes. Negative ARCs were only found at less inclusive taxonomic ranks, when considering stem age, and when rates varied among clades. This was the case both in ecologically and time-dependent processes. Together, our results warn against direct interpretations of single ARC estimates and advocate for a more integrative use of ARCs across age types and taxonomic ranks in diversification studies. [Birth–Death models; crown age; diversity dependence; extinction; phylogenetic structure; speciation; stem age; taxonomy; time dependence; tree simulations.]

Explaining the causes of the heterogeneous distribution in species numbers (richness) among taxa, communities and regions, and across time, is a fascinating and long-standing problem in evolutionary biology (Darwin 1859; Wallace 1878; Bokma et al. 2014). While many factors have been postulated to explain the heterogeneous distribution of richness we observe in nature, species richness is ultimately the result of the interplay between speciation and extinction, that is, the diversification process. Diversification processes can be represented by various models (Morlon 2014), including the classical 'time-dependent' and the 'ecologically dependent' models. In time-dependent processes, the rate at which new species are generated (speciation rate, λ) and the rate at which species become extinct (extinction rate, μ) vary as a function of time. These models predict that richness is either expanding unbounded through time and space (Yule 1925; Nee et al. 1992) or that it is controlled by increases in μ (Raup et al. 1973; Pyron and Burbrink 2012) or by decreases in λ through time (Morlon et al. 2011). In ecologically dependent processes, the speciation and extinction rates vary according to ecological factors such as the number of species alive at a given time (diversity-dependent process). In these models, richness is expected to be bounded by a macroevolutionary carrying capacity or by extrinsic ecological factors (Mittelbach et al. 2007; Rabosky 2009a).

To evaluate different diversification dynamics one can use empirical phylogenetic and/or taxonomic data and apply a maximum likelihood or Bayesian approach to determine the diversification model that best explains the data (e.g., Hey 1992; Nee et al. 1992; Rabosky 2006a, 2014; Alfaro et al. 2009; Morlon et al. 2010, 2011; Etienne et al. 2011). When phylogenetic data are not available or phylogenies are incomplete, it is possible to use summary statistics —such as the maximum clade richness or the correlation between clade age and species richness (the age–richness correlation, ARC)— to distinguish among alternative hypotheses of diversification (Ricklefs and Renner 1994; Ricklefs et al. 2007; Rabosky 2009b; Pyron and Burbrink 2012). The ARC is particularly useful because it allows direct evaluation of the effect of time —measured as clade age— on species richness. Intuitively, a positive relationship should indicate that clade age determines richness distribution patterns. A nonsignificant or negative relationship indicates that other factors explain these patterns. For example, a negative ARC could arise if differences in diversification rates rather than time explain the heterogeneous distribution of richness among taxa (Ricklefs and Renner 1994; Magallón and Sanderson 2001).

Evaluations of previous intuitions with simulations have indicated that ARCs are negative when richness is bounded (by ecological factors, Rabosky 2009b,

2010; or by extinction, Pyron and Burbrink 2012). A more recent study has shown that when ARCs are estimated using the stem age of clades (stem-ARCs), a taxonomic classification based on time can also generate null or negative ARCs in diversification processes of unbounded richness (Stadler et al. 2014). This was not observed with ARCs estimated using the crown age of clades (crown-ARCs), revealing a conflict between ARCs estimated using crown or stem ages within the same diversification process. Accordingly, it was suggested that only crown-ARCs could be informative about the underlying diversification process (Stadler et al. 2014), with positive relationships expected from processes of unbounded richness and null or negative relationships expected from processes of bounded richness. However, this has not been explicitly evaluated.

Since the crown-ARC/stem-ARC conflict seems to arise only in some types of taxonomic delimitation (Stadler et al. 2014), it is natural to wonder if different taxonomic ranks could affect ARC estimations differently or even provide inconsistent evidence about the relationship between the age and richness of clades. If this is the case, can a particular taxonomic rank inform us better than others about the true ARC? For example, could the genus level, which has been considered to be more natural than other taxonomic ranks (Humphreys and Barraclough 2014), be more informative than more inclusive ranks, such as orders or families? Thus, accounting for the hierarchical nature of taxonomy is fundamental to determine the informative potential of ARCs in diversification studies. In this work, we first develop and implement a two-state birth–death model based on Rabosky et al. (2012), to simulate phylogenies incorporating the origin of higher taxa as the process of hierarchical emergence of attributes (any morphological, ecological, etc. trait inherited to all the descendants of a species) that can be used to assign monophyletic named groups (i.e., taxa) to nested categories (i.e., ranks) in a hierarchical arrangement equivalent to common taxonomical practice. To assess the informative breadth of the simulated ARC trends, we characterize empirical ARCs from different taxonomic ranks (ranging from more inclusive —e.g., orders— to less inclusive —e.g., genera) obtained from extant amphibians (Lissamphibia), birds (Aves), mammals (Mammalia), squamate reptiles (Squamata), and flowering plants (Angiospermae), using stem and crown ages. We find that our model reproduces the empirical ARC trends, suggesting that it captures relevant features of taxonomic practice that might be affecting ARCs in the biological systems analyzed. This allows us to establish crown- and stem-ARC expectations in different ecologically and time-dependent diversification models when richness is categorized into nested taxonomic ranks and when phylogenetic structure is considered. We discuss the validity of current ARC interpretations and ways forward in the study of diversification processes using the relationship between clade age and richness.

