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The Interaction of Phylogeny and Community Structure: Linking the Community Composition and Trait Evolution of Clades

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Title page

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Biosketch: All authors' research interests focus on the intersect between ecology, evolutionary biology, and biostatistics. WDP focuses, in particular, on the use of phylogenies to infer how ecological assembly and function operates, and the role of phylogenies in conservation prioritisation.

Article title: The interaction of phylogeny and community structure: Linking the community composition and trait evolution of clades

Running title: Clades' variation in community composition

1 Abstract

Aim.

Community phylogenetic studies use information about species' evolutionary relationships to understand the ecological processes of community assembly. A central premise of the field is that species' evolution maps onto ecological patterns, and phylogeny reveals something more than species' traits alone about ecological mechanisms structuring communities such as environmental filtering, competition, and facilitation. We argue, therefore, that there is a need to better understand and model the interaction of phylogeny with species' traits and community composition.

Innovation.

We outline a new approach that identifies clades that are eco-phylogenetically clustered or overdispersed, and then assesses whether those clades have different rates of trait evolution. Eco-phylogenetic theory would predict that the traits of clustered or overdispersed clades might have evolved differently, either in terms of tempo (fast or slow) or mode (*e.g.*, under constraint or neutrally). We suggest that modelling the evolution of independent trait data in these clades represents a strong test of whether there is an association between species' ecological co-occurrence patterns and evolutionary history.

Main conclusions.

Using an empirical dataset of mammals from around the world, we identify two clades of rodents whose species tend not to co-occur in the same local assemblages (are phylogenetically overdispersed), and then find independent evidence of slower rates of body mass evolution in these clades. Our approach, which assumes nothing about the mode of species' trait evolution but rather seeks to explain it using ecological information, presents a new way to examine eco-phylogenetic struc-

ture.

Keywords: beta-diversity, trait evolution, mammals, phylogenetic scale, competition, environmental filtering

2 Introduction

Community phylogenetics (eco-phylogenetics) represents an attempt to link the evolutionary history of species to their present-day ecological interactions (Webb, Ackerly, McPeek, & Donoghue, 2002; Cavender-Bares, Kozak, Fine, & Kembel, 2009). The field is young but controversial, and some of its fundamental assumptions have been criticised (notably by Mayfield & Levine, 2010). Many community phylogenetic studies invoke niche conservatism (reviewed in Wiens et al., 2010) to assert that phylogenetic distance is a measure of distance in niche space, making phylogenetic structure a metric of ecological structure. Under such niche conservatism, phylogeny is often assumed to serve as a reasonable proxy for unmeasured functional traits [as the 'Phylogenetic Middleman'—Swenson (2013); see also Peres-Neto, Leibold, & Dray (2012)]. Although useful, such use undervalues phylogeny, which could be used to place (rather than approximate) species' trait and distribution data within the context of past evolutionary and biogeographical processes that have shaped current patterns of species' distributions and co-occurrences. In current approaches, we cannot disentangle species' functional trait evolution from their functional trait ecology because we use phylogeny as a measure of both. There is, therefore, a need to better integrate evolutionary history into community phylogenetics that parallels advances in the field of comparative analysis, where phylogeny is increasingly viewed as the inferential backbone for models of species' trait evolution, not simply as a statistical correction (*e.g.*, Freckleton, Cooper, & Jetz, 2011).

One of the earliest, and most commonly used, applications of community phylogenetic methods is to disentangle the impacts of niche-based processes such as environmental filtering and competition on community assembly (Webb, 2000; Cavender-Bares, Keen, & Miles, 2006). Here, it is assumed that a community of closely-related species (phylogenetic clustering) reflects environmental filtering on the basis of phylogenetically conserved traits, while the converse (phylogenetic overdispersion) implies competitive exclusion (Webb et al., 2002). A growing awareness that phylogenetic structure does not always match trait variation, even when assumptions of niche conservatism hold (Mayfield & Levine, 2010; Godoy, Kraft, & Levine, 2014; Cadotte, Davies, & Peres-Neto, 2017), has led many to separately estimate the phylogenetic and functional trait structures of communities and then contrast them (*e.g.*, Kraft & Ackerly, 2010; Graham, 2012). Critically, however, such comparisons

do not capture the *interaction* between functional traits and phylogeny, *i.e.*, how different ecological patterns in different clades may have arisen (evolved) and so shaped present-day species' distributions and co-occurrences. Because multiple ecological and evolutionary processes interact to affect eco-phylogenetic structure within the same phylogeny some clades may be functionally or phylogenetically overdispersed while others are clustered: only a clade-based approach can detect and unpick these conflicting signals (see also Leibold, Economo, & Peres-Neto, 2010). Figure 1 gives a conceptual example of how common ecological processes can produce variation among clades' eco-phylogenetic structure. Using differences in ecological pattern among clades to guide questions about ecological assembly is a form of phylogenetic natural history (Uyeda, Zenil-Ferguson, & Pennell, 2018).

It is already well-appreciated in the eco-phylogenetic literature that different clades might demonstrate conflicting patterns, hinting at the interaction of ecological and phylogenetic structure (Ndiribe et al., 2013; Elliott, Waterway, & Davies, 2016). For example, the phylogenetic scale (*e.g.*, clade crown age) of a study, and its relationship with spatial scale (*e.g.*, spatial extent) has itself become an object of study (see Swenson, Enquist, Pither, Thompson, & Zimmerman, 2006; Vamosi, Heard, Vamosi, & Webb, 2009; Graham, Storch, & Machac, 2018). Parra, McGuire, & Graham (2010) were among the first to examine the contribution of different clades to an overall metric of phylogenetic structure. Later work expanded node-based analysis to consider the separate structures of individual clades (Pearse, Jones, & Purvis, 2013), and others have examined clade-wise variation in environmental and biogeographic structure (Leibold et al., 2010; Borregaard et al., 2014). Surprisingly, these advances in the measurement of clade-based eco-phylogenetic structure have been disconnected from clade-based advances in trait evolution (*e.g.*, Beaulieu, Jhwueng, Boettiger, & O'Meara, 2012; Mazel et al., 2016) and phylogenetic diversification (*e.g.*, Davies et al., 2004; Rabosky, 2014). This is despite early work linking the order of trait evolution to community composition (Ackerly, Schwilk, & Webb, 2006; Silvertown, Dodd, Gowing, Lawson, & McConway, 2006).

We suggest that one of the key assertions of community phylogenetics is that the evolution of species' traits is tied to their present-day ecological co-occurrences (Webb et al., 2002; Cavender-Bares et

al., 2009). A strong test of this assertion would be to link variation in the tempo or mode of trait evolution among clades with independent evidence of variation of community composition within those same clades. This goes beyond independently testing for phylogenetic structure of assemblages and traits (Swenson, 2013): it tests hypotheses that specific clades' traits should evolve differently to cause, or as a consequence of, changes in the community composition of those clades (see figure 1). Our approach looks to validate the assertion that variation among clades' co-occurrences is a product of the interaction of phylogeny with ecology using independent trait data. Here we extend the β-diversity framework of Legendre & De Cáceres (2013) to quantify how the co-occurrence patterns of phylogenetic clades vary across sites. Using this method it is possible to detect clades whose species do, and do not, tend to co-occur (clustered and overdispersed clades; Webb et al., 2002), and thus detect and disentangle variation in ecological structure across the tree of life.

