Phylogenetic scale in ecology and evolution

Catherine H. Graham [1], Antonin Machac [2,3,4], David Storch [3,4]

[1] Department of Ecology and Evolution, 650 Life Sciences Bldg, Stony Brook University, Stony Brook, NY 11794, USA – [2] Center for Macroecology, Evolution, and Climate, Natural History Museum of Denmark, Universitetsparken 15, DK 2100 Copenhagen – [3] Department of Ecology, Vinicna 7, 12844 Prague 2, Czech Republic – [4] Center for Theoretical Study, Jilska 1, 11000 Prague 1, Czech Republic.

Email contacts: CHG: catherine.graham@stonybrook.edu, AM: A.Machac@email.cz, DS: storch@cts.cuni.cz.

Author for correspondence: Catherine H. Graham

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Abstract

It has been widely acknowledged that many phenomena in ecology and evolution depend on spatial and temporal scale. However, important patterns and processes may vary also across the phylogeny and depend on phylogenetic scale. Though phylogenetic scale has been implicitly considered in some previous studies, it has never been formally conceptualized and its potential remains unexplored. Here, we develop the concept of phylogenetic scale and, building on previous work in the field, we introduce phylogenetic grain and extent, phylogenetic scaling and the domains of phylogenetic scale. We use examples from published research to demonstrate how phylogenetic scale has been considered so far and illustrate how it can inform, and possibly resolve, some of the longstanding controversies in evolutionary biology, community ecology, biogeography and macroecology. To promote the concept of phylogenetic scale empirically, we propose methodological guidelines for its treatment.

Introduction

Numerous patterns in ecology and evolution vary across the phylogenetic hierarchy (Fig. 1). Species diversity declines with latitude across higher taxa but not necessarily across their constituent families and genera (Kindlman *et al.*, 2007). Phylogenetic delimitation of species pools influences our inferences about the processes that form local communities (Cavender-Bares *et al.*, 2009). Many other, similar examples further illustrate that patterns in ecology and evolution often depend on phylogenetic scale (Fig. 1). Yet, unlike the extensively developed concepts of spatial and temporal scale where scale dependence in the patterns and processes driving variation in diversity has long been acknowledged (Wiens, 1989; Levin, 1992), the importance of phylogenetic scale has only recently begun to be recognized. Here, we formalize and develop the concept of phylogenetic scale, summarize how it has been considered across disciplines, provide empirical guidelines for the treatment of phylogenetic scale, and suggest further research directions.

Inspired by the concept of spatial scale (Wiens, 1989; Levin, 1992), we define phylogenetic scale in terms of phylogenetic grain and phylogenetic extent (Box 1). Phylogenetic grain refers to the elementary unit of analysis, defined in terms of tree depth, taxonomic rank, clade age, or clade size. Phylogenetic extent refers to the entire phylogeny encompassing all these units. Exploring multiple grains and extents should provide relevant insights about the mechanisms that have produced a pattern of interest. For example, the number of families in the fossil record appears to be constant while the number of genera seems to increase continually over geological time, suggesting that different mechanisms produce genus-level and family-level diversity (Benton & Emerson, 2007). In community ecology, clade-wide analyses typically suggest that communities have been shaped by environmental filters while focused analyses of narrowly defined clades often implicate a suite of additional mechanisms (e.g. competition, mutualisms, dispersal limitation; Cavender-Bares *et al.*, 2009). Different patterns, and by extension different inferences about the underlying processes, might therefore emerge across the continuum of phylogenetic scales.

The concept of phylogenetic scale seems particularly pertinent given the growing body of research and statistical methods to explore the increasingly accurate and ever more complete phylogenetic data (Table 1). Yet, few studies have extended the explorative strategies to systematically investigate phylogenetic scale-dependence (upscaling, downscaling), delimit phylogenetic domains of ecological theories (e.g. niche conservatism, environmental filtering and competition), or test the universality of ecological laws (e.g. species-abundance distributions, latitudinal gradients). We contend that the full potential of the phylogenetic data, and the methods at hand, have not yet been fully realized, and further progress might be precipitated by a more focused and formalized treatment of phylogenetic scale, akin to that commonly applied across temporal and spatial scales (Wiens, 1989; Levin, 1992).

Here we overview the variety of ways in which different disciplines have either implicitly or explicitly considered phylogenetic scale, highlighting their respective benefits and pitfalls. We further propose how these efforts might be consolidated under one conceptual and empirical framework that would provide the common ground for cross-disciplinary discussion. In particular, we define and formalize the concept of phylogenetic scale, distinguish between phylogenetic grain and extent, scale-dependence, phylogenetic scaling and the domains of scale. We also provide practical guidelines for the treatment of phylogenetic scale across empirical studies, using the data and statistical methods currently available. We hope this will inspire further debate, draw more focused attention to the subject, and advance the notion of phylogenetic scale in ecology and evolution.