MATERIALS AND METHODS

Expected Diversification Processes: Modeling a Hierarchical Taxonomy

As an approximation to modeling a hierarchical taxonomy, we extended the birth–death model implemented by Rabosky et al. (2012) to allow a hierarchical origin of taxa. The model incorporates an origination rate parameter (Φ) that controls the frequency at which higher taxa arise. Briefly, the process starts with a branch that represents a single species. This branch can speciate through cladogenesis and generate two branches with rate λ; it can go extinct with rate μ; or it can undergo an origination event with rate Φ, and become a higher taxon. The origin of a higher taxon is not a branching event; it should be understood as an event such as the acquisition (or loss) of a distinctive attribute (*sensu lato*, e.g., morphology, function) that is inherited by all the descendants of the branch on which it occurred. Because each origination event occurs only once during the process, the associated distinctive properties would correspond to synapomorphies of the resulting clade, which are used to identify clade membership. The first node descending from the branch on which the origination event occurs represents the crown node of the higher taxon. Descending branches have the same three possibilities: they can speciate, go extinct, or become a higher taxon of the next rank. The first origination event to occur along a lineage will correspond to the most inclusive taxon, belonging to the highest rank (i.e., first rank); the next event to occur within that lineage will delimit groups of second-highest rank (i.e., second rank), and so on (Fig. 1). Therefore, small-numbered ranks correspond to highly inclusive taxa closer to the root of the tree, such as classes and orders, whereas ranks with high numbers correspond to least inclusive taxa, closer to the tips of the tree, such as families and genera.

Two or more origination events can occur by chance on the same branch, but this will not change its rank; rather, the rank level of any given branch is determined by the number of branches toward the root of the tree that have undergone origination events (Fig. 1). Our model does not simulate morphological change, and branch lengths are neither proportional to any measure of morphological distance (e.g., distinctiveness) nor to the number of origination events that occur on the same branch. Speciation and extinction probabilities can be constant or variable among clades by introducing the parameter α as the probability of a diversification rate shift occurring on any given branch. The timing of higher-taxon origination events are drawn from an exponential distribution with parameter $\beta = \lambda + \mu + \Phi + \alpha$. The probability of each type of event is proportional to β. Origination probability is constant in all models evaluated in this study, but it could be modified to vary through time, and in a diversity-dependent manner.
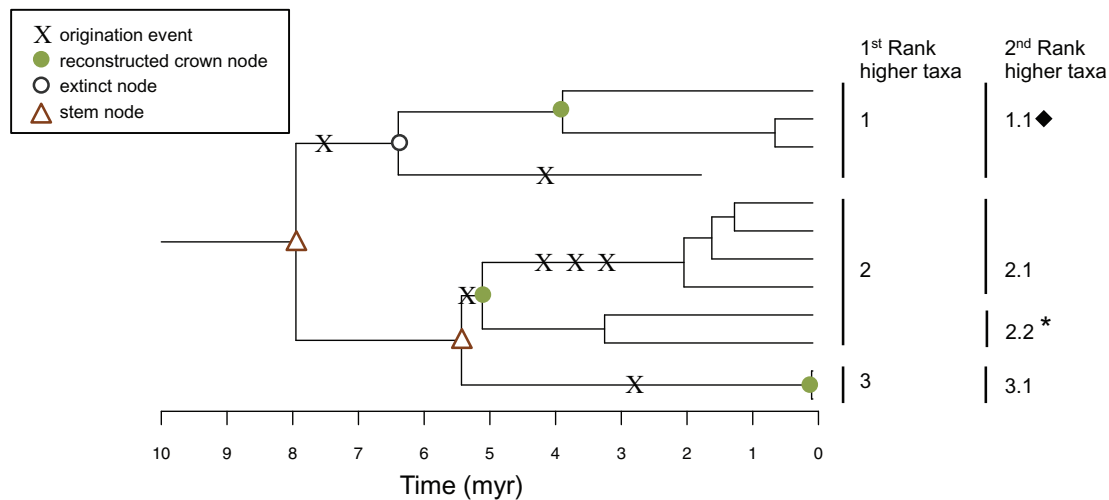
FIGURE 1. Example tree simulated with the model of hierarchical origin of higher taxa proposed in here. Highertaxon origination events (X) can occur at any branch. The node descending from the highertaxon origination event deepest in the tree corresponds to the crown node of a 1st rank higher taxon (filled circles). The node subtending the branch where the origination event occurred represents the stem node of the higher taxon (open triangles). Nodes in which any of the two daughter branches went extinct cannot define higher taxa (empty circles). To preserve monophyly, a clade that lacks origination events but is sister to a higher taxon, is defined as a higher taxon of the same rank as its sister, as exemplified by taxon 2.2 (asterisks). Clades with fewer origination events are assigned to all less inclusive taxonomic ranks generated during the simulation, as exemplified by taxon 1.1 (filled diamonds). This *a posteriori* highertaxon delimitation guarantees the inclusion of all lineages in a clade at all ranks.

Simulations

We conducted tree simulations under the general model described above by developing R code available in the package RPANDA (Morlon et al. 2016). Tree simulations were run for 50 time units or until 5000 extant tips were reached. Initial λ values for each model were set to generate large trees (> 500 extant tips; Supplementary Table S1 available on Dryad at http://dx.doi.org/10.5061/dryad.2b7d5). Since small trees could still be generated by chance, we ran simulations until 500 large trees were obtained for each diversification model described below. Analyses were performed on large trees only.

As a null model of a time-dependent process with unbounded richness, we first considered constant rates of speciation and extinction through time and among clades. We evaluated the effect of extinction by constraining μ to be a constant proportion of λ at any point in time, so that we could explore the effect of different turnover regimes: absent (μ = 0), low (μ = 0.2λ), moderate (μ = 0.5λ), and high turnover (μ = 0.9λ). To assess the effect of a hierarchical taxonomy, we considered three different origination rate regimes: low (Φ = 0.5λ₀), moderate (Φ = λ₀) and high origination (Φ = 1.3λ₀). When origination rate is low, few higher taxa arise and diversity is partitioned among few taxonomic ranks. As origination rate increases, eventually exceeding speciation rate, more higher taxa arise and diversity becomes more partitioned, generally among less inclusive taxonomic ranks. An example can be extracted from flowering plants. Order Malvales (e.g., cotton, chocolate) and order Piperales (e.g., black pepper) have roughly similar species richness (~6000

and ~4000, respectively). However, Malvales includes a much higher number of families and genera (10 and 338, respectively) than Piperales (4 and 17, respectively). This indicates that similar species richness is partitioned in a larger number of higher taxa in Malvales than in Piperales, suggesting a higher rate of origin of ecological, morphological, etc. descriptive attributes in the former group than in the latter.

