

## Point of View

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### On the Selection and Analysis of Clades in Comparative Evolutionary Studies

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**Abstract.**—Researchers commonly present results of comparative studies of taxonomic groups. In this review, we criticize the focus on named clades, usually, comparably ranked groups such as families or orders, for comparative evolutionary analyses and question the general practice of using clades as units of analysis. The practice of analyzing sets of named groups persists despite widespread appreciation that the groups we have chosen to name are based on subjective human concerns rather than objective properties of nature. We demonstrate an effect of clade selection on results in one study and present some potential alternatives to selecting named clades for analysis that are relatively objective in clade choice. However, we note that these alternatives are only partial solutions for clade-based studies. The practice of analyzing named clades obviously is biased and problematic, but its issues portend broader problems with the general approach of employing clades as units of analysis. Most clade-based studies do not account for the nonindependence of clades, and the biological insight gained from demonstrating some pattern among a particular arbitrary sample of groups is arguable. [Clades; comparative biology; taxonomic groups.]

Comparative evolutionary studies often analyze multiple clades separately to test trends of character correlation, speciation rate, or some other macroevolutionary property. Clade-based studies may use techniques specific to taking the clade as unit of analysis (e.g., Corfield et al. 2015) used order as a covariate in regression analyses), or may involve simply performing treewide analyses on multiple separate subtrees (e.g., Sánchez-Reyes et al. 2017) conducted separate analyses of Tetrapod classes/orders). Whole-tree lineage-based approaches (e.g., those that incorporate reconstructions of internal branch states) do not require breaking a tree into multiple subtrees, that is, clades, but this subdivision often is done to examine whether some trend occurs in multiple parts of the tree. Although operationally well understood (see, e.g., the distinction between reconstruction-based “uncensored” and clade-based “censored” applications in the program Brownie [O’Meara et al. 2006]), the conceptual bases of clade-based studies have remained largely unexamined. Here, we criticize a common approach in clade-based studies, the use of taxonomic groups for analysis, and offer some alternative approaches to clade selection. This discussion leads to questions regarding the value of clade-based studies in general.

phenotypic evolution of named groups persists. Most commonly, clades of comparable Linnaean rank (e.g., families) are compared. Baker et al. (2015) compared size evolution among mammal orders, Muller et al. (2019) compared genome evolution among subfamilies within a plant family (Bromeliaceae), and Saladin et al. (2019) compared “phylogenetic turnover” of assemblages among Amphibia, Aves, Mammalia, and Squamata, for example (additional examples: Corfield et al. 2015: bird orders; Miller and Wiens 2017: Amniote classes; Sánchez-Reyes et al. 2017: higher taxa [e.g., Amphibian families, Angiosperm orders]; Castro-Insua et al. 2018: Mammal families; Carta et al. 2018: Angiosperm superorders; González-del-Pliego et al. 2019: Amphibian families).

The selection of named clades for comparison involves choosing from the groups we humans have elected to recognize. Historically the choice to name a group was based on perceptions of distinctiveness and important traits (e.g., Mammalia = the clade including species with mammary glands), an approach that in modern form may employ genetic divergence cutoffs (e.g., Yarza et al. 2014). Today, many decisions to “split” or “lump” taxonomic groups appear driven by a taxonomic Goldilocks principle, whereby named groups of a particular rank must include neither too many nor too few species/taxa within them according to some subjective human concern (e.g., the large number of species in the genus *Anolis* is considered “a hindrance to scientific communication” [Nicholson et al. 2013, p. 13]; botanists are said to favor genera with many species “so as to help in keeping their names (and, possibly, their diagnostic traits) in mind” [Minelli 2016]). The continuing use of taxonomic ranks (genera, families, orders, etc.) exacerbates the illusion of biological significance of named groups, as the nomenclatural