In this paper, our fundamental goal is to test whether variation in present-day eco-phylogenetic structure can be used to predict past patterns of trait evolution. Our approach has two components: (1) the use of a novel β-diversity approach to detect clustered and overdispersed clades, and (2) the use of existing macro-evolutionary approaches to test whether those same clades have different rates or modes of trait evolution in comparison with the rest of the phylogeny. While we cannot experimentally test a causal link between present-day ecological structure and past evolution, we argue our approach provides a strong inferential test in the form of specific hypotheses about structures that are common across datasets. We apply our method to global mammal data (Fritz, Bininda-Emonds, & Purvis, 2009; Jones et al., 2009; Thibault, Supp, Giffin, White, & Ernest, 2011), where we find evidence for slower rates of body mass evolution in present-day overdispersed clades. By linking variation in clades' ecological co-occurrences to variation in clades' trait evolution, we show the power of phylogeny as data to help understand the evolution of ecological community assembly.

3 Methods

All software referred to below in *italics* are packages for the *R* environment (R Core Team, 2017), and novel code written for this project is released in *pez* (in the function family *clade.var*; Pearse et al., 2015, to be added after acceptance, and currently in the Supplementary Materials). The Supplementary Materials contain code (that, using *suppdata*, also fetches all data; Pearse & Chamberlain, 2018) that reproduces our empirical example in its entirety.

3.1 Overview and motivation

It is often relevant to determine whether species within an assemblage are more related (phylogenetically *clustered*) or less related (phylogenetically *overdispersed*) compared to some expectation of assembly from a larger set of species, from which patterns we hope to infer some ecological mechanism. However, as outlined above, there is a growing understanding that such patterns are not necessarily uniform among the clades within a phylogeny (Leibold et al., 2010; Parra et al., 2010; Pearse et al., 2013; Borregaard et al., 2014; Graham et al., 2018). Indeed, phylogenetic clustering is an inherent property of *clades*: a phylogenetically clustered assemblage must have, by definition, one or more over-represented clades. Below we describe how these clade-wise patterns of clustering and overdispersion can be mapped onto a phylogeny, using an extension of existing approaches to partition β-diversity (where β-diversity is the variation in community composition among sites in a region of interest; Legendre & De Cáceres, 2013). By testing for differences in the evolution of such clades, we are able to evaluate the linkages between ecological and evolutionary processes, moving phylogeny from a proxy for traits to data to be explored in the context of traits.

Figure 2 shows two assemblages ('A' and 'B') in an eight-species phylogeny; one of the clades is clustered, the other overdispersed. The general principle is clearer with species' presence ('1') and absence ('0') data, but the calculations are the same for species' abundances. While the variance (σ^2) of each species' occupancy of the two sites is the same ($1/2$), by summing the species' occupancies within each clade the variance increases in the clustered clade but decreases in the overdispersed clade. When compared with simulations that provide null expectations of the expected variance in

different clades, it is therefore possible to locate significant clustered and overdispersed clades across different ecological assemblages. We note that the standard advice when calculating β-diversity of abundance data is to work with a transformed data matrix (typically a Hellinger transformation; Legendre & Gallagher, 2001). We do not do so here for clarity, and note that our simulations indicate our method is robust to such untransformed data.

Once clades with different patterns of eco-phylogenetic dispersion have been identified, we can test whether the evolution of *independent* trait data differs within those clades (following Beaulieu et al., 2012). It is, of course, equally possible to test for variation in the evolution of clades first, and then to test the community composition of those clades using our β-diversity approach, as the two procedures are performed independently. In such cases, clades with outliers in a PGLS regression (see Freckleton et al., 2011), or the output from methods such as SURFACE (Ingram & Mahler, 2013), `bayou` (Uyeda & Harmon, 2014), or `BAMM` (if shifts in speciation/extinction were of interest; Rabosky, 2014) could be used to select candidate clades. These clade-level tests directly map variation in ecological and evolutionary structure onto each other. Within this framework, phylogeny is not a mere proxy for missing species' trait data (Mace, Gittleman, & Purvis, 2003; Srivastava, Cadotte, MacDonald, Marushia, & Mirotchnick, 2012; Swenson, 2013): the interaction between phylogenetic, community composition, and trait data provides novel insight into how evolutionary history is linked with ongoing ecological processes.

We suggest that the main source of novelty in our approach is the comparison of trait evolution among clades with different co-occurrence patterns. Additionally, our method of detecting ecological variation among clades is novel, although alternative methods could be developed (*e.g.*, extensions of phylogenetic fields approaches; Villalobos, Rangel, & Diniz-Filho, 2013). While there exist various approaches capeable of measuring clades' patterns of eco-phylogenetic dispersion, our method is distinct from them. Firstly, and most importantly, it is a method for detecting variation in clade-level compositions (*c.f.* Ives & Helmus, 2011). Secondly, it compares multiple sites (*c.f.* Pearse et al., 2013) simultaneously as it measures β-diversity (figure 2 shows its application to two sites but the summations are the same for more than two sites and this is not a pairwise method). Thirdly, it does not seek to find clades that contribute to an overall pattern (*c.g.* Parra et al., 2010) but rather

identify contrasting patterns among clades. Finally, it models all species simultaneously and so does not compare species' individual drivers of presence/abundance, making it capable of detecting clade-wide overdispersion (*c.f.* Leibold et al., 2010; Borregaard et al., 2014).

Because our clade-wise test of phylogenetic dispersion is novel, so too are our definitions of overdispersion and clustering (*c.f.* Webb, 2000; Webb et al., 2002; Cavender-Bares et al., 2009). Here we define a clustered clade not on the sole basis of presences within a single site, but rather the pattern of presences and *absences* across *multiple* sites. For example, the clustered clade in figure 2 would not traditionally have been considered clustered in site B. To emphasise this distinction, we refer to our patterns of phylogenetic structure as β-clustering and β-overdispersion.

3.2 Extensions of β-diversity and significance tests

The method of Legendre & De Cáceres (2013) estimates β-diversity as the variance in the site-by-species data matrix after some appropriate transformation of the data. In this context, our β-diversity partitioning extends the measurement of species' individual contributions to total variance (*sensu* Legendre & De Cáceres, 2013) to consider clades' contributions. This allows ecologists interested in comparing the contributions of species ((SCBD indices in Legendre & De Cáceres, 2013)) and sites ((LCBD indices in Legendre & De Cáceres, 2013)) to β-diversity patterns to also compare the contributions of clades. While we focus solely on phylogenetic clades in this manuscript, we see no reason why this approach could not be applied to other (hierarchical) groups of species, such as those produced using functional traits (Petchey & Gaston, 2006) and interactions between species (Poisot, Guéveneux-Julien, Fortin, Gravel, & Legendre, 2017).

We suggest two ways to assess the significance of a clade's departure from the expected variance (the clade-level variances, σ^2, in figure 2). The first is an 'exact' method based on the expectation of variances, and is described in the Supplementary Materials. The second method is based on the comparison of observed clade variances with null distributions of variances estimated via permutation (*e.g.*, reshuffling species' identities across the phylogeny, reviewed in Gotelli, 2000; Miller, Farine, & Trisos, 2017). Ranking a clade's observed variance among its null variances would reveal

whether a clade has unusually high or low variance. The null model approach protects against cases where a clade whose members are entirely absent or omnipresent within a set of communities is highlighted as a clade with low variance (*i.e.*, displaying no, or trivial, pattern).