Next, we allowed speciation and extinction rates to vary among clades with a rate shift probability of α = 0.05 and an initial λ class (Supplementary Table S1). Given a rate shift event occurring on a randomly chosen branch, a new λ class was drawn from a gamma distribution with shape parameter $k = 0.1$, generating a distribution of new λ classes that are generally small but that can occasionally take high values.

As the null model of an ecologically dependent process with bounded richness, we implemented linear diversity-dependent change in speciation rate, allowing carrying capacity (K) and initial speciation rate (λ₀) to shift among clades with a probability of α = 0.01. The process starts with a given initial value of K and λ₀ (Supplementary Table S1 available on Dryad). Speciation rate decreases following the equation described by Nee et al. (1992) and used by Rabosky (2006b) and Rabosky and Lovette (2008), in which the speciation rate at any point in time ($λ_t$) is bounded by the number of species at that time (N_t) and by K:

$$\lambda_t = \lambda_0 (1 - N_t / K)$$

Given a rate shift event, a randomly chosen branch is assigned new K and λ₀ classes drawn uniformly from the

intervals (50, 500) and (e^{-6}, 1), respectively. This branch and its descendants no longer belong to the initial K and λ_0 classes and will continue to evolve under the new class until another shift event occurs.

In both models of among-clade rate variation, we implemented Φ values that resulted in approximately the same number of ranks generated in the constant-rate models under high origination (Supplementary Table S1 available on Dryad). The effect of extinction was evaluated with the same four turnover regimes described above.

Empirical Diversification Processes: Age and Richness Data from Extant Taxa

We selected published molecular dating studies of various biological systems from which we could gather data on stem and crown ages from more than 80% of taxa within at least two different taxonomic ranks. The final data set comprised a dated tree sampling > 80% amphibian species (De Lisle and Rowe 2015); a dated tree encompassing > 85% squamate genera (Pyron and Burbrink 2014); a mammal family-level dated tree generated with a supermatrix approach (Meredith et al. 2011); a maximum clade credibility tree obtained with TreeAnnotator (Rambaut and Drummond 2007) from a species-level dating study of birds (Hackett backbone; Jetz et al. 2012); and a family-level dated tree encompassing > 87% flowering plant families (Magallón et al. 2015).

Richness counts were obtained following the taxonomy from the specialized databases of the Amphibian Species of the World 6.0 (Frost 2015); The Reptile Database (Uetz and Josek 1995); The Mammals Species of the World, 3rd edition (Wilson and Reeder 2005); and the Angiosperm Phylogeny Website (Stevens 2001). Richness counts of bird taxa were obtained following the master taxonomy from the Jetz et al. (2012) study, available in their electronic supplementary material.

ARC Estimation

To accurately estimate correlations between richness and any biological attribute within a phylogenetic framework and to avoid false positive ARC estimates (Rabosky et al. 2012), nonindependence (autocorrelation or phylogenetic structure) of the data must be assessed and corrected. As a null model for the presence of phylogenetic structure, most tests use a Brownian motion model of association of normally distributed characters (or Brownian motion scaled to a link function if characters follow a distribution different from a Gaussian; Hadfield and Nakagawa 2010). This model is used to account for variation and covariation between characters, which are then used to estimate variance-corrected contrasts at each node as the average of derived character values (Felsenstein 1985). Ideally, the nature of the distribution of age and richness data should be taken into account. However, the methods usually applied to ARC estimation assume a normal distribution of characters. Concerns have also been raised about how contrasts are estimated, which might be unsuitable for species-richness data (Agapow and Isaac 2002; Isaac et al. 2003). These concerns have promoted the development of alternative methods (see Agapow and Isaac 2002), that, nonetheless, seem to present other problems (Freckleton et al. 2008). For the objectives of this study and for comparative purposes with previous research (e.g., Rabosky 2009b; Rabosky et al. 2012; Stadler et al. 2014; Hedges et al. 2015), we selected two approaches that have been commonly used in recent years to estimate age–richness relationships. First, to account for phylogenetic structure we employed Pagel's (1999) lambda (Λ) test within a phylogenetic generalized least squares (PGLS) framework (Freckleton et al. 2002), performed with the pgls function in the R package CAPER (Orme et al. 2013). Briefly, Λ is estimated with maximum likelihood (ML) and 95% confidence intervals are obtained to infer the model that best explains covariation between clade age and log-transformed richness data (i.e., residuals of the relationship of log-transformed richness regressed on clade age). A Λ value of 0 indicates phylogenetic independence of the data (residuals are randomly distributed across the phylogeny) whereas a value of 1 indicates that traits covary following a Brownian motion model and that there is phylogenetic structure (residuals are more similar among closely related lineages). Λ can also take intermediate values, indicating a weak phylogenetic structure explained by a different, unknown model of character association (Freckleton et al. 2002) or by a non-Gaussian character distribution Hadfield and Nakagawa 2010). This makes the Λ test particularly useful to detect phylogenetic structure in characters that might not behave following Brownian motion. Second, we estimated ARCs with the Spearman's rank test, a method that does not account for phylogenetic structure, using the cor.test function in the R base package STATS (R Core Team 2014).

ARCs were estimated with these two methods at all taxonomic ranks available from the simulated and empirical phylogenies. PGLS analyses were performed using higher-level phylogenies. To produce these, the original species-level phylogenies were pruned to leave only one representative per taxon at the corresponding taxonomic rank. Except for flowering plants and mammal orders and families, non-monophyletic taxa were found in most empirical data sets. To evaluate the effect of non-monophyletic taxa, we estimated ARCs including and excluding them.