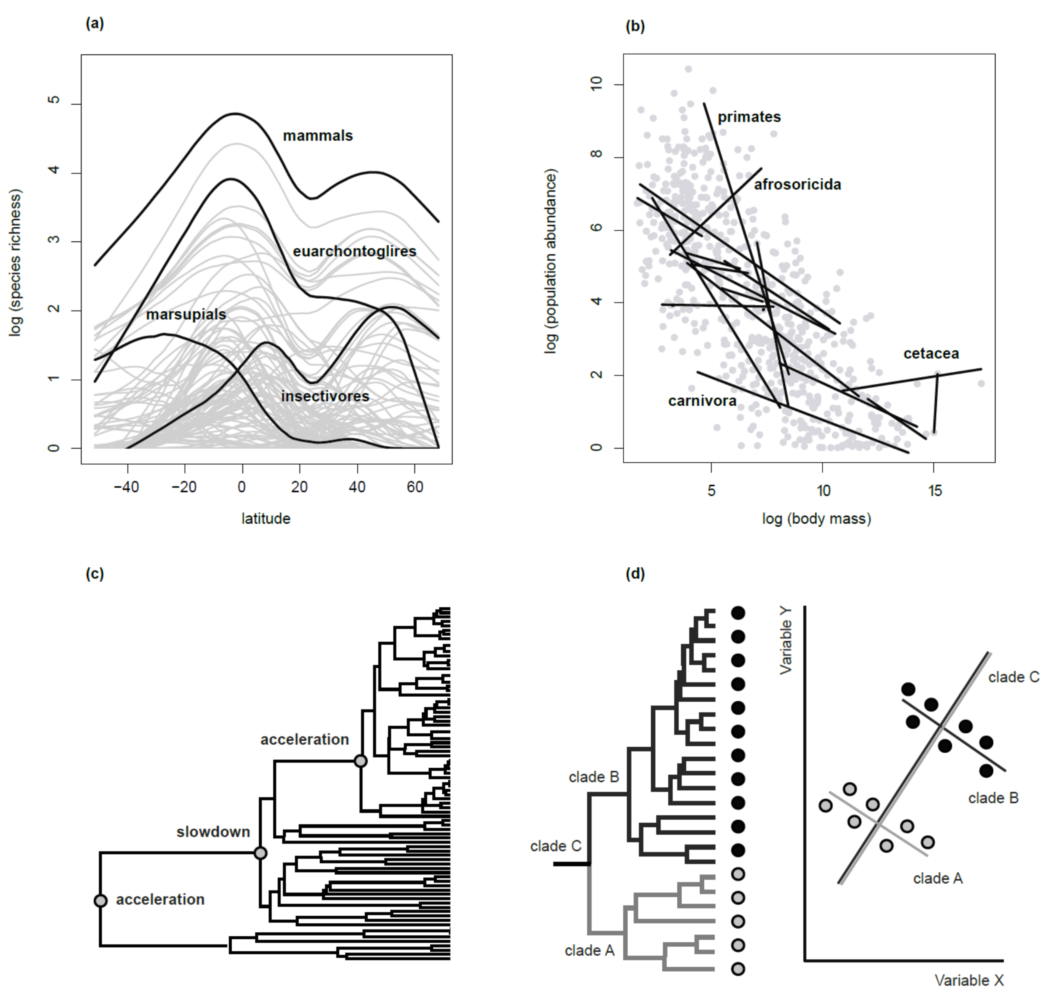
Phylogenetic sale in ecology and evolution

Phylogenetic scale has been considered to varying degrees in ecology and evolution, from being largely neglected to being relatively well-developed. In this section, we describe research that has implicitly or explicitly considered phylogenetic scale and suggest how different disciplines might further benefit from this concept.

Evolution and diversification

Evolutionary diversification and disparification are known to vary across phylogenetic scales but have rarely been thoroughly studied in this context. Even though a suite of methods is commonly used to explore these processes across the phylogeny (Alfaro *et al.*, 2009; Rabosky *et al.*, 2012) (Table 1), most studies report the recovered patterns without a focused examination of their scale-

Figure 1. Examples of patterns that vary across phylogenetic scales. (a) The latitudinal diversity gradient. Mammal diversity decreases with latitude across large clades but many other patterns emerge across small clades, including inverse ones (selected clades depicted in black). (b) The dependence of population abundance on body mass. The dependence is negative across large phylogenetic scales (mammals depicted in grey) but varies substantially across small scales (selected orders depicted in black). (c) Diversification dynamics. Slowdowns detected over some phylogenetic scales might be accompanied by accelerations over both larger and smaller scales. (d) Statistical correlations. Even though the depicted variables are negatively correlated within each of the two subclades, the correlation becomes positive when the subclades are studied together. The data were taken from the IUCN (http://www.iucnredlist.org) and PanTHERIA (http://esapubs.org/Archive/ecol/E090/184/default.htm).