3.3 Simulations testing clade-level variation in β-diversity

We used simulations to verify our method's ability to detect variation in assemblage composition among clades. Below we describe each parameter of the simulation, listing each parameter in *italics* and its values across the simulations (in parentheses). We simulated phylogenies of n_{spp} species (either 50 or 100) following a pure-birth Yule process (using *geiger*; Pennell et al., 2014). We then selected a focal clade containing either 5–10% or 10–20% of the species in the phylogeny, and simulated a trait under Brownian motion (root set to 0, also using *geiger*; Pennell et al., 2014) across the entire phylogeny with a σ^2 (0.5, 1, 1.5, 2, 2.5; σ^2_{tree}), excluding the focal clade, for which traits were simulated with σ^2 a multiple of 10 greater or lesser than across the entire tree ($\times 10^{-3}, 10^{-2.75}, 10^{-2.5}, ..., 10^{3}$; σ^2_{clade}). We then simulated community assembly across n_{site} sites (either 50 or 100) based on the simulated trait values: in each site, we randomly selected a species and then drew community members based on their trait distance from the first randomly selected species. Species with absolute differences in simulated traits ≥ 1 from the focal species were assigned a probability of membership of 0, and a species with a difference of $|0.5|$ would have a probability of 0.5. We acknowledge that this mapping between trait difference and probability of co-occurrence is arbitrary, but its simplicity makes it straightforward to consider the impact of a variety of parameter combinations and thus makes our results easier to generalise. In related simulations, however, we saw little evidence that varying this relationship qualitatively affected our method's performance.

These simulations represent a form of ecological assembly that is deliberately agnostic with regard to any particular ecological mechanism (*e.g.*, facilitation, competition, or environmental filtering), but, as illustration, they can be matched to the scenario of environmental filtering shown in figure 1. In regards to patterns of co-occurrence, a clade can evolve faster than the rest of the phylogeny

(such that $\sigma^2_{clade} > \sigma^2_{tree}$ in our simulations), in which case we would expect close-relatives to rarely co-occur within a clade (a β-overdispersed clade; see figure 2). A clade can also evolve slower than the rest of the phylogeny ($\sigma^2_{clade} < \sigma^2_{tree}$), in which case we would expect close-relatives to frequently co-occur (a β-clustered clade; see figure 2). Even in simulations where $\sigma^2_{clade} = \sigma^2_{tree}$, we still evolved a separate trait for the focal clade, making this an extremely conservative test of our method as assembly was always based on a different trait in the focal clade.

We repeated simulations across all combinations of our parameter values, and an additional 20 times for each combination with identical σ^2_{tree} and σ^2_{clade}, resulting in a total of 2160 simulations. For each simulation, we ranked the observed variance of the focal clade within $9,999$ permutations (the observed value was included as part of the null distribution, totalling $10,000$ values for each null distribution), swapping species' identities on the phylogeny and keeping everything else constant. These rankings provide probabilities under the null hypothesis: values greater than 0.975 suggest β-clustering (at $\alpha_{5\%}$) and values lesser than 0.025 suggest β-overdispersion. The comparisons to the null distributions provide a test of whether our method can reliably detect β-overdispersion (ranked in the bottom 2.5% when $\sigma^2_{clade} > \sigma^2_{tree}$), β-clustering (ranked in the top 2.5% when $\sigma^2_{clade} < \sigma^2_{tree}$), and whether it is vulnerable to false-positives (ranked in the top or bottom 5% when $\sigma^2_{clade} = \sigma^2_{tree}$—a type I error). Note that clades are hierarchically nested, and so they are not necessarily independent. While we make reference to this in the discussion, we do not conduct simulations to investigate this further, as it is a feature that has been discussed at length in the literature (*e.g.*, Alfaro et al., 2009). We draw the reader's attention to the fact that we conducted these simulations over a range of parameter values, with the explicit aim of finding the conditions under which our method performs well and where it underperforms (*i.e.*, across the range of parameters in our simulations).

3.4 Empirical example: rodent communities

There are two steps to our empirical analysis. In our first step, we examine the β-diversity of all lineages, and use these calculations to detect the clades that most strongly depart from the overall β-diversity patterns. In our second step, we fit a model of trait evolution across the complete

phylogeny to assess whether the evolution of those same clades differs from that of the rest of the phylogeny. Our aim is to evaluate whether clades with different β-diversity in the present show evidence of different trait evolution in the past. Above, we argued that this forms a strong test of the imprint of past evolution on present-day ecology, as it sets up explicit hypotheses across different datasets.

To provide an empirical example of our approach, we present an analysis of a rodent dataset. We took data from a mammal community dataset (Thibault et al., 2011), phylogeny [Bininda-Emonds et al. (2007), updated by Fritz et al. (2009)], and body mass from a large database for mammal traits (Jones et al., 2009). This community dataset covers a number of continents and community types, and body mass is known to be a good proxy for ecological interactions in rodents (see Thibault et al., 2011). Excluding species not covered in all three datasets (community, phylogeny, and traits) left us with abundance information for 483 species across 939 sites (assemblages) worldwide. Following the method described above, we identified clades' β-diversity and assessed statistical significance by comparison to $9,999$ species-identity randomisations (Kembel et al., 2010).

We fitted Brownian motion and Ornstein-Uhlenbeck (OU) models using *OUwie* (Beaulieu et al., 2012) to the (log-transformed) body mass data. We contrasted models with shared and varying parameters for our clades identified as having significantly different ecological β-diversity (see above); support for Brownian and OU models with different parameters for these clades would suggest a link between ecological trait-based assembly and trait evolution. *OUwie* requires the user to specify which clades are to be tested for differing rates of trait evolution, and our β-diversity analyses (see above) provided this information. Where hierarchically-nested clades were identified, we selected the oldest clade as this is more conservative (the 'cascade' problem; see Discussion) and parameter estimation is more accurate in larger clades (Beaulieu et al., 2012). In the Supplementary Materials, we present results of a series of permutation tests that we performed to ensure that our evolutionary model-fitting was not biased towards finding support for particular evolutionary hypotheses.

4 Results

Results from our simulations are presented in table 1 and figure 3, and show that our method powerfully and reliably detects variation in phylogenetic structure among clades. Our method has strong statistical power to detect β-clustering (higher variance within a clade; the red line in figure 3), and a somewhat reduced power to detect β-overdispersion (lower variance within a clade; the blue line in 3). As shown in table 1, however, greater sampling modifies this: sampling 100 species across 100 sites additively increases the ranking of the observed variance by 10% (*i.e.*, from the .85 quantile to the .95) in comparison with 50 species across 50 sites. Our method shows a tendency to spuriously suggest support for β-clustering (*i.e.*, overall inflated type I error rates in simulations of 24% at two-tailed $\alpha_{5\%}$; see figure 3), but again this varies depending on the context. As shown in table 1, focal clades that make up large proportions of the total data are more likely to be erroneously identified as β-clustered: if the focal clade contains 10 of the 100 species in a system ($n_{sites} = 50$, σ^2=1) the predicted quantile is 0.77, but if the clade contains 20 species (*i.e.*, 20% of the species) that prediction rises to 0.95. Neither of these expected quantiles are statistically significant at $\alpha_{5\%}$ (*i.e.*, they are all < 0.975) and so this is not indicative of the method having problems with type I error rates. As we highlighted above, we explored a wide parameter space in our simulations to highlight where our method performs well and where it performs poorly. Thus, the raw results plotted in figure 3 do not necessarily reflect our average expectations for performance of our method.