RESULTS

Expected ARC Patterns

Analyses of data on age and richness simulated with the model of hierarchical taxonomy show that ARCs vary across taxonomic ranks (Figs. 2 and 3). This was

(a) Constant rates

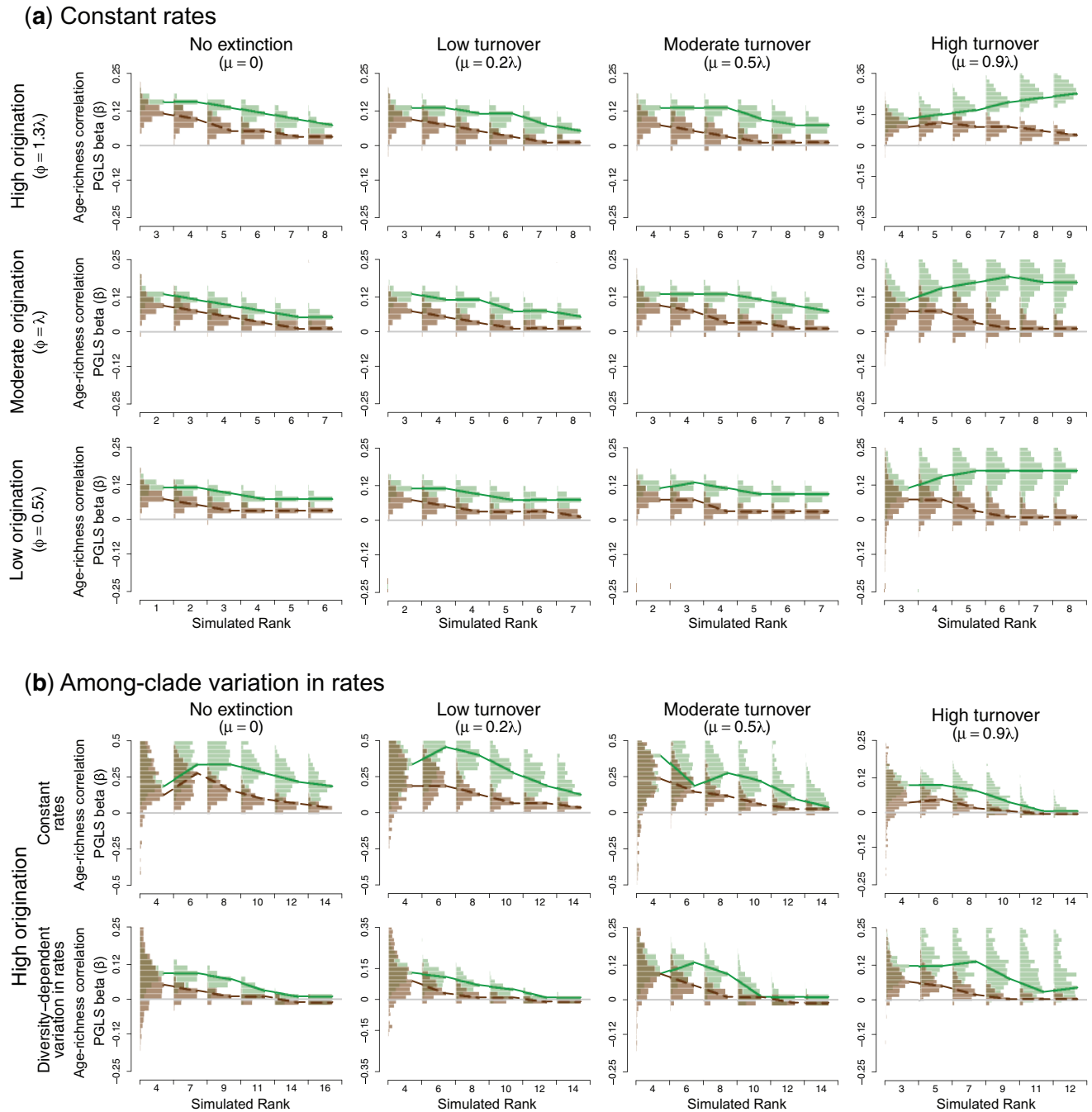**(b)** Among-clade variation in rates

FIGURE 2.   Expected relationship between clade age and species richness inferred with phylogenetic generalized least squares (PGLS). X-axis numbers denote simulated taxonomic ranks, from the most to the least inclusive. At each simulated taxonomic rank, ARCs are estimated using crown ages (crown-ARCs) and stem ages (stem-ARCs). A solid line across distributions connects crown-ARC modes of each rank while a dashed line connects stem-ARC modes. PGLS was applied to data simulated under models of constant speciation and extinction rates (a) and of among-clade variation in speciation and extinction (b) with no rate change through time (b – top row), and with diversity-dependent rate variation (b – bottom row). Different extinction (increasing μ from left to right) and origination rates (increasing φ from bottom to top in (a); for (b) we only show results obtained with a high origination) were considered. To facilitate comparisons, results are shown for the six ranks displaying the most extreme ARC values of each model. The horizontal gray line indicates a correlation of zero.

detected with both PGLS and Spearman's rank test. ARC variation across simulated ranks seems to be controlled mainly by origination and extinction rate parameters. In constant rate models, age and richness data appear to lack phylogenetic structure, since Λ