#### ANALYSIS OF NAMED CLADES

##### *The Clades We Name Reflect Human Foci*

Despite widespread and longstanding appreciation of the biological insignificance of named taxonomic groups (e.g., Laurin 2010), the practice of comparing biological properties such as diversification rates and rates of

comparability of ranks fallaciously suggests some evolutionary comparability of groups with the same rank (de Queiroz and Donoghue 1988). This problem has manifest historically in repeated and biologically meaningless attempts to explain differences in (e.g.) species diversity between (e.g.) genera using ecological rather than psychological arguments (see discussion in Dubois 1988; Minelli 2000; Laurin 2010), and currently by the issues discussed in this article. We note two issues related to this discussion. First, our comments have nothing to do with monophyly of taxa; we are assuming all named groups are clades. Second, the adoption of phylogenetic nomenclature (Cantino and de Queiroz 2010) likely would alleviate the temptation to analyze named groups, because in that case there would be no illusion of comparability between clades of the same rank.

Whether based on “important” traits, the Taxonomic Goldilocks Principle, assumed biological comparability of groups at some taxonomic rank, or some other anthropogenic rule, a set of named groups is arbitrary with respect to the universe of clades that could be compared. If we are interested in learning about nature rather than the consequences of our naming decisions, then these criteria of selection are a potential problem for comparative studies of named groups.

Justifications for comparative study of named groups such as orders usually focus on the existence of key traits in named clades (mammals with endothermy, e.g.). Such foci are reminiscent of the classification claims of evolutionary taxonomists who emphasized key traits, operational rules, or practicality over phylogeny as a basis for taxonomy (e.g., Ashlock 1979). Almost nobody argues for the recognition of paraphyletic or polyphyletic groups based on such arbitrary concerns anymore, but apparently our lingering biases still permeate our comparative evolutionary studies.

It might be argued that a set of families or phyla is as good as any other set of clades for testing comparative hypotheses. This supposition would be true if results are insensitive to choice of clades to compare. That is if, for example, some correlation between a trait and “diversification rate” found in analyses of families was also found when some other sample of clades was analyzed, then use of named groups as units of analysis might be reasonable. Fortunately, this contention is easily testable (see below for an example). Unfortunately, currently few if any studies test the effect of clade selection on conclusions.

Below we discuss alternatives to the selection of clades for analysis based on taxonomy. Although these approaches are each suitable only for particular kinds of study and are each flawed in unique and shared ways, they all lack the main demerit of the taxonomic approach; that is, dependence on human bias rather than objective properties of nature.

#### *Other Options: Random Selection of Clades*

The approach of comparing a set of randomly selected clades seems analytically attractive as a substitute for taxonomy-based selection. However, we note two problems with this approach. First, random selection of clades may result in a set of units that seem even less equivalent than a set of comparably ranked taxonomic groups. For example, one could end up with comparison of a recently diverged clade of two species with an anciently diverged clade of thousands of species. Second, the nested nature of clades means that any random selection of clades is likely to come with statistically unsatisfactory nonindependence issues (i.e., applying Felsenstein’s [1985] classic arguments to clades rather than species), even if compared clades do not overlap in content. For any rooted strictly bifurcating tree, the maximum number of contained subclades that are independent is two, regardless of tree size or shape. Although perhaps not immediately obvious, this rule is easy to appreciate if we imagine choosing two independent subclades within a rooted tree (independent in the sense that neither is nested within the other), then attempt to choose a third independent clade. Any clade (where a clade includes some ancestor and all its descendants) chosen will either be nested within one of the two selected clades, more closely related to one clade than the other, or outside of the smallest clade containing both of the initially selected clades, thus rendering the initially selected clades as nonindependent (i.e., sharing history with each other) relative to the third selected clade. Therefore, two is the limit for independent subclades within a rooted bifurcating tree. This nonindependence problem is not a consequence of attempting random selection of clades, but rather affects any comparison of more than two clades. Comparisons of vertebrate classes, for example, do not tend to account for the fact that squamates share some 30 myr of evolutionary history with birds separate from mammals.