In our analyses of the rodent dataset, we focused on two clades (marked on figure 4): the *Sciuridae* (squirrels) and their sister family the *Gliridae* (dormice), and the *Echimyidae* (a Neotropical rodent family) and some close relatives within what is sometimes called the *Caviomorpha* (*e.g.*, South American rodents like the guinea pig). We refer to these two groups as the 'squirrels' and 'cavies', respectively. Both these clades were identified as having low variance (phylogenetic β-overdispersion). Note that our method also detected clades indicative of β-clustering (high variance). As the low-variance clades are nested within these high-variance clades, we suggest they might reflect important eco-evolutionary shifts. The detection of both phylogenetic β-clustering and β-overdispersion demonstrates the ability of our method to reveal both kinds of structure in

empirical datasets.

We find that the squirrel and cavi clades were also characterised by different rates of trait evolution (table 2). The top four models, with δAIC less than 5, all supported different rates of body mass evolution for these two clades in comparison with the rest of the phylogeny. The alternative hypothesis, that trait evolution is constant across the squirrels, cavies, and the rest of the mammal phylogeny, was the fifth-ranked model with a δAIC of 14.9 and so has little support (Burnham & Anderson, 2002). The lowest-AIC model favoured a simple three-rate Brownian motion model in which the rate of body mass evolution in squirrel and cavi clades is significantly slower, most notably in the squirrel clade. In the Supplemental Materials we present additional simulations that test whether our findings are a result of a bias in our phylogenetic or trait data. These simulations reveal that, if anything, our data are biased *against* the pattern that we observe, and so give greater strength to our findings.

5 Discussion

We have presented a novel method for identifying clades (groups) of species whose co-occurrences differ from other species across a set of communities. Simulating species' phylogenies and trait-based community assembly processes, we demonstrated that the method reliably detects shifts in the variance of species' occupancies, identifying different phylogenetic structures. Most importantly, however, we have also shown, using empirical data, that the tempo of trait evolution shifts within clades associated with differing present-day assemblage compositions. To the best of our knowledge, this is the first test of the hypothesis that the evolution of traits within a clade is associated with its co-occurrence patterns. By linking variation among clades' co-occurrence patterns with independent evidence for variation in those clades' rates of trait evolution, we have found evidence for an interaction between evolutionary and ecological information. We argue that our approach, combining evidence of both ecological and evolutionary patterns, has more power to answer questions about the underlying eco-evolutionary drivers of community assembly than methods focusing singularly on phylogenetic or trait data alone.

5.1 Variation in β-diversity in community phylogenetics

The use of phylogeny as a proxy for ecological process has been criticised. It has been argued that there is little need for phylogeny if we already have functional traits (Swenson, 2013), and phylogenetic pattern rarely maps directly onto ecological process (a critique that applies equally to functional traits; Mayfield & Levine, 2010). However, we have suggested one central premise of community phylogenetics is that there is an association between the evolution of species' traits and the phylogenetic structure of the communities in which they are found. For example, that competition among species might drive character displacement, such that co-occurring species differ in their functional traits. Many community phylogenetic studies, like ours, examine the tempo and mode of trait evolution within their system (*e.g.*, Swenson et al., 2006; Kraft, Cornwell, Webb, & Ackerly, 2007), but few have asked how trait evolution and community phylogenetic structure are linked and feed back into each other. Simple measures of phylogenetic signal assume complete,

or at least unbiased, taxon sampling (Pagel, 1999; Blomberg, Garland, & Ives, 2003), and so eco-phylogenetic structure, which, by definition, implies non-random taxonomic representation, may mask underlying (true) patterns of trait evolution. Our approach offers a coherent framework to test for links between the macro-evolutionary dynamics of clades and their present-day community compositions. We acknowledge that our study does not sample or examine all rodent species, and that other processes undoubtedly influenced body size evolution. Nonetheless, we were able to detect a significant association between trait evolution and species' co-occurrences, and this strong test in independent data suggests that incomplete taxon sampling is unlikely to have biased our findings.

Despite conceptual issues, the utility of phylogeny in predicting species' traits (Guénard, Legendre, & Peres-Neto, 2013), Janzen-Connell effects (Gilbert & Webb, 2007), invasion success (Strauss, Webb, & Salamin, 2006), and ecosystem function (Cadotte, Albert, & Walker, 2013) suggests phylogeny will remain a useful (Tucker, Davies, Cadotte, & Pearse, 2018), if imperfect (Cadotte et al., 2017; Mazel et al., 2018), proxy in ecology for some time. Yet we suggest that phylogeny is more than just a surrogate for unmeasured traits, and that it provides us with the ability to link patterns and processes in ecology and evolution. Here, we map patterns in separate ecological assemblage and species trait datasets onto each other, linking them by treating phylogeny in and of itself as data in two separate analyses. Our approach does not invoke niche conservatism, but rather seeks to understand how traits have evolved and can explain patterns of species co-occurrences across local communities (though other spatial units, such as biogeographical zones, could equally be considered). As such, there is no requirement that closely related species are more ecologically similar or compete more strongly, eco-phylogenetic assumptions that have been heavily criticised (Cahill, Kembel, Lamb, & Keddy, 2008; Mayfield & Levine, 2010). Our results simply support a link between the ecological interactions (as measured by β-diversity) of clades and the evolutionary history of those clades. The evolutionary patterns we observe come from interactions, or the absence of interactions, that occurred over millions of years, potentially in assemblages very different to those we see today. Our analyses indicate that these past interactions have left an imprint on present-day community assembly, and imply that future evolutionary trajectories may be influenced by

present-day species interactions.

In our analysis of small mammal assemblages, we showed that the cavi and squirrel clades, whose members tended not to co-exist (their clade variances were low), have lower rates of trait evolution (table 2). Rodent body size is a driver of ecological competition (Bowers & Brown, 1982; Ernest, 2005), and our results are consistent with slower evolution of body size being a driver of variation in the present-day composition of our small-mammal assemblages. The clades we have focused on are relatively small and young (see figure 4), and previous work (Ackerly et al., 2006; Silvertown et al., 2006) has suggested that traits that evolve early and late in the evolutionary history of a clade may affect ecological assembly differently. Our results imply that it is not just the timing of body size evolution that may be important, but also its rate of evolution. We do not yet know what caused this slow-down in the capi and squirrel clades and whether these associations are driven by changes in diversification rate (which can be confounded with trait evolution; FitzJohn, 2010). There is, however, some evidence that younger clades tend to co-occur more than older ones (Pearse et al., 2013; Parmentier et al., 2014). We caution, however, that our results are correlational. While our OU models' greater α parameters might be consistent with strong stabilising selection [Uyeda & Harmon (2014); but see Pearse et al. (2018)], as with any historic study of biogeography we cannot definitively rule out some other process driving the patterns we have detected. In particular, we do not consider the impact of (historic) dispersal limitation on species' distributions.

5.2 Method performance

We show that our method has good statistical power, and compares favourably to the widely used NRI (often called SES_{MPD}) and NTI (SES_{MNTD}) metrics of phylogenetic community structure, for which statistical power can be (in some circumstances) less than or equal to 20% (Kraft et al., 2007) and 60% (Kembel, 2009). In some cases, however, we observed inflated type I error rates relative to these other methods (see below for discussion). In many ways these are unfair comparisons, given that our approach makes use of information from multiple sites (although the number of species with phylogenetic structure is comparable), which we would argue is a strength of our method.