were null with crown and stem ages and across all simulated ranks (Supplementary Fig. S1 available on Dryad). Accordingly, ARCs display very similar trends with PGLS and Spearman's test. In general, ARC values decrease as taxonomic rank becomes less inclusive.
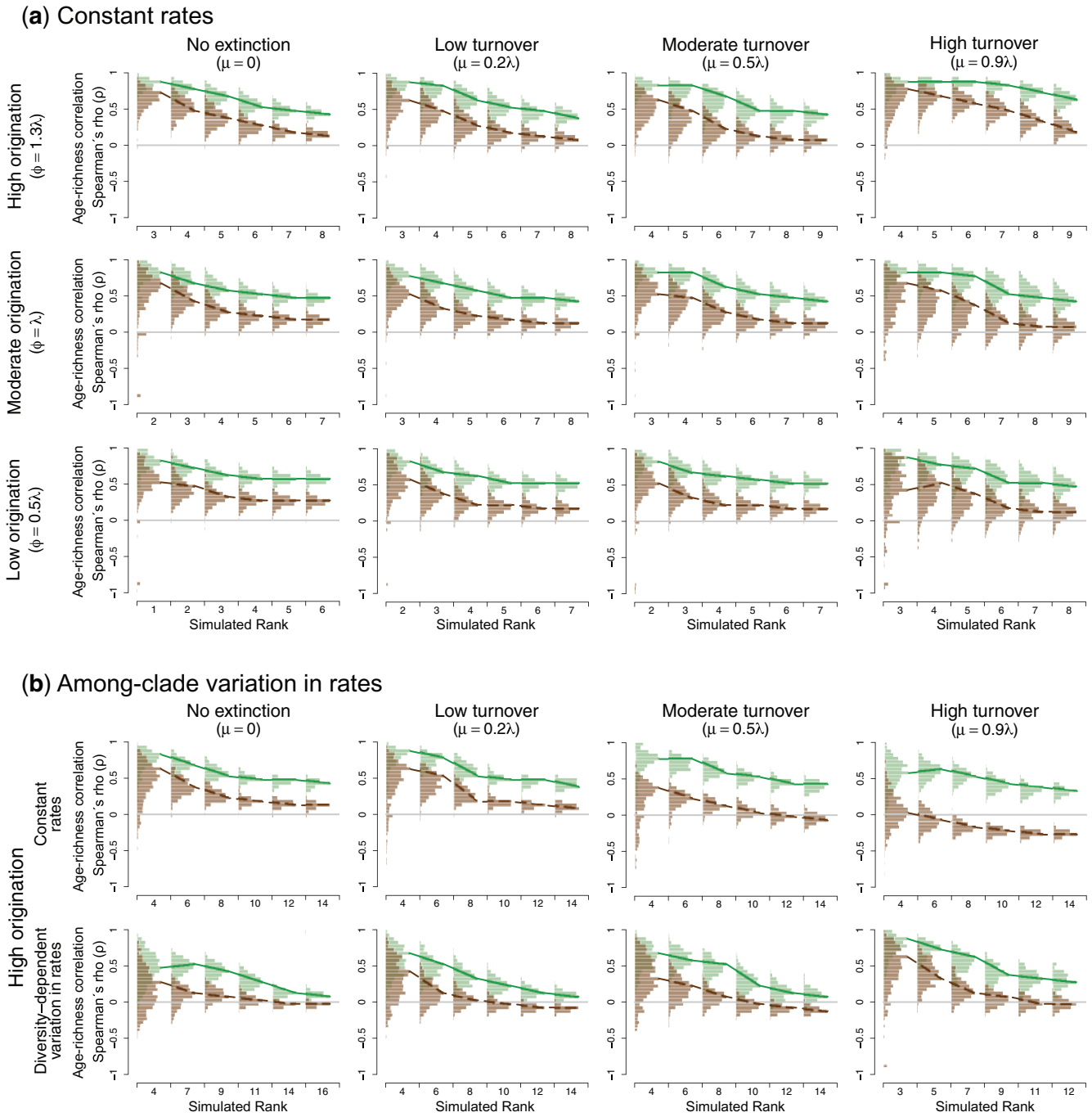
(a) Constant rates

(b) Among-clade variation in rates

FIGURE 3.   Expected relationship between clade age and species richness inferred with Spearman's rank test. *X*-axis numbers denote simulated taxonomic ranks, from the most to the least inclusive. At each simulated taxonomic rank, ARCs are estimated using crown ages (crown-ARCs) and stem ages (stem-ARCs). A solid line across distributions connects crown-ARC modes of each rank while a dashed line connects stem-ARC modes. Spearman's test was applied to data simulated under models of constant speciation and extinction rates (a) and of among-clade variation in speciation and extinction (b) with no rate change through time (b – top row), and with diversity-dependent rate variation (b – bottom row). Different extinction (increasing μ from left to right) and origination rates (increasing φ from bottom to top in (a); for (b) we only show results obtained with a high origination) were considered. To facilitate comparisons, results are shown for the six ranks displaying the most extreme ARC values of each model. The horizontal gray line indicates a correlation of zero.

Decrease in ARCs is more pronounced when either origination or extinction rates are moderate to high (Figs. 2a and 3a). When estimated with PGLS and when extinction is moderate to high (Fig. 2a), ARCs can increase in high taxonomic ranks and subsequently decrease. ARCs tend to stabilize and become almost equal across lower taxonomic ranks. ARC stabilization is reached more slowly as extinction increases (Figs. 2a

and 3a; Supplementary Fig. S2 available on Dryad). Under the constant rate models, crown- and stem-ARCs are always positive.

When rates are allowed to vary among clades, Λ takes a range of intermediate values up to 1 among higher simulated ranks. Λ values decrease until they are null at lower simulated ranks (Supplementary Fig. S1 available on Dryad). Despite the presence of phylogenetic structure at higher simulated ranks, PGLS and Spearman's ARC estimates display the same general trends. We observe that both crown- and stem-ARCs decrease with taxonomic rank. However, crown-ARCs remain nonnegative across taxonomic ranks, even in the model of diversity-dependent decrease in rates (Figs. 2b and 3b). In contrast, stem-ARCs are positive at high taxonomic ranks but take negative values at low taxonomic ranks, when extinction is moderate to high, in both models of among-clade rate variation (Figs. 2b and 3b).

Empirical ARC Trends

Empirical ARCs resulting from the analyses including and excluding non-monophyletic taxa were very similar (Supplementary Tables S2 and S3 available on Dryad). Here, we only present and discuss results from the analyses including non-monophyletic taxa (Figs. 4 and 5). Pagel's (1999) test applied to empirical age and richness data reveals different degrees of phylogenetic structure among biological systems (Supplementary Fig. S3 and Supplementary Table S4 available on Dryad). In all amphibian data sets, Λ estimates are almost null and significantly different from 1, indicating that age and richness covary independently of phylogeny. This is also observed in stem age–richness data of flowering plants orders and families, in crown and stem age–richness data of squamate infraorders and orders, and in stem age–richness data of squamate genera. Crown age–richness data of squamate genera and families also have almost null Λ, albeit not significantly different from 1 and with large confidence intervals, preventing to confidently assess phylogenetic independence in these data sets. This was also the case for mammal superorders and orders, and for bird orders. In contrast, Λ estimates are significantly different from 0 in bird families and genera, revealing the presence of phylogenetic structure in birds at lower taxonomic ranks. Since Λ was also significantly different from 1 in these data sets, it indicates that a Brownian motion model does not account for the detected phylogenetic autocorrelation, and that a different character association model should explain phylogenetic structure. This is also the case for crown age–richness data of flowering plant families. Crown age–richness data of flowering plant orders and stem age–richness data of mammal families display high and intermediate Λ estimates, respectively, suggesting the presence of some degree of phylogenetic structure in these data. However, the test was not significantly different from 0 and confidence intervals were wide, preventing to confidently assert the presence of phylogenetic structure. A Brownian motion model of character association was not detected in any data set. Intermediate levels of phylogenetic structure can also occur when character distributions are non-Gaussian (Hadfield and Nakagawa 2010).