BOX 1: The concept of phylogenetic scale

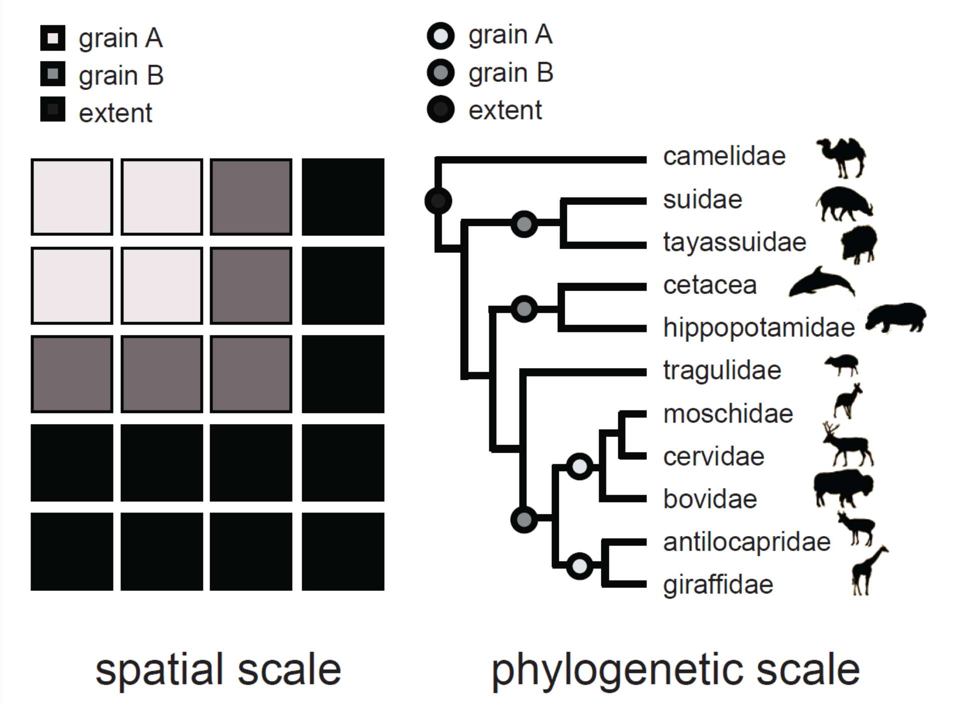
The concept of scale is based on the fact that some entities can be ordered, or placed on a scale (*scala* means *ladder* in Latin). For example, continents contain biomes, ecoregions, and localities, giving rise to spatial hierarchy. Similarly, large clades contain small clades, creating phylogenetic hierarchy which defines phylogenetic scale. However, clades are not always nested, in which case standard measures might be needed to order the clades along the scale continuum. These measures might include time (clade age) but also clade size (number of species within a clade) or the degree of molecular, phenotypic, or ecological divergence within a clade. These measures will be inherently correlated across mutually nested clades but might become decoupled across non-nested clades (e.g. old clades will not necessarily be most diverse) (Box 2).

In the concept of spatial scale, **grain** and **extent** are usually distinguished. Grain refers to the area of the basic unit analyzed (e.g. ecoregion) while extent refers to the total area analyzed (e.g. continent). Phylogenetic scale can be defined analogically, such that phylogenetic grain refers to the basic unit of analysis (e.g. species, genera, families) and phylogenetic extent to the total phylogeny that would encompass all the units analyzed (e.g. class, phylum).

Even though taxonomic ranks are commonly used to define phylogenetic scale, they are not always comparable (e.g. genera in mammals are not comparable to genera in insects), and standardized measures might be better suited to define phylogenetic scales across distant taxa (e.g. taxon age, taxon size). However, even these measures might not ensure entirely that the analyzed taxa are fully comparable. For example, clade age might reflect the degree of phenotypic divergence across clades, but some clades might be more diverged than others despite being of similar age. The same limitations apply to the measures of spatial scale because spatial grains of standardized sizes might not ensure comparability across species of dramatically different home range sizes (Wiens 1989). Therefore, the most suitable measure and definition of the phylogenetic scale should be dictated by the biological properties of the organismal system (e.g. body size, generation time, rates of phenotypic evolution) and the question under study (e.g. phenotypic divergence, diversification dynamics, diversity patterns).

In some cases, it may be useful to work with non-standardized grains which represent more natural units of analysis (e.g. islands in spatial scaling or island faunas in phylogenetic scaling). The extents will then be defined correspondingly, so as to cover all of the units analyzed (e.g. all islands or the entire biotas across islands). Finally, grain and extent are defined only in relation to each other. The grain from one study can therefore act as an extent in another study, or vice versa.

FIGURE (Box 1): Geographic and phylogenetic scale.



dependence. However, focused examination of patterns across scales may precipitate the resolution of several outstanding controversies in the field.

One such controversy revolves around the dynamics of diversity and diversification. It has been debated whether the dynamics are expansionary, such that regional and clade diversity accumulate constantly over time (Benton & Emerson, 2007; Wiens, 2011; Harmon & Harrison, 2015), or whether the dynamics are ecologically limited, such that diversity tends toward an equilibrium (Rabosky, 2009; Rabosky & Hurlbert, 2015). Empirical evidence suggests that genera with dozens of species often expand in terms of their diversity (Benton & Emerson, 2007; Wiens, 2011) whereas higher taxa with thousands of species seem to be mostly saturated at their equilibrium diversity (Rabosky & Hurlbert, 2015). Island radiations and fossil evidence also indicate that clades often expand, seemingly without bounds, during the initial phases of their diversification but eventually reach an equilibrium and saturate (Alroy, 1996; Benton & Emerson, 2007; Glor, 2010; Quental & Marshall, 2013). It is therefore possible that diversification varies systematically across phylogenetic scales such that seemingly contradictory dynamics (i.e. expansionary and equilibrial) might be detected even within the same phylogenetic tree. If this is the case, the debate as to whether the dynamics are expansionary or equilibrial might not prove particularly productive and should perhaps be reframed in terms of phylogenetic scale. For example, we could investigate phylogenetic scales over which the different dynamics prevail, the scale-related factors that determine the shifts between the dynamics, or how the dynamics combine across scales and nested clades of different ages and sizes to produce emergent diversification dynamics.