Phylogenetic Generalised Linear Mixed Models (Ives & Helmus, 2011) also use many sites at once, and our results compare favourably to this approach (87% detection rate for phylogenetic clustering, 53% for overdispersion, but with fewer sites than in our study). It is important to note, however, that these alternative methods are intended to answer different questions, and none of them were designed to measure what we term β-dispersion. We make these comparisons simply to demonstrate that our approach performs reasonably in comparison with others, even in simulations where the number of species in a focal clade could be as low as 5 and the datasets themselves small (50 species or sites).

Our simulations show that, in cases where the focal clade makes up a large proportion of the species under study (in our simulations, over 20%) type I error rates could be inflated. We do not feel that this is of concern, for several reasons. First, within our framework, clades must be detected as significant both in terms of their present-day co-occurrence patterns and also their historic trait evolution. As such, spurious identification of structured clades would tend to weaken any association between their ecology and evolution. Second, it is rare that ecological assemblages are truly randomly structured: the norm is for them to display some degree of phylogenetic structure (Vamosi et al., 2009). We suggest most biologists may be more interested in detecting the difference between β-overdispersion and β-clustering, not β-overdispersion or β-clustering versus random assembly. This is the case in our empirical example, where we examined clades that were β-overdispersed whose sisters were β-clustered. We also note that type I error rates can be even higher for other, more commonly used, metrics of phylogenetic structure. For example, SES_{MPD}, when estimated by taxa-shuffling ('richness') null distributions such as we employ here, can have type I error rates of c. 50% (Kembel, 2009; Miller et al., 2017).

5.3 Potential methodological extensions

Like similar approaches (Parra et al., 2010; Pearse et al., 2013; Borregaard et al., 2014), our method does not directly consider nestedness (see also Ulrich, Almeida-Neto, & Gotelli, 2009), where the significance of a clade 'cascades' up into higher super-sets of hierarchical groupings (*c.f.* the 'trickle-

down' problem in diversification analysis; Purvis, Nee, & Harvey, 1995; Moore, Chan, & Donoghue, 2004). One possible extension would be to compare each clade with the *summed* clades subtending it (not, as in the method we are presenting, the species within it). As such each clade in a fully resolved phylogeny would have its variance compared with the variances of the two clades subtending it (our supplementary code permits this). Significance could be tested through null permutation, as done in this study, or potentially through nested ANOVAs. However, we suggest that this cascading is not so much a limitation but rather a matter of interpretation; that a group is β-clustered because it contains other β-clustered groups does not strike us as problematic. A balanced approach could limit the study to particular clades on the basis of age or other variable of interest, or to hold problematic clades constant in null randomisations.

We also note that our approach for identifying ecological patterns among clades does not incorporate phylogenetic branch lengths. Branch lengths inform models of trait evolution, and so for our purposes of mapping *independent* evolutionary pattern onto ecological pattern we consider it undesirable to have branch lengths play a role in both aspects. For those interested in incorporating branch lengths in other situations, a simple approach would be to multiply each species' abundance by its evolutionary distinctiveness (Isaac, Turvey, Collen, Waterman, & Baillie, 2007) or another measure of its phylogenetic uniqueness (*e.g.*, Redding & Mooers, 2006; Cadotte et al., 2010; Hipp et al., 2018). However, depending on the question at hand this might 'average out' the signal of interest. For example, if community composition varies with phylogenetic scale (Webb et al., 2002; Cavender-Bares et al., 2009; Vamosi et al., 2009), it might be better to model the standard effect size (SES; *sensu* Kembel, 2009) of node variance as a function of node age (see Pearse et al., 2013).

5.4 Conclusion

We suggest that the identification of clades with different co-occurrence patterns is of at least as much interest as the summary statistics that have been used frequently to describe overall phylogenetic assemblage structure but which map only poorly to ecological process. Further, we

see the establishment of links between assemblage structure and the evolution of species' traits as a central goal of community phylogenetics that has rarely been achieved. As a field, community phylogenetics is well-placed to take advantage of recent advances in trait evolution (Pennell & Harmon, 2013; Nuismer & Harmon, 2015) and eco-phylogenetic theory (Pigot & Etienne, 2015). We have outlined here an approach to directly test links between the processes of community assembly and the evolution of species' traits. As we gain a firmer grasp of assemblages' phylogenetic structure, we can begin to model it as data, not merely measure its pattern.

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Data accessibility statement

No new data are released as part of this manuscript; the mammal phylogeny is from Fritz et al. (2009), the mammal trait data from Jones et al. (2009), and the mammal assemblage data from Thibault et al. (2011). All simulations and analysis `R` code are released in the supplement.

Figure legends

Figure 1. Linking clades' evolution and community assembly. Here we give an example of how clade-level variation in community structure (the tendency for close/distant relatives to co-occur) might arise. We consider a set of species that are initially filtered within some biogeographic (or meta-community) context; perhaps the clade is widespread but not all its members are present in every continent/region, for example. A trait, represented by the size of the circles at the tips of the phylogeny, evolves across the phylogeny, but evolves faster in one clade (the red branches) and slower in another (the blue branches). Ecological community assembly on the basis of this trait, regardless of mechanism, will result in different eco-phylogenetic structures across these clades. Re-framing our eco-phylogenetic analysis in terms of clades allows for the generation of falsifiable hypotheses about how species' ecology and evolution interact. In this study, we use evidence of variation in the co-occurrences within clades to test for variation in the evolution of those traits. It would also be possible to find clades with differing evolutionary patterns, and then use these to test for differing methods of ecological assembly and co-existence within those same clades. We emphasise that this diagram is but one example of how ecological assembly and the macro-evolution of species' traits could interact. While we do not show the interaction of fitness and niche differences on species' co-occurrence (*sensu* Chesson, 2000; Mayfield & Levine, 2010), we see no reason our approach could not be applied to more complex models of ecological assembly. Equally, while there may be null models that allow investigators to partial out the influences of some of these patterns and processes, the aim of our approach is to statistically model, and so better understand, them. The eco-phylogenetic terms in this diagram match onto those in figure 2 where we outline our new method, and the colours match onto those in figure 3 where we test our method's statistical power through simulation and figure 4 where we apply our method to an empirical dataset.

Figure 2. Overview of variance-based method for the detection of variation in clades' eco-phylogenetic structure. A horizontal dashed line splits the phylogeny into two clades: one has an overdispersed community phylogenetic structure (close relatives are unlikely to co-occur), and the other a clustered structure (close relatives are likely to co-occur). It is these two kinds of eco-phylogenetic structure that our method aims to detect, and that we suggest, in the main text,

could be termed β-overdispersion and β-clustering to emphasise their focus on eco-phylogenetic structure across multiple sites simultaneously. A vertical grey dashed line separates species and grouped clade calculations. To the left of the vertical line, the occurrences of each species in two assemblages (A and B) are shown alongside the variance (σ^2) of each species' occurrences across the assemblages; all species have the same variance ($1/2$). To the right of the vertical line, community occurrences for the species have been summed: the variance of these occurrences is now much lower for the overdispersed clade and much higher for the clustered clade. For simplicity, we use binary presence-absence data in only two sites as an illustration, but this method can be applied to species' abundances within any number of assemblages. While there is an analytical expectation for clade-level variances (see text) we recommend using ecological null models to assess the significance of clade-level patterns. Note that when more than two sites are considered, a single variance value for each species is calculated across all species' presences and absences (or abundances).