Both the nonindependence and nonequivalency problems are addressable using *ad hoc* approaches—nonindependence using standard phylogenetic corrections and nonequivalency by restricting random clade selection to particular ranges of clade size or age—but the broader question of the value of clade-based studies remains (see below).

#### *Other Options: Timeslice*

The approach of comparing clades of equal age (Fig. 1; e.g., Roalson and Roberts 2016) may be most similar in spirit to the taxonomic selection approach as usually implemented (i.e., with comparison of named clades of the same rank), and it may hold the best hope as a replacement if comparison of clades is to continue. This approach would force a fundamental shift in clade comparison analyses, as clades not normally grouped together would become units (datapoints) dependent on the particular timeslice adopted. For

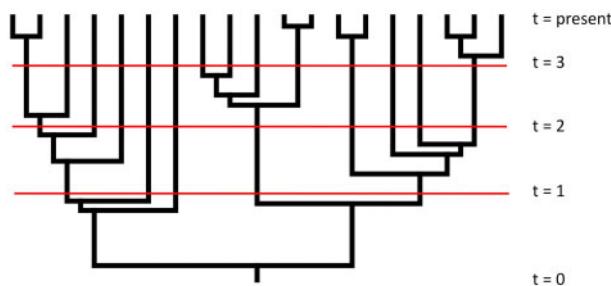


FIGURE 1. The timeslice approach involves comparing clades of equal age across a dated tree. Comparisons of clades at timeslices 1 ( $n=5$  clades), 2 ( $n=10$  clades), 3 ( $n=14$  clades) involve alternative nonindependent analyses.

example, if we endeavor to compare Tetrapod clades and select a timeslice at the Triassic-Jurassic boundary, the datapoints are mammals, birds, crocodylians, cryptodire turtles, pleurodire turtles, tuataras, dibamid squamates, nondibamid squamates, frogs, salamanders, and caecilians, according to one phylogenomic estimate (Shen et al. 2011). Note that this set is a minimum. If extinct taxa and denser taxon sampling were incorporated, still more nonstandard clades would result. However even if one is comfortable with adopting a new set of comparisons that subdivides classically unitary clades like turtles and squamates, it must be recognized that the timeslice approach does not solve the nonindependence problem discussed above. Taxonomic comparisons are not only subjective, but control for neither time nor evolutionary relationship; the timeslice approach controls for time but maintains the same issues of nonindependence due to evolutionary relationship.

#### *Other Options: Maximal and Random Sister Clade Comparisons*

Many workers make use of sister clade comparisons, for example, under diversification tests proposed by Slowinski and Guyer (1993) or Paradis (2012). The nomenclatural comparability of ranked groups such as genera or families may encourage analytical comparisons of sister clades of the same rank (e.g., Jansson and Davies 2008; Clarke et al. 2016), but there is no scientific reason to restrict sister clade analyses to named groups. Alternative kinds of sister clade comparisons include trait- or diversity-based selection of sisters, maximizing the number of sister clade comparisons, or random selection of sister clades. Trait-based comparisons of diversification in sister clades are common (e.g., Mitterboeck et al. 2016; Poore et al. 2017) and subject to known biases (e.g., Maddison 2006). We discuss the latter two approaches below.

For any rooted phylogenetic tree, the maximum number of sets of independent sister clade comparisons is equal to the number of sister-tip pairs in the tree. A proof of this fact could proceed inductively, starting with the simplest informative rooted tree (i.e., three