Evolutionary disparification may also vary across the phylogeny because traits (phenotypic, behavioral, but also molecular) diverge at different rates and, therefore, are conserved over different phylogenetic scales (Freckleton *et al.*, 2002). Even though the dynamics of trait divergence and niche conservatism have been the subject of much research, clear generalizations about their scale-dependence have not yet emerged. In most cases, physiological traits that largely determine the extent of species distributions seem conserved over extensive phylogenetic scales (Freckleton *et al.*, 2002) while habitat- and diet-related traits that mediate species coexistence locally are generally labile and conserved over small scales (Buckley *et al.*, 2010). However, the opposite pattern has also been observed where physiological tolerances are conserved over small scales while habitat, diet, body size, and feeding method remain unchanged for most of a clade's history (Price *et al.*, 2014).

These mixed results suggest that temporal scale may be insufficient to fully capture the variance in niche conservatism. Niches and traits may evolve at different rates even across closely related clades (e.g. due to clade-specific selection regimes, genetic architecture, pleiotropy) that span similar temporal scales. For example, one clade may have undergone an explosive radiation on an island while another accumulated only limited morphological, ecological, and species diversity on the mainland. In such a case, it would be useful to use a time-independent measure of phylogenetic scale, such as the degree of molecular or phenotypic divergence, to delimit clades that are mutually comparable. Consequently, the concept of phylogenetic scale may encourage a more realistic and potentially more accurate way of thinking about trait evolution and niche conservatism.

Community ecology

Patterns of community phylogenetic structure, and hence the inferred processes that shape communities, can vary with phylogenetic scale (Cavender-Bares *et al.*, 2009; Munkemuller *et al.*, 2014). Community ecology represents one of the disciplines where patterns and processes have already been analyzed in relation to phylogenetic scale, illustrating the theoretical and empirical potential of the concept. However, while community phylogeneticists have long been aware of this fact (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009), most studies routinely do not recognize the influence of phylogenetic scale on their results.

To study the phylogenetic structure of a community, researchers calculate standardized community metrics (e.g. the net relatedness index, NRI; Table 1) that compare the observed values to the null expectation based a model in which species are drawn randomly from a regional species pool. Different phylogenetic delimitations of the species pool can produce different results which provides insights into the mechanisms that mediate local coexistence of different suites of species (Cavender-Bares *et al.*, 2009; Lessard *et al.*, 2012). Species pools that encompass large phylogenic extents often indicate that the studied communities were formed by environmental filters while narrowly defined pools produce results suggestive of competition, mutualism, or dispersal limitation within the community (Swenson *et al.*, 2007; Parra *et al.*, 2011).

The interpretation of community structure has been recently under increasing scrutiny because different processes can produce similarly structured communities (Mayfield & Levine, 2010; Gerhold *et al.*, 2015) and a single metric may not capture community structure well enough to identify the processes that may have produced it (Gerhold *et al.*, 2015). The evaluation of how community structure changes across phylogenetic scales, potentially using recently developed statistical approaches (see Table 1) might be a particularly powerful strategy to capture community structure more completely and disentangle the interplay of processes that have produced the community. We also advocate that community metrics are complemented by experimental results if possible (Godoy *et al.*, 2014). Taken together, despite some of the recently raised limitation of community phylogenetics, further advances in the field are certainly possible (e.g. analysis of multiple metrics across phylogenetic scales; experimental work targeting different scales) and hold the promise of a more conclusive interpretation of community-level patterns and the ecological processes behind them.

Biogeography and niche conservatism

Biogeographic patterns, such as species distributions and diversity gradients, are largely shaped by ecological niche conservatism (Wiens & Graham, 2005), and much literature been dedicated to the question whether or not the niches are conserved (Freckleton *et al.*, 2002; Wiens & Graham, 2005; Losos, 2008). Instead of investigating whether niches are conserved or not, however, we should perhaps ask over which phylogenetic scales they are conserved and how this scale-dependence contributes to biogeographic patterns.