Figure 3. Simulations showing how method performance increases with effect size. In grey, the observed variances' quantiles are shown for when there was no difference between the model of trait evolution in the focal clade and the rest of the phylogeny. The mean of these values, along with the percentage of values lying beyond the 2.5% and 97.5% quantiles, are shown in black. In light blue, the probabilities for the β-overdispersed (low variance; $\sigma^2_{clade} > \sigma^2_{tree}$) are shown, along with a quasi-Binomial GLM prediction in darker blue. In orange, the probabilities for the β-clustered (high variance; $\sigma^2_{clade} < \sigma^2_{tree}$) are shown, along with a quasi-Binomial GLM prediction in red. At an $\alpha_{5\%}$, a predicted quantile of 0.025 or 0.975 would provide statistical support for the focal clade being β-clustered or overdispersed, respectively. None of these curves account for the additional explanatory variables used in the models in table 1, and thus these curves are conservative but can be interpreted in the context of the parameters within table 1 to generate predictions for any parameter combination. These figures show the raw data (*i.e.*, each point is the result of a single simulation) used to parameterise the models shown in table 1. In the main text, we define the terms β-overdispersion and β-clustering as referring to eco-phylogenetic structures in clades across sites.

Figure 4. Empirical mammal results showing associations between clades' co-occurrences

and their rates of body mass evolution. To the left and right, the phylogeny of all 483 mammals in the study. Two large red circles on the nodes of each phylogeny indicate the two 'squirrel' and 'cavi' clades tested in the evolutionary analysis (see text and table 2). The left-hand phylogeny is coloured according to the ranking of the clades' variances; a quantile of 0 (red; see legend) would indicate a clade whose variance was lower than all $9,999$ null permutations, and a quantile of 1 (blue; see legend) a clade whose variance was higher than all $9,999$ null permutations. In the centre, a site-by-species matrix of relative abundance in all 939 assemblages, with a colour-scale indicating relative abundance (see legend at bottom; more abundant species in red, absent species in white). Each of the 939 assemblages (sites) is a column in this matrix, and each of the species a row that maps onto the phylogenies to the left and right. This represents the raw data used to calculate the clades' variances. The right-hand phylogeny is shaded according to a reconstruction of body mass (g) across the phylogeny (using `phytools`;g Revell, 2012). Although this reconstruction does not explicitly model variation in rate among clades, variation in size across its branches can be seen. In the main text, we define β-overdispersion and β-clustering as eco-phylogenetic structures of overdispersion and clustering that are detectable only across multiple sites simultaneously.