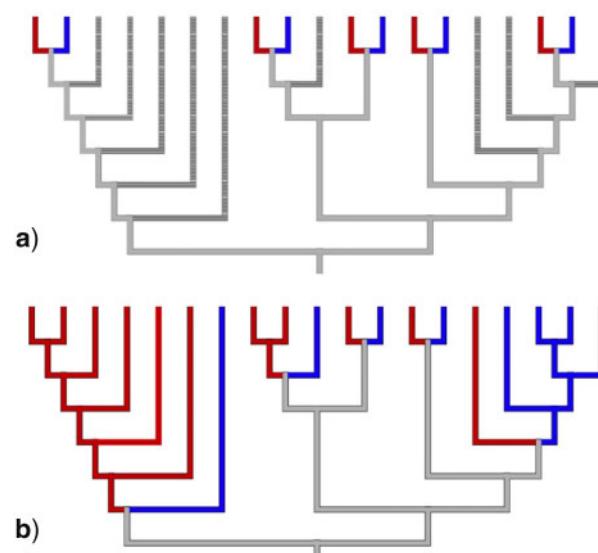


FIGURE 2. Alternative maximizations of the number of independent sister clade comparisons in a particular 19-taxon tree. The maximum number of sister clade comparisons in a tree of this shape is five. a) Maximization of recent comparisons; b) maximization of phylogenetic depth.

taxa) and demonstrating that only additions of taxa that increase the number of sister-tip pairs will increase the number of independent sister clade comparisons. This characteristic of rooted trees does not mean that sister tips must be compared in order to maximize the number of comparisons. One might, for example, desire to select the deepest possible comparisons while still maximizing the number of clades compared. Two obvious ways to perform maximum sister clade comparisons are to maximize either recency or depth of comparison. Maximizing recent comparisons involves comparing as many pairs of sister tips as possible (perhaps an unlikely comparison in practice), whereas maximizing depth will involve comparing subsets of the tree composed of ladderlike (pectinate) structure. Figure 2a shows a maximum number of sister clade comparisons while maximizing recency; Figure 2b shows a maximum number of sister clade comparisons while maximizing depth of comparisons. Under the latter scheme, one could compare pairs of species (choosing one from the larger clade) or a clade to its sister lineage, depending on the goals of the study.

The above maximization approach ensures only a particular kind of comparison relative to tree shape, that is, comparison of a single taxon with its sister taxon or clade. One also could maximize the number of sister clades compared under a randomization procedure. This procedure would need to proceed in stepwise fashion, as each selection of a sister clade pair restricts the universe of possible independent pairs remaining in the tree. Figure 3a–d show a sample sequence of random selection of sequentially compatible independent pairs of sister clades; Figure 3e–g show three potential outcomes of such a procedure.