Diversity gradients vary dramatically across taxa (Fig. 1), and this variation may result from the fact that climatic niches are conserved over different phylogenetic scales across taxa (Wiens & Donoghue, 2004; Buckley *et al.*, 2010). In mammals, many ancient lineages failed to colonize high latitudes (e.g. treeshrews, sloths, armadillos), presumably because their physiological tolerances have been conserved over larger phylogenetic scales than those of lineages (e.g. rabbits and hares) that have not only invaded high latitudes, but also diversified there (Buckley *et al.*, 2010). This occasional breakdowns of niche conservatism, which typically span only a short period in the history of a clade and limited phylogenetic scales, sometimes precipitate diversification episodes that significantly enrich the diversity of the regional biota (e.g. ray-finned fishes and angiosperm plants) (Glor, 2010; Rabosky *et al.*, 2013). The phylogenetic scale over which niches are conserved may consequently contribute to the formation of diversity patterns.

Diversity patterns may be further influenced by the effects of niche conservatism on regional extinctions (Cahill *et al.*, 2013). Many genera whose climatic niches were conserved over phylogenetic scales that extended beyond the timeframe of the climatic changes during the Pleistocene were wiped out by these changes (e.g. North American trees, European megafauna) (Stuart, 1991; Jackson & Weng, 1999). Yet, the Pleistocene changes in climate have exterminated only few families, perhaps because climatic niches are less conserved at the family-level than at the genus-level (Freckleton *et al.*, 2002). The extinction footprint of climate change therefore likely depends on the phylogenetic scale at which climatic niches are conserved. Evaluating scale-dependent vulnerability to extinction seems particularly relevant in the face of the on-going worldwide changes in climate and land use, and the results of such research might afford insights into the patterns of loss of phylogenetic diversity. In sum, even though it has long been recognized that niches are conserved to varying degrees, few studies have systematically investigated this variation across the phylogeny despite the potentially promising insights that such an investigation could contribute to the study of biodiversity patterns.

Macroecology

Macroecologists, concerned mostly with statistical patterns across large spatial and temporal scales, rarely consider phylogenetic scale in their research. Yet, cross-scale comparisons can identify statistical patterns (e.g. latitudinal diversity gradient, body size distributions, species-area relationship, species-abundance distributions) that are truly universal and those that disintegrate across phylogenetic scales (Storch & Sizling, 2008). Phylogenetic scale may therefore inform us about the generality of statistical patterns in ecology and about the mechanisms (e.g. mathematical, geometric, random sampling, or biological) that likely produced them.

Many of the patterns originally considered universal have later been shown to disintegrate across certain phylogenetic scales. The latitudinal diversity gradient, as discussed above, provides a very intuitive example where the pattern holds across most higher taxa (e.g. mammals, birds, amphibians, reptiles, plants) but often breaks down across their constituent lower taxa that encompass limited phylogenetic scales (e.g. penguins, hares, aphids, ichneumonids, Proteacea) (Kindlman *et al.*, 2007; Fig. 1a). Likewise, species abundance and body mass are negatively correlated across birds and mammals (Damuth, 1981), but the correlation disappears across narrowly defined taxa (Isaac *et al.*, 2011) and even becomes positive in some tribes of birds (Cotgreave & Stockley, 1994; Fig. 1b). Within large phylogenetic extents, small-bodied species can reach high abundances because their low metabolic requirements raise the carrying capacities of their populations. However, within restricted phylogenetic extents, local abundance becomes constrained by competition between closely related species, and large-bodied species become locally abundant because of their competitive superiority, thus reversing the directionality of the correlation between body size and population abundance across phylogenetic scales (Cotgreave & Stockley, 1994; Fig. 1b).

Theoretical and empirical exploration of the variation of macroecological patterns across phylogenetic scales may shed light into the universality of these patterns. The species-area relationship (SAR) and species-abundance distribution (SAD) were traditionally believed to universally conform to certain mathematical forms (the power-law function and the lognormal distribution, respectively) (Preston, 1948; Rosenzweig, 1995). However, if two sister clades follow power-law SARs and lognormal SADs which differ in their parameters, it can be proven mathematically that the clade containing both sister taxa cannot follow either the power-law SAR or the lognormal SAD (Storch & Sizling, 2008; Sizling *et al.*, 2009). Therefore, even though some macroecological patterns represent classic examples of ecological laws, cross-scale analyses can indicate that they are not truly universal, and, as was the case for the relationship between species abundance and body mass, can sometimes provide insights into the biological mechanisms behind them.

The fact that some statistical patterns do not hold across phylogenetic scales implies either that the theories that assume patterns are universal (e.g., those theories based on geometry) are fundamentally ill-founded; instead a pattern possibly pertains to select phylogenetic scales only (Storch & Sizling, 2008). The latter would suggest that phylogenetic scales form phylogenetic domains (Box 2) within which the processes hypothesized by a theory operates, and the explicit delimitation of these domains might further inform the theory (see Box 2).

Phylogenetic scale in practice

The above overview demonstrates that the consideration of phylogenetic scale varies across fields, both in terms of the approach used to consider phylogenetic scale and the vocabulary used to describe it. Therefore, there is value in developing a common language to discuss and study phylogenetic scale. There are two general approaches with which phylogenetic scale can be considered in ecological and evolutionary research. One is exploratory, where patterns are identified across a range of phylogenetic scales and then explained in the light of specific events or mechanisms. The other approach relies on testing a priori hypotheses, which are based on mechanisms that presumably take place at a given phylogenetic scale. Both approaches have their strengths and either may be appropriate, depending on the objective of a given study; however, we advocate the hypotheses testing approach for most questions.

