

SPECIAL FEATURE PAPER: NEW OPPORTUNITIES AT THE INTERFACE BETWEEN ECOLOGY AND STATISTICS

Trees, branches and (square) roots: why evolutionary relatedness is not linearly related to functional distance

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Summary

1. An increasingly popular practice in community ecology is to use the evolutionary distance among interacting species as a proxy for their overall functional similarity.
2. At the core of this approach is the implicit, yet poorly recognized, assumption that trait dissimilarity increases linearly with divergence time, that is all evolutionary time is considered equal. However, given a classic Brownian model of trait evolution, we show that the expected functional