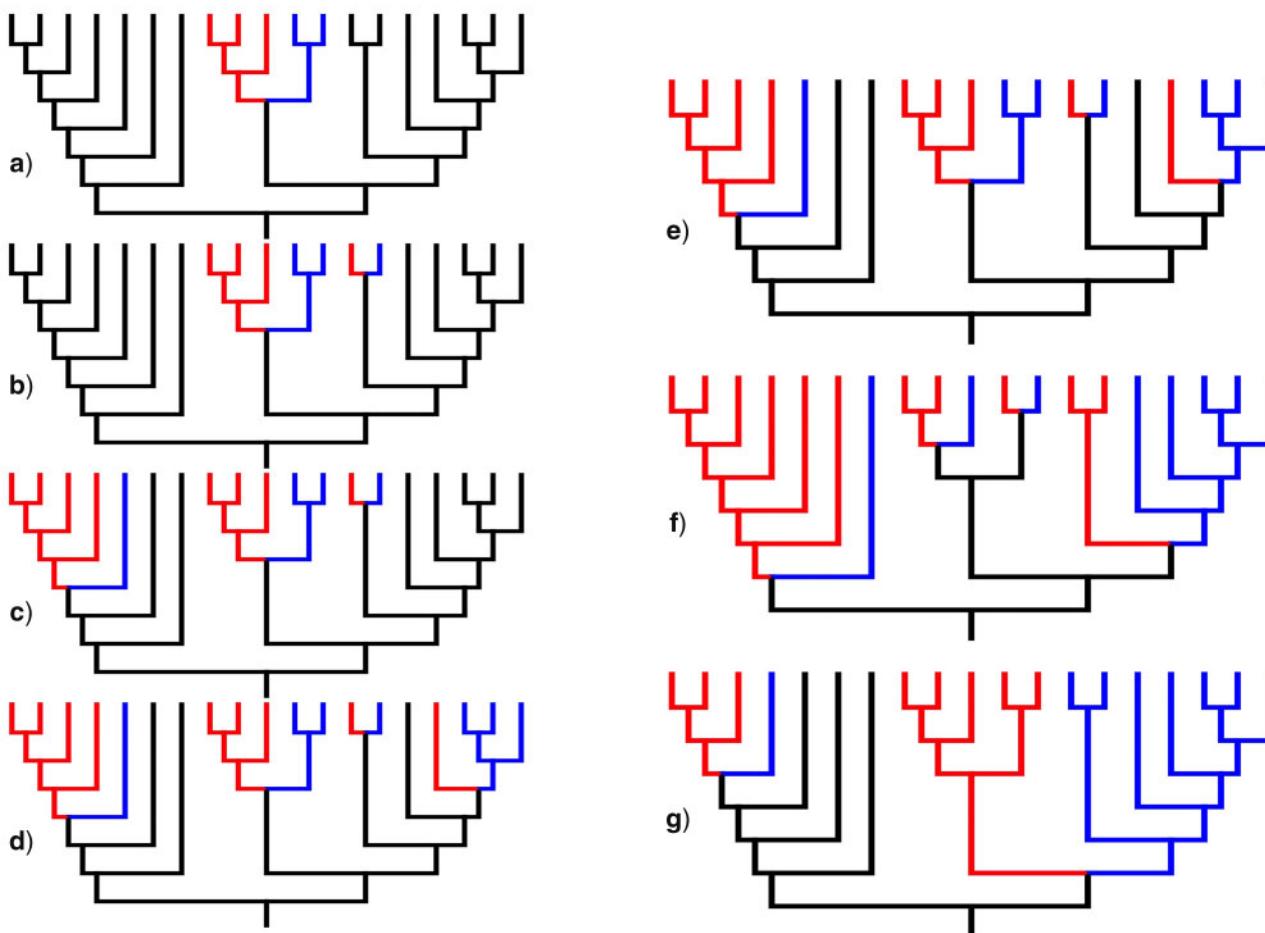


FIGURE 3. Random selection of independent sister clade comparisons. (a–d) One sequence of random selection of sister clades; (a, then b, then c, then d: four sister clade pairs); (e–g) alternative potential final selections of independent sister clade comparisons resulting from sequential random selection of sister clades.

#### *Other Options: Lineage-Based Approaches*

As discussed above, comparing named groups for diversification rate or trait evolution, even named clades strongly associated with favored traits, is only indirectly informative about nature and beset with nonindependence issues. Conversely, the comparison of lineages—segments of phylogenetic trees—across entire phylogenies is a form of potentially rigorous hypothesis testing. The means for making such comparisons are in continual development (e.g., Felsenstein 1985; Maddison 1990; Maddison et al. 2007; O'Meara 2012; O'Meara and Beaulieu 2016; Uyeda et al. 2018) and represent the most precise and rigorous options for testing trends across evolutionary history. To put it simply, comparative methods that account for phylogenetic nonindependence by analyzing lineages across whole phylogenies solve most if not all of the problems discussed in this essay.

#### *An Example*

In order to illustrate an effect of analyzing named groups versus a set of temporally comparable clades,

we reexamine a portion of the results of Baker et al. (2015) using the timeslice methodology described above. Baker et al. (2015) tested whether named mammalian clades (mostly orders) increased in body size over evolutionary time and concluded that such an increase had occurred. Note first that it would be difficult to consider mammalian orders to be comparable in any nontaxonomic sense. The studied mammal orders vary in age from 98.9 Ma to 55.8 Ma, differ in number of taxa, and share varying degrees of evolutionary history (e.g., Lagomorpha and Rodentia share some 10 myr of history separate from Afrotheria).