To study the effects of phylogenetic scale, one can evaluate how a specific attribute of interest (such as diversification rate, niche conservatism, geographic distribution, statistical relationships) changes with phylogenetic scale. These attributes may vary randomly or systematically across the

Table 1. Ecological and evolutionary attributes that often vary across phylogenetic scales. Each attribute is listed along with examples of methods for its evaluation.

Field	Examined attribute	Examples of evaluation methods
Evolution and diversification	diversification mode	coalescent inference to distinguish between accelerations, slowdowns, and saturation (Morlon *et al.*, 2010)
	diversification rate	product-moment estimators (Magallon & Sanderson, 2001), equal-splits measures (Jetz *et al.*, 2012)
	slowdown strength	gamma statistic (Pybus & Harvey, 2000)
Community ecology	community structure	phylometrics (NRI, NTI, MNND, MPD) (Webb *et al.*, 2002)
	phylogenetic diversity	Faith's PD (Faith, 1992)
Biogeography and macroecology	form of the relationship	linear, polynomial, exponential, lognormal functions
	strength of the relationship	Pearson's correlation, Spearman's correlation, regression slope
Niche conservatism	phylogenetic signal	Pagel's lambda (Freckleton *et al.*, 2002), Blomberg's K (Blomberg *et al.*, 2003)
	evolutionary rates	Brownian motion model (Felsenstein, 1985), Ornstein-Uhlenbeck model of trait evolution (Hansen, 1997)

BOX 2: Research across phylogenetic scales

Many attributes, such as diversification rate, niche conservatism, or community structure, vary across phylogenetic scales (Table 1). They may vary in three different ways:

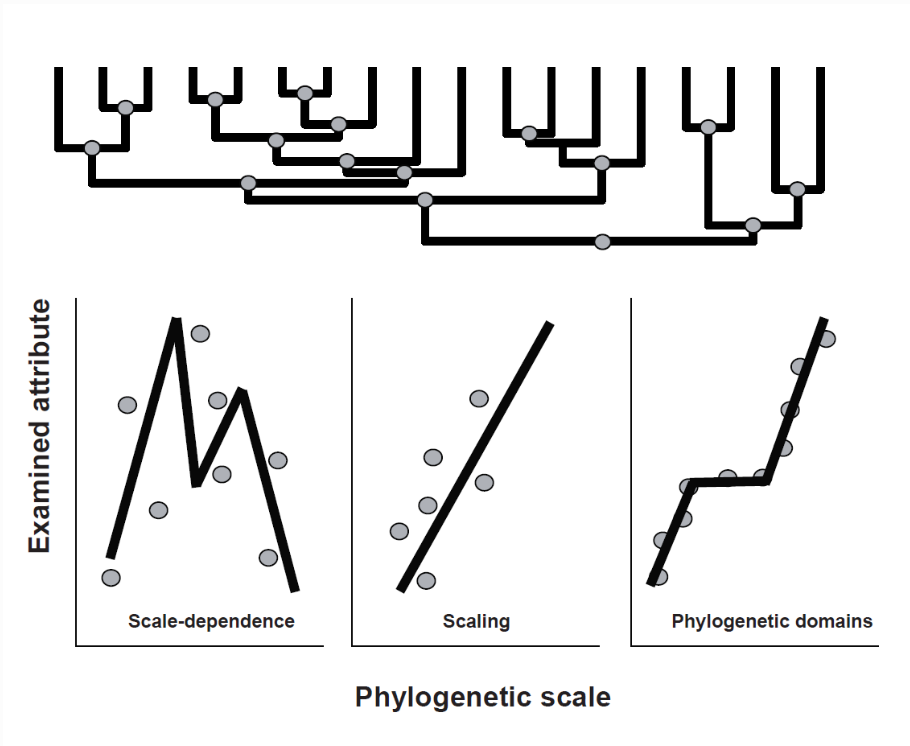
(a) Scale dependence refers to the situation when the studied attribute varies across phylogenetic scales without any obvious trend. In this case, the suitable scale of investigation should be defined a priori, based on the objective of the study. The results from one scale will be difficult to extrapolate to other scales.

(b) Scaling occurs when the attribute of interest varies systematically along the scale axis. The interpretation of scaling is at least threefold, depending on the underlying mechanism (note that only one of the interpretations is biological):

1. **Statistical scaling** is a sample-size effect whereby the statistical power of the analysis increases with clade size. Consequently, the attribute under study appears to change systematically from small clades to large clades (Machac *et al.*, 2012). While the inferred values of the attribute itself may be technically correct, their systematic variation across scales is biologically irrelevant.
2. **Methodological artifacts** result when a statistical analysis becomes increasingly misleading toward the deep nodes of the phylogeny, resulting in incorrect and potentially biased estimates for the attribute of interest (e.g. ancestral reconstructions under dispersal-vicariance models tend to suggest that the ancestor occupied all of the regions examined) (Ronquist, 1997). Methodological artifacts can be mitigated under various statistical corrections or when the results are validated using supplementary data, such as fossils.
3. **Phylogenetic scaling in the strict sense** occurs when the studied attribute changes across scales because the underlying biological process changes. True scaling can therefore inform us about the processes which generate the patterns observed across scales. If the scaling can be described mathematically, it may allow to extrapolate across scales, even those not included in the original study, i.e. *downscale* or *upscale* the patterns under study.