Despite the presence of phylogenetic structure, PGLS and Spearman's test provide very similar ARC estimates, both in terms of the sign of the correlation and the significance of the test (Figs. 4 and 5). Considering only the sign of ARC estimates, the empirical relationship between age and richness across taxonomic ranks holds within the same age type in all biological systems studied, except for mammal stem-ARCs estimated with Spearman's test, which are negative within superorders and families but positive within orders (Fig. 5b). The significance of the correlation test is also consistent across taxonomic ranks in amphibians, flowering plants, mammal stem-ARCs, and squamate and bird crown-ARCs. In mammal crown-ARCs and squamate and bird stem-ARCs, significance is achieved at lower taxonomic ranks, but not always so at higher ranks (Fig. 5).

Similar to ARC patterns simulated with the model of hierarchical taxonomy proposed here (Figs. 2 and 3), empirical ARC estimates tend to decrease at lower taxonomic ranks (Fig. 4). The only exceptions are stem-ARCs from flowering plants and mammals, in which we detect a moderate increase at lower ranks. In these two groups, ARC estimates obtained with stem and crown ages are decoupled: crown-ARCs are significantly positive whereas stem-ARCs are negative and nonsignificant. In birds and squamates, stem-ARCs are weaker than crown-ARCs, but both are always positive, and in most cases, significant. In amphibians, ARC estimates are almost equal with both age types and across taxonomic ranks, being positive but not significantly different from 0.

DISCUSSION

Simulations represent a fundamental tool to provide expectations from null models for hypothesis testing at macroevolutionary timescales. A good simulation framework must incorporate all elements potentially affecting the behavior of the parameters used to describe the null model of interest in order to allow us to reach accurate interpretations. In diversification studies, taxonomy appears to be an element that must be considered to understand comprehensively biodiversity patterns and processes. Paleobiologists have investigated the effect and validity of using higher taxa to study biodiversity patterns in the fossil record, with encouraging results (e.g., Raup et al. 1973; Wagner 1995; Robeck et al. 2000; Soul and Friedman 2015). In the study of the relationship between age and richness of extant clades, some forms of taxonomic delimitation have been demonstrated to affect ARC estimates (Stadler et al. 2014). However, the different implementations of taxonomic criteria have hampered the establishment of a
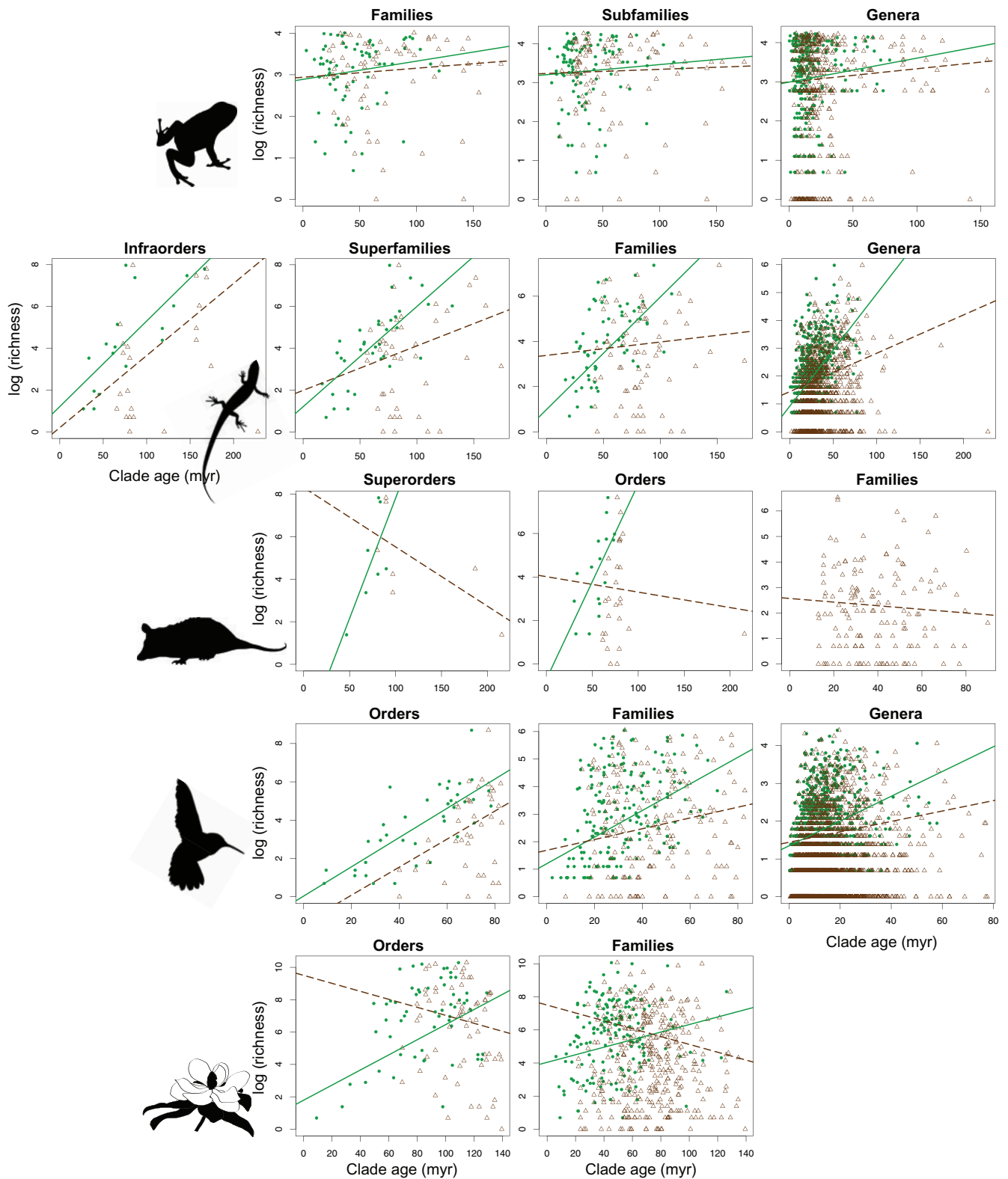
FIGURE 4.   Empirical relationship between clade age (filled circles for crown and open triangles for stem age) and richness of higher taxa from different taxonomic ranks of amphibians, scaled reptiles, mammals, birds, and flowering plants, estimated with phylogenetic generalized least squares (PGLS). Lines represent the fitted relationship between crown age and richness (solid) and between stem age and richness (dashed). Organismal silhouettes are available from www.phylopic.org. Material is presented unmodified. Mammal material was provided by Sarah Werning under a CC by 3.0 license (creativecommons.org/licenses/by/3.0/).
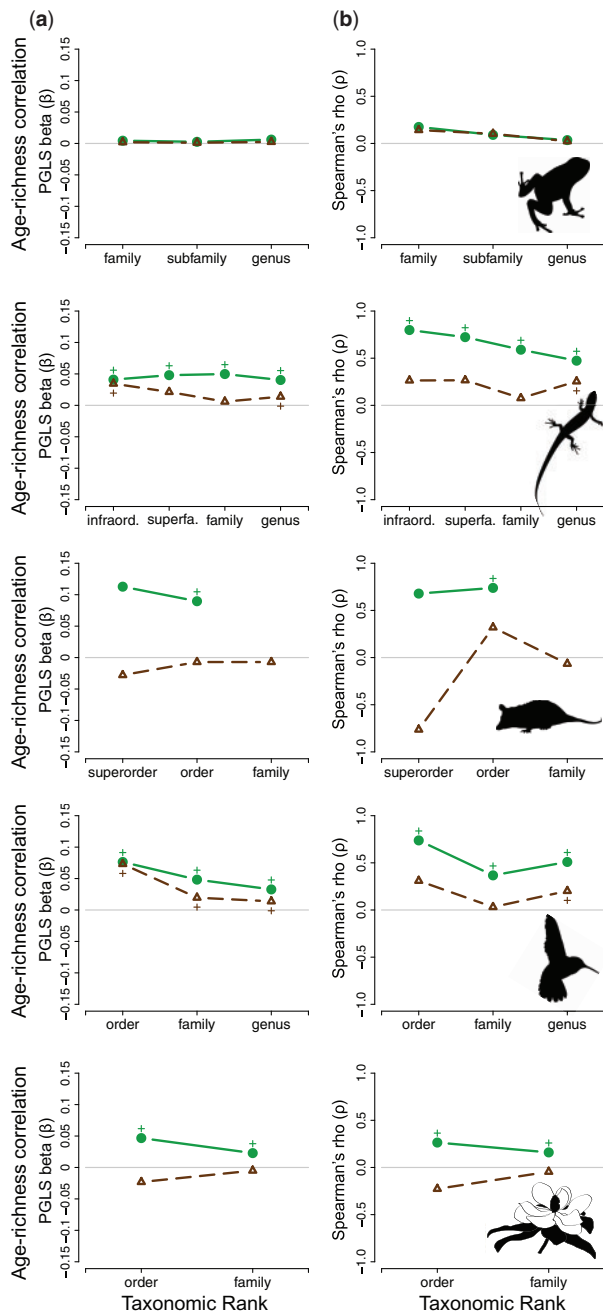
FIGURE 5.   Relationship between crown age and richness (filled circles, solid lines) and between stem age and richness (open triangles, dashed lines) of higher taxa from different taxonomic ranks of amphibians, scaled reptiles, mammals, birds and flowering plants, as estimated with a) phylogenetic generalized least squares (PGLS) and b) Spearman's rank test. A horizontal gray line is drawn at β (or ρ) = 0; + significant correlation (P ≤ 0.05). Exact values are shown in Supplementary Table S2 available on Dryad. Organismal silhouettes are available from www.phylopic.org. Material is presented unmodified. Mammal material was provided by Sarah Werning under a CC by 3.0 license (creativecommons.org/licenses/by/3.0/).