Figures

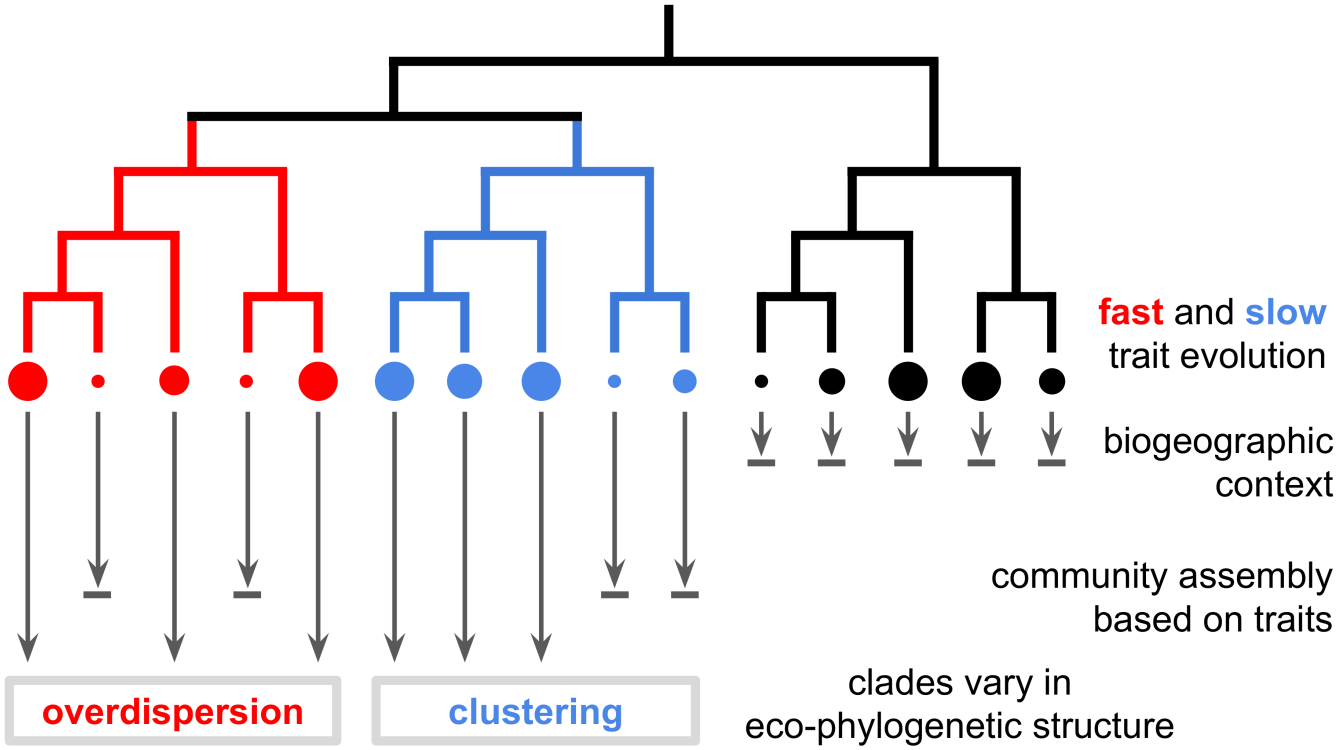

Figure 1

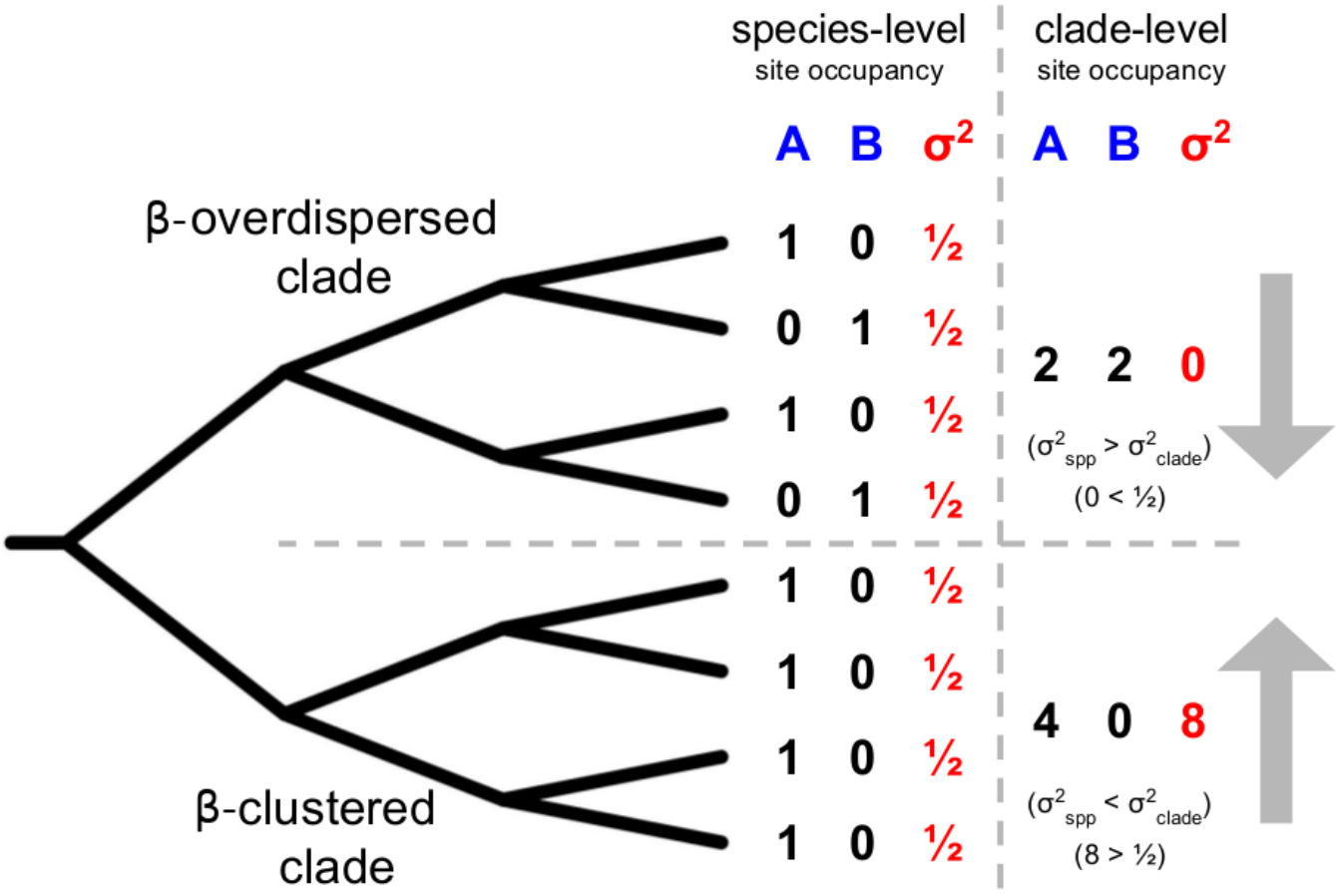

Figure 2

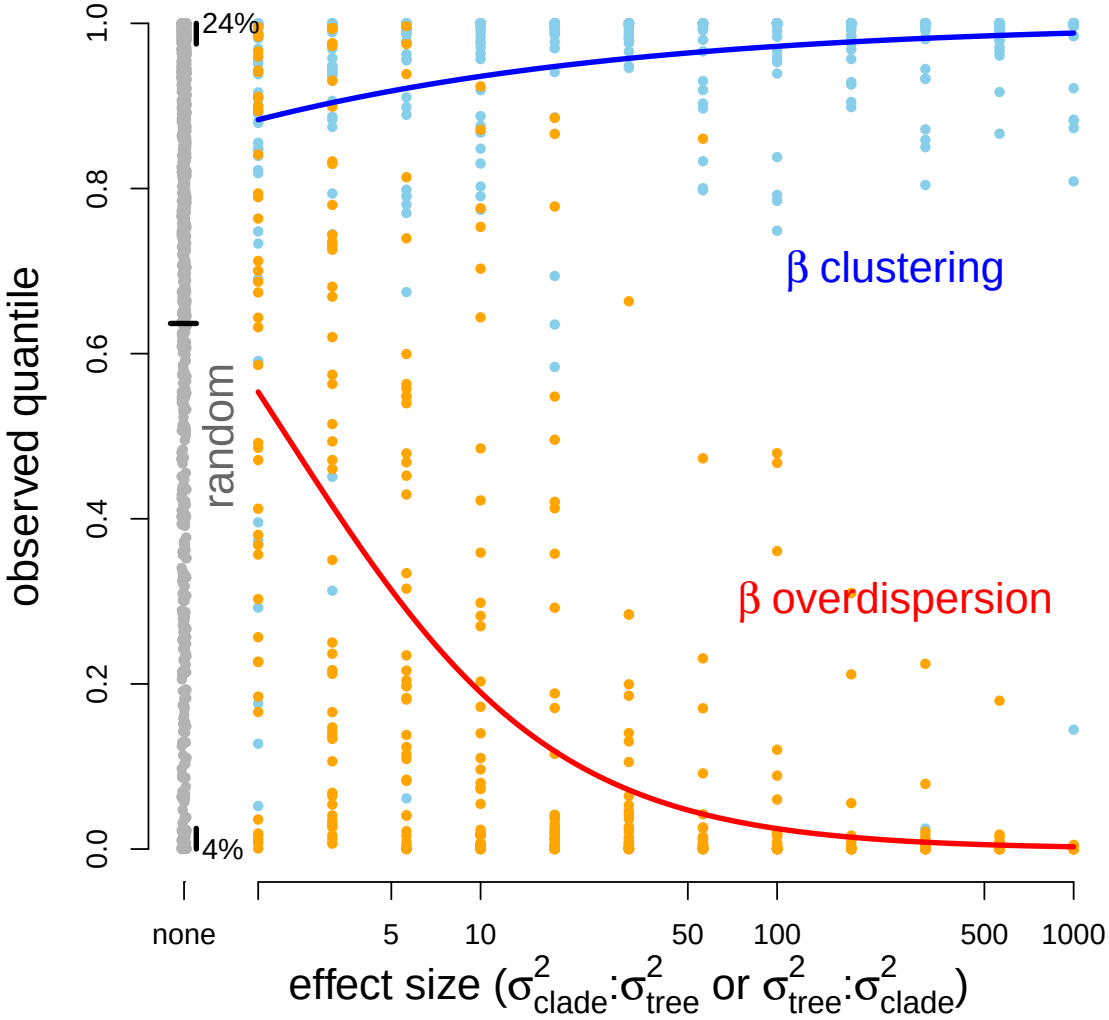
observed quantile
0.0
0.2
0.4
0.6
0.8
1.0
24%
4%
random
β clustering
β overdispersion
none
5
10
50
100
500
1000
effect size (σ^2_{clade}:σ^2_{tree} or σ^2_{tree}:σ^2_{clade})