(c) Domains of scale refer to the segments of the phylogeny (e.g. taxonomic units, tree depth, distinct clades) within which the attribute of interest appears relatively unchanged. The attribute might change abruptly between domains, indicating changes in the underlying biological processes. Therefore, it should be possible to extrapolate across phylogenetic scales within domains, but not across scales between them.

FIGURE (BOX 2): Numerous attributes can be studied across phylogenetic scales. These may include diversification measures, statistical relationships between ecological variables, parameters of frequency distributions, metrics that describe community phylogenetic structure, or measures of niche conservatism (see Table 1). Phylogenetic scale can be defined in terms of clade age, clade size, taxonomic rank, the degree of molecular or phenotypic divergence, etc., depending on the question under study.



phylogeny, be more prevalent at particular scales, or stay unchanged across a discrete set of mutually nested clades (Box 2). We refer to the latter as a domain of phylogenetic scale which, in analogy to spatial domains (Wiens, 1989), corresponds to a segment of phylogeny that reveals homogeneity in the attribute of interest. In this section, we consider conceptual and methodological approaches to explore patterns which are phylogenetic scale-dependent.

Choice of phylogenetic scale

While most researchers are aware that the choice of scale can influence inferences about patterns or processes, all too often the choice of scale, be it spatial, temporal or phylogenetic, is influenced by data availability or other logistical concerns. Instead, the scale of an investigation should be chosen based on a specific objective or question whenever possible. For example, phylogenies of higher taxa may not be appropriate for evaluating the processes of community assembly that typically take place across small phylogenetic scales. To test the hypothesis that competition reduces species coexistence locally, for example, small phylogenetic scales (e.g. genera, or clades where species can be reasonably assumed to compete with each other should be preferred to large scales where most species are unlikely to compete (e.g. the entire classes, such as birds and mammals). However, even with a specific question at hand, it can be difficult to choose a single most appropriate phylogenetic scale. Therefore, evaluating multiple phylogenetic extents or grains should be considered.

Multiple phylogenetic scales

Simultaneous consideration of multiple phylogenetic scales may be particularly important in large phylogenies because different clades within such phylogenies may show different patterns with respect to the attribute of interest (e.g. diversification rate, the strength of niche conservatism, patterns of community phylogenetic structure) (Figure 1). For example, Cetacean systematists had long been perplexed as to why there is little correspondence between diversification dynamics estimated from the fossil record and phylogenetic trees (Quental & Marshall, 2010; Morlon *et al.*, 2011). The correspondence between the two datasets emerged only when diversification dynamics were evaluated independently for clades within cetaceans (whales, dolphins, and porpoises) as opposed to cetaceans as a whole. In this case, each clade appeared to have its own dynamics which were obscured when the entire tree was evaluated (Morlon *et al.*, 2011).

In some cases, it may be difficult or even undesirable to specify, a priori, a specific set of scales. It might be instead more illuminating to study how the attribute of interest varies across an inclusive range of scales. There are several approaches, originating in community phylogenetics, which allow for such cross-scale analyses and return results for each node of the phylogenetic tree (Leibold *et al.*, 2010; Pavoine *et al.*, 2010; Borregaard *et al.*, 2014; Table 1). For example, the method developed by Borregaard *et al.* (2014) identifies nodes whose descendant clades underwent conspicuous geographic, phenotypic, or ecological shifts. In evolutionary research, evaluation of all nodes is not uncommon, and multiple tools have been developed to identify shifts in diversification rates and clades with conspicuously fast or slow diversification (Alfaro *et al.*, 2009; Rabosky, 2014; Table 1). However, statistical analyses that would include all nodes of the phylogeny remain relatively scarce (e.g., Buckley *et al.*, 2010; Machac *et al.*, 2012), and most studies analyze selected clades only, despite the often cited concerns that the selection of clades is rarely random, reflects our prior biases, and might influence the analysis profoundly (Phillimore & Price, 2008).

Two potential issues associated with the evaluation of all nodes are data non-independence and nestedness. Non-independence can be readily accommodated by widely used comparative methods (e.g. PIC, PGLS) (Hurlbert, 1984; Felsenstein, 1985). These methods typically estimate the same parameters as their conventional counterparts (e.g. intercepts, regression slopes, group means) but adjust the confidence intervals of these parameters based on the inferred degree of phylogenetic correlation in the data (Hurlbert, 1984; Felsenstein, 1985). The nestedness of the data is more difficult to accommodate. For example, the diversification rate of a clade is inherently determined by the rate values across its constituent sub-clades. Nestedness therefore extends beyond the phylogenetic correlation of rate values and reflects how the value for a clade is produced by the sub-clade values. This information cannot be readily accommodated under the currently available comparative methods whose phylogenetic corrections consequently cannot guarantee proper estimates of statistical significance across nested data. For these reasons, we argue that parameter estimates can be extracted, compared, and analyzed across nested clades, but their significance needs to be interpreted cautiously. New theory that would illuminate how different attributes of interest (e.g. diversification rates, regression slopes, phylogenetic signal) combine and compound across nested hierarchies, as well as the methods to capture these correlations, are clearly needed.