We applied a timeslice of 86 Ma to the mammalian tree using a new data set based on Baker et al. (2015). This point in mammalian evolutionary history results in a similar number of clades recovered by Baker et al. (2015). We used the time calibrated phylogeny for mammals produced by Fritz et al. (2009) and a comprehensive data set of mammalian body mass compiled from Ernest (2003) and Jones et al. (2009). Prior to analysis, we log transformed body mass and pruned the phylogeny and data set to include only taxa present in both, resulting in  $n=3845$  species (vs.  $n=3321$  in Baker et al. (2015)).

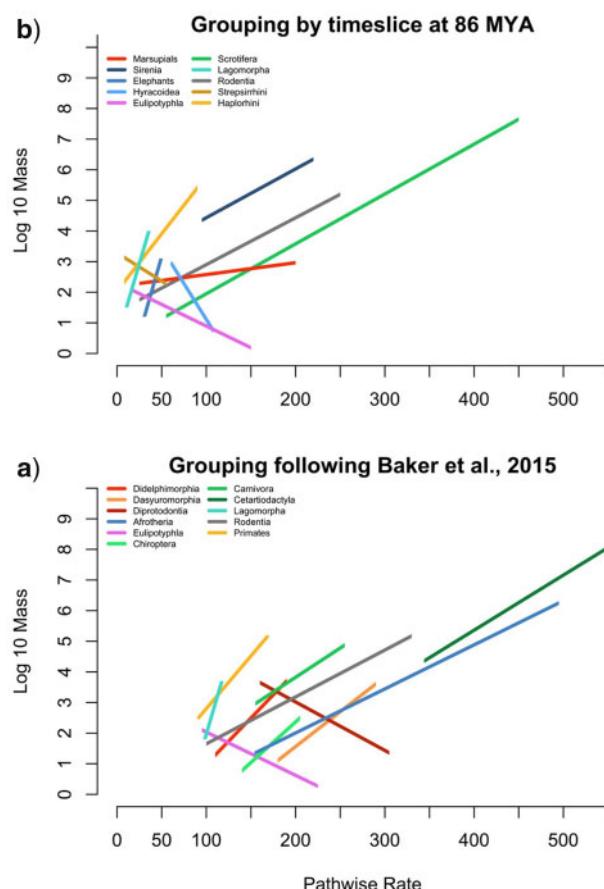


FIGURE 4. Log<sub>10</sub> body mass versus phylogenetic pathwise rate, as presented in Baker et al. (2015) to show changes in body mass over evolutionary time. Results using a) comparably ranked taxonomic clades as units and b) timeslice approach to identifying clades at 86 MYA described in text.

Branch lengths were rescaled by rate of morphological evolution in BayesTraits V3.0.2 (Meade and Pagel 2019) using Phylogenetic Generalized Least Squares. Pathwise rate (i.e., sum of rescaled branch lengths from root-to-tip) and log transformed body mass were recovered for all taxa. We analyzed the sample of clades that result from the taxonomic criterion of Baker et al. (2015, i.e., orders) and analyzed the set of clades that result from a timeslice at 86 Ma. Body size was regressed on pathwise rate for each clade of the two grouping schemes. All clades recovered at 86 Ma have preexisting names and we secondarily apply them here to simplify our presented results. We recovered 14 clades that diverged at or before 86 Ma using the timeslice method and 7 of these met the authors' criterion for minimum number of taxa ( $n \geq 40$ ) to be statistically informative. However, we present results for three additional groups containing fewer than 40 taxa in order to increase our sample size.

Figure 4a shows results of analyses using taxonomic orders and Figure 4b shows the timeslice results using the graphical presentation employed by Baker et al. Not surprisingly, the timeslice approach produces a

different data set, i.e., a different set of analyzed clades, than the taxonomic approach. Revealed subtleties include a mixed signal within primates (body size increasing in Haplorhini, decreasing in Strepsirrhini) and a lumping of three closely related orders found to increase in body size into a single increasing clade (i.e., Carnivora, Chiroptera, and Cetartiodactyla are analyzed as Scrotifera). Overall, the taxonomic analysis resulted in nine clades increasing in body size and two decreasing, whereas the 86 Ma timeslice analysis shows seven increasing and three decreasing. Thus the effect of analyzing this alternative set of clades is to call into question the strength of the time-body size relationship. For example, under a sign test assuming increase and decrease in body size are equally likely (and ignoring the nonindependence of clades as datapoints), the taxonomic results show significant increase at level 0.05 [ $P = 0.035$ ], whereas the timeslice results do not [ $P = 0.206$ ]. We note that this exercise is neither a reanalysis of Baker et al.'s (2015) data nor a definitive statement on mammal size evolution (see e.g., Bokma et al. (2016)). Our goal is simply to provide a counterexample to the supposition that choice of clades for analysis does not matter.