Figure 3

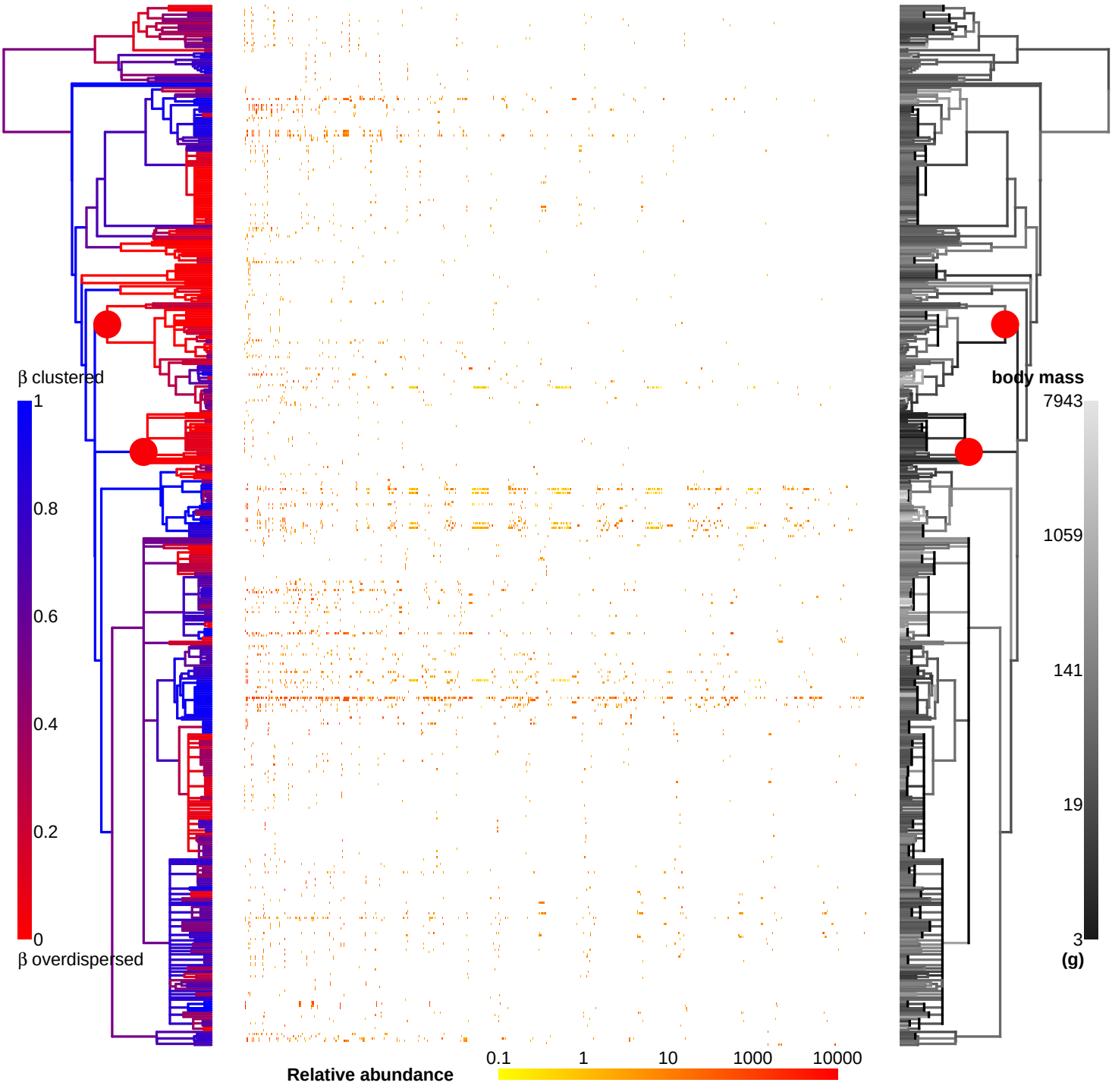
β clustered
1
0.8
0.6
0.4
0.2
0
β overdispersed
body mass
7943
1059
141
19
3
(g)
0.1
1
10
1000
10000
Relative abundance

Figure 4

Tables

	Estimate	Std Err	z	p
Intercept ($n_{spp} = n_{sites} = 50$)	−0.5964	0.4288	−1.39	0.1649
$log_{10}(\frac{\sigma^2_{tree}}{\sigma^2_{clade}})$	0.8362	0.1543	5.42	0.0000
n_{clade}	0.4772	0.0829	5.76	0.0000
σ^2_{tree}	0.1238	0.2099	0.59	0.5555
Contrast—$n_{spp} = 100$	−0.3004	0.3862	−0.78	0.4370
Contrast—$n_{sites} = 100$	0.3508	0.2383	1.47	0.1416

(a) β-clustering (higher variance)

	Estimate	Std Err	z	p
Intercept ($n_{spp} = n_{sites} = 50$)	1.0324	0.2851	3.62	0.0003
$log_{10}(\frac{\sigma^2_{clade}}{\sigma^2_{tree}})$	−2.2238	0.1565	−14.21	0.0000
n_{clade}	−0.0149	0.0257	−0.58	0.5627
σ^2_{tree}	−0.1043	0.1488	−0.70	0.4836
Contrast—$n_{spp} = 100$	−0.0686	0.2123	−0.32	0.7467
Contrast—$n_{sites} = 100$	0.0082	0.1665	0.05	0.9609

(b) β-overdispersion (lower variance)

	Estimate	Std Err	z	p
Intercept ($n_{spp} = n_{sites} = 50$)	0.7030	0.0292	24.10	0.0000
n_{clade}	0.0153	0.0029	5.19	0.0000
σ^2_{tree}	−0.0439	0.0168	−2.61	0.0092
Contrast—$n_{spp} = 100$	−0.0021	0.0237	−0.09	0.9298
Contrast—$n_{sites} = 100$	−0.0173	0.0189	−0.92	0.3599

(c) Null (no difference in variance)

Table 1: **Simulations showing how method performance varies as a function of phylogeny and clade size, rate of trait evolution, and effect size**. Each sub-table shows the results of modelling the observed quantiles of focal clades' variances in simulations of β-clustering (higher variance; a), overdispersion (lower variance; b), and random assembly (null, no difference; c) across the simulations. At an $\alpha_{5\%}$, a predicted quantile of 0.025 or 0.975 would provide statistical support for the focal clade being β-clustered or overdispersed, respectively. Generalised Linear Models with a quasi-binomial error structure were used to account for non-normality of errors in the β-clustering (a) and overdispersion (b) models, and so coefficients are reported on the logit scale. In (a), a greater statistical power to detect β-clustering is most strongly associated with the number of species in the focal clade and the difference in evolutionary rate between the focal clade and the rest of the phylogeny (deviance: $null_{529} = 105.98$ and $residual_{524} = 67.07$; estimated $dispersion = 0.30$). In (b), a greater statistical power to detect overdispersion is most strongly associated with the difference in evolutionary rate between the focal clade and the rest of the phylogeny and the number of sites sampled (deviance: $null_{531} = 262.32$ and $residual_{526} = 138.95$; estimated $dispersion = 0.34$). In (c), there is a slight tendency for larger focal clades to appear more β-clustered, and for faster-evolving traits to drive β-overdispersion, even when focal clades evolve under the same model as the rest of the phylogeny ($F_{4,919} = 11.99$; $r^2 = 4.96\%$; $p < 0.0001$). We recommend that more attention should be paid to coefficient sizes than statistical significance in these models, since statistical significance can be driven by sample size and these are the results of simulations.

θ_0	θ_c	θ_s	σ_0	σ_c	σ_s	α_0	α_c	α_s	δAIC
—	—	—	53	32	1.12	—	—	—	0.00
2.14±0.42	5.38±1.53	2.00±1.39	52	30	1.12	0.00			1.13
2.14±0.42	5.38±720.76	2.05±0.52	51			0.00	0.00	49	1.54
2.15±0.42	352.83±159.69	-15.44±130.72	52	30	1.1	0.00	0.00	0.00	5.00
—	—	—	58			—	—	—	14.90
2.17±0.44			58			58			16.90
2.14±0.44	5.32±1.70	1.96±1.25	57			57			17.00

Table 2: **Results of log(body mass) evolutionary modelling**. Above are the θ (optimum), σ (rate), and α (rate of return to optimum) estimates, along with AIC and δAIC values, for all trait evolution models. Each row represents a different model; '—' is used to indicate when a parameter is not fit in a model, and where only a single estimate for a parameter is given (*e.g.*, θ_0) only a single parameter was fit across the whole phylogeny. Thus rows one and four represent Brownian motion (models with no optima), and all other rows are variants of Ornstein-Uhlenbeck models. In subscripts of parameters, 'c' refers to the 'capi' clade, 's' to the 'squirrel' clade, and '0' to the remainder of the phylogeny. See text and figure 4 for a description of these species making up each clade. The α and σ estimates have been multiplied by 10^{-4} for brevity of presentation. The four most likely models according to δAIC all contain clade-level variation, strongly supporting different patterns of evolution in the clades highlighted by the variation in β-diversity among clades (see text).