Phylogenetic scaling

Statistical methods that evaluate all clades (nodes) in a given phylogeny (Pavoine *et al.*, 2010; Borregaard *et al.*, 2014; Rabosky, 2014) can be used to explore phylogenetic scaling. Scaling is a systematic trend along the scale axis in the attribute of interest. For example, diversification rate or net relatedness index (NRI; Webb *et al.*, 2002) may change systematically with increasing phylogenetic scale (Cavender-Bares *et al.*, 2009).

Phylogenetic scaling should be most prevalent across mutually nested clades because the patterns associated with larger clades are determined by the patterns of clades nested within them (or vice versa). For example, diversification rate of a clade is determined by the rate values of its subclades, similarly as species richness of a spatial plot is determined by the richness of its subplots. Consequently, it should be possible to predict the value of an attribute (e.g. diversification rate, regression slopes, phylogenetic signal) at a particular phylogenetic scale from the knowledge of those values across other scales, much like it is possible to estimate species richness within large geographic areas, based on the knowledge of richness within small areas (Storch *et al.*, 2012). When characterized mathematically, phylogenetic scaling should allow for predictions across phylogenetic scales not covered by the phylogeny at hand (i.e. upscaling or downscaling).

Domains of phylogenetic scale

When moving along the scale axis, the values of an attribute might sometimes change abruptly. Such discontinuities provide the opportunity to delimit domains of phylogenetic scale (Box 2). Domains are discrete segments of a phylogeny, such as monophyletic clades, taxonomic ranks, or tree depth, which show homogeneity in the attribute of interest (i.e. diversification rate, statistical correlation, or phylogenetic signal). By definition, the attribute does not vary substantially within a domain but changes between domains. Phylogenetic domains may therefore provide insights into the processes which operate over different segments of a phylogenetic tree.

Traditionally, phylogenetic domains were delimited by taxonomists whose objective was to organize species into biologically meaningful units, such as families, orders, or classes. These units are based mostly on morphological and ecological attributes. However, phylogenetic domains can also consist of clades that show diversification homogeneity, similar rates of morphological evolution, or similar life-history trade-offs. Therefore, the domains may be delimited based on key innovations, episodes of historical dispersals, or extinction events, but also statistically, using quantitative methods without the prior knowledge of the evolutionary history of a clade. While the statistical approach may be more transparent and reproducible, the resulting domains may be harder to interpret biologically. Nonetheless, statistically delimited domains may reveal otherwise unnoticed evolutionary events and potentially important breaks in the clade's history that may have shaped its extant diversity.

Phylogenetic domains may also facilitate statistical inference, given that most comparative methods assume that the attributes analyzed are homogeneous (e.g. regression slopes do not vary across genera within the analyzed family, diversification is homogenous across the analyzed lineages) and return spurious results when applied to clades that show a mixture of patterns and processes (Morlon *et al.*, 2011; O'Meara, 2012). Phylogenetic domains may therefore help to identify when comparative methods report reasonably reliable results and when their conclusions must be interpreted with caution because the results span different domains and the underlying assumptions have been violated.

Conclusion

It is well established that different processes dominate over different spatial and temporal scales. Phylogenetic scale, however, has received limited attention although much research in ecology and evolution relies on molecular phylogenies (Table 1). Explicit consideration of phylogenetic scale, scale dependence, phylogenetic scaling, and the domains of phylogenetic scale can therefore inform multiple disciplines in the field (e.g. diversification analysis, community ecology, biogeography and macroecology).

We have discussed phylogenetic scale largely in isolation from spatial and temporal scales, but these types of scale will often be related. For instance, competitive exclusion may be prominent among closely related species within local communities over short time periods (Cavender-Bares *et al.*, 2009). In contrast, plate tectonics might influence deeper nodes in a phylogeny and operate over broad geographic and temporal scales (Willis & Whittaker, 2002). In some notable cases, however, the scales may not be related. Diversity anomalies, such as New Caledonia or Madagascar, represent examples of decoupling where rich biotas that encompass extensive phylogenetic scales diversified in a relatively small region (Warren *et al.*, 2010; Espeland & Murienne, 2011). In contrast, recent radiations within grasses and rodents have had a large geographic footprint but encompass only limited phylogenetic scales (Edwards *et al.*, 2010; Edwards & Smith, 2010) (Edwards et al. 2010). Evaluating when different types of scale are coupled (or decoupled) may yield new insights into the evolutionary history of different clades and regions (Willis & Whittaker, 2002).

We hope that the perspective presented here will spur further theoretical, empirical, and methodological research. Explicit consideration of phylogenetic scale may turn our focus away from the importance of particular mechanisms (diversification, trait evolution, niche conservatism) toward the appreciation for the interplay of multiple processes which together, but over different phylogenetic scales, shape the diversity of life.

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