#### USE OF CLADES AS UNITS OF ANALYSIS

The alternative approaches to clade selection presented above (random, timeslice, random/maximal sister clade) solve the subjectivity and comparability problems of clade selection to varying degrees. However, none of them addresses a fundamental problem with clade-based studies. Namely, the issue of nonindependence between analyzed units. There are approaches that both analyze clades as units and attempt to account for clade interrelationships (e.g., Baker et al. 2015), thus solving the nonindependence problem. However, the end results of such studies still are difficult to interpret biologically. That is, it is not clear why trends among some arbitrary set of clades should be of interest. The statements that "Passeriformes speciated faster than Sphenisciformes" or "mammals have higher metabolic rates than frogs" are factually true but only tangentially informative as explanations of the natural world. Such statements simply tell us how two arbitrarily selected groups differ, which is not a question about natural evolutionary patterns. The association of particular traits with compared clades—e.g., endothermy with mammals, ectothermy with squamates; perching or song with Passeriformes, nonvolant ecology with Sphenisciformes—does not solve the problem, but rather points the way to more precise and informative research questions. If one is interested in comparing the effects of "endothermy" and "ectothermy" (or perching/song, or body plan, or terrestriality...) one should compare evolutionary lineages that are rigorously reconstructed as such under suitable phylogenetic correction.

## CONCLUSIONS

In this essay, we have attempted to point out potential problems inherent to the comparison of (monophyletic, usually comparably ranked) named groups. Some of these points have been made previously (see e.g., [Dodd et al. 1999](#); [Isaac et al. 2003](#)), yet analyses of families, orders, and genera continue to be published in high profile journals. We present some alternative approaches for selecting clades for analysis that may be justified with reference to randomization or maximization of data. These approaches address the subjectivity and noncomparability issues inherent to taxonomy-based clade selection but still share some weaknesses with the taxonomic approach.

Our analysis herein does not negate the results of all previous clade-based studies, but it does call into question the effect of using a single arbitrary set of nonindependent datapoints to test a hypothesis. The dozens or hundreds of previous studies that have employed clade-based approaches should be reconsidered with reference to the sensitivity of their results to choice of clades for analysis and, if clade interrelationships were not accounted for, the nonindependence of clades.

It is possible that clade-based approaches still are scientifically useful as computationally simpler (the approach used by [Jezkova and Wiens \(2017\)](#) requires neither a fully resolved species tree nor knowledge of states for particular species) stepping-stones pointing the way to more rigorous studies. In the future, perhaps such investigations will proceed according to timeslice-like approaches (Fig. 1) suitably corrected for the shared phylogenetic history of analyzed clades (see e.g., [Baker et al. 2015](#)), and resulting conclusions will direct rigorous whole-tree lineage-based studies.

In closing, we make two recommendations for future work. First, we suggest that clade-based studies that analyze only comparably ranked taxonomic groups be abandoned. Choice of clades to analyze affects results (e.g., Fig. 4), and there is no reason to favor those results that are most explanatory for subjectively human-recognized groups. Second, if clade-based studies are still to be undertaken, then analyzed clades should be corrected for phylogenetic relationship, and alternative sets of clades should be analyzed to assess the sensitivity of results. We will leave it to future workers to determine whether such approaches are worthwhile when there exist alternative, whole-tree, lineage-based techniques that allow for more rigorous tests of hypotheses than are possible under clade-based approaches.

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