null taxonomic model applicable to different organisms (Stadler et al. 2014). The model of hierarchical origin of higher taxa developed here reproduces different ARC

trends observed in common taxonomic ranks of a wide variety of biological systems, appearing as a potential good tool to study the expected behavior of ARCs under alternative diversification scenarios.

When diversification rates are constant through time and among clades, time is the only factor expected to explain variation in species richness (Rabosky 2009b; Stadler et al. 2014). Our simulation framework is consistent with this expectation (Figs. 2a and 3a): the relationship between age and richness of clades is positive when time is considered since crown or stem age in constant rates diversification models. Nevertheless, we observe that stem-ARCs are weaker than crown-ARCs. The difference in ARC estimates generated by the use of crown or stem ages cannot be explained by unusually long stem branches generated by extinction (Pyron and Burbrink 2012), since it also arises in the absence of extinction (Figs. 2a and 3a). Hence, the simple fact that stem ages are older than crown ages should be weakening stem-ARCs compared to crown-ARCs. Furthermore, the strength of the relationship between time and richness varies with taxonomic rank, weakening as rank becomes less inclusive. ARC variation across taxonomic ranks has not been documented before and is difficult to explain. It might be related to the presence of monotypic taxa, which are usually represented in more than one taxonomic rank. If monotypic taxa appear early in the tree, they could affect the age and richness variance structure of less inclusive ranks. More tests are needed to evaluate if monotypic taxa can effectively weaken the relationship between age and richness across taxonomic ranks.

When diversification rates vary among clades but are constant through time, richness is positively correlated with crown ages but negatively or not correlated with stem ages, only with certain forms of taxonomic delimitation (Stadler et al. 2014). In our simulations, less inclusive taxonomic ranks display this ARC pattern (Figs. 2b and 3b, top row), which also emerges in diversity-dependent diversification processes (Figs. 2b and 3b, bottom row). Hence, earlier work reporting positive relationships between crown age and richness should not necessarily be interpreted as time explaining richness patterns (Stephens and Wiens 2003; Wiens et al. 2006; McPeek and Brown 2007; Escudero and Hipp 2013), since ecologically dependent processes can generate that relationship too. Positive crown-ARCs and null or negative stem-ARCs have been obtained using PGLS among tribes of sedges (Escudero and Hipp 2013) and families and genera of mammals and birds (Hedges et al. 2015), and have been interpreted as evidence for time dependency and rate constancy. Of the simple models considered in this study, those that allowed among-clade varying rates (either constant through time or varying in a diversity-dependent manner) and a high extinction are the only ones producing ARC patterns consistent with the ones observed in those groups.

We note that stem-ARCs previously reported in Rabosky et al. (2012) for amphibians and birds differ from the ones obtained here. This might be a

consequence of the use of different dated phylogenies in each study, which differ in topology and in dating methodology, likely resulting in differences in estimated clade ages. The effect of phylogenetic uncertainty and of error in age estimation on descriptive statistics of the diversification process is an important issue that should be addressed in future work. Our simulated ARCs show the ideal case in which we know clade ages precisely. In this context, our results suggest that stem-ARCs are more useful than crown-ARCs to reveal characteristics of the underlying diversification process. Considering both crown and stem ages to estimate correlations might prove useful to reveal the presence of extinction. However, neither crown- nor stem-ARCs can be used to distinguish between bounded and unbounded diversity scenarios, as previously proposed (Rabosky 2009b; Pyron and Burbrink 2012; Rabosky et al. 2012).

Phylogenetic structure is another factor that has been posited to affect ARC behavior (Rabosky et al. 2012). When we assume Brownian evolution ($\Lambda = 1$; Supplementary Fig. S4 available on Dryad) to estimate ARCs applying PGLS to data with no phylogenetic structure, correlations appear overestimated as compared to those obtained using the phylogenetic structure model inferred from the data (ML Λ values; Fig. 2; Supplementary Fig. S1 available on Dryad) and using a method that does not account for phylogenetic structure (Spearman's test; Fig. 3). A similar bias appears in the complementary case when richness evolves with a high degree of phylogenetic structure and a non-phylogenetic method is used to estimate ARCs (Rabosky et al. 2012). This raises the need for more work to correctly account for phylogenetic structure before attempting to estimate correlations. For the moment, the results presented here suggest that when phylogenetic structure is weak, non-phylogenetic methods are as effective and valid as PGLS to estimate ARCs.

The models of among-clade variation reproduce to some degree the empirical lineage-through-time plots of the biological systems presented here (Supplementary Figs. S5 and S6 available on Dryad). In the models of rate variation among clades, we also detect some negative values of Pybus and Harvey (2000) gamma statistic (Supplementary Fig. S7 available on Dryad). However, the distribution of simulated gamma values tends toward null or positive estimates, showing that our model does not reproduce all properties of real phylogenies. The simulations also produced more taxonomic ranks than those generally established by common taxonomic practice, preventing the establishment of a formal correspondence between empirical and simulated taxonomic ranks. Since we aimed to generate complete trees (including extinct branches; Nee et al. 1992), simulation of very large trees (with >5000 extant tips) required substantial computational resources, hindering simulations with certain parameter values (e.g., high diversification rate). Hence, we only used a small range of parameter

values not estimated from the empirical data to conduct the simulations. To implement a formal comparison between observed and expected properties of higher taxa, our model needs to be computationally optimized to perform predictive *a posteriori* simulations using parameters estimated from empirical data. At present, there are many methods to estimate speciation and extinction rates (Morlon 2014), but there are very few methods to estimate origination rate from extant taxa. A framework to estimate origination rate in a constant birth–death scenario has been developed (Maruvka et al. 2013), and it could be extended to accommodate diversification rate variation. It is also important to highlight that we only considered a model of constant origination through time, which implies that more origination events occur as species number increases, resulting in more higher taxa accumulating toward the present. However, it is unknown if we should expect something similar in real higher taxa and if it is not the case, how it can affect ARCs. Simulated clade richness frequency distributions per taxonomic rank (Supplementary Fig. S8 available on Dryad) are in some ways similar to the empirical ones (Supplementary Fig. S9 available on Dryad). Given the sensitivity of the results to the origination rate parameter observed, exploration of the effect of different forms of higher-taxon accumulation—such as protracted or diversity-dependent origination—should be evaluated.

In the last decade, the correlation between age and species richness of higher taxa has extensively and increasingly been used to explore the effect of time versus ecological effects on the heterogeneous distribution of species among taxa and regions. Overall, these studies have reported contradictory conclusions regarding the relationship between age and richness (e.g., McPeek and Brown 2007; Rabosky et al. 2012; Hedges et al. 2015). In this study, we show that the conflict probably comes from the fact that ARCs have been estimated using different taxonomic ranks, age types, and correlation estimation methods. Moreover, previous interpretations have relied on ARCs estimated from one taxonomic rank only. In the study of the latitudinal diversity gradients, it has been observed that ecologically and time-dependent diversification models cannot be differentiated with a simple estimate of the relationship between age and richness of clades (Hurlbert and Stegen 2014), conforming to our concerns. ARCs should be used with caution as supporting evidence in diversification analyses. Whenever possible, we encourage researchers to estimate ARCs considering different taxonomic ranks available in their data sets, and to carefully analyze their trends. A null or negative ARC should not be taken as evidence in favor of diversification processes that bound species accumulation, since processes of unbounded diversity can generate such relationships between age and richness as well. However, it can be used to document among-clade rate variability in general. It is important to note that we only considered few diversification models from the wide variety available in the literature. The evaluation of other models such

as diversification limited by area or by extinction might change ARC interpretations. Moreover, ARC patterns described here might not hold for subgroups evolving within a general diversification process. For example, Passerine birds have consistently portrayed negative ARCs (Ricklefs 2006; Rabosky 2009b), differing from the ARC patterns portrayed by the whole class reported here and elsewhere (Stadler et al. 2014). Finally, we emphasize the importance of incorporating a higher-taxon origination parameter in simulation frameworks, as it appears to have a relevant effect on the behavior of descriptive statistics of diversification dynamics, whose importance for the study of richness patterns should not be neglected.

Supplementary Material

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.2b7d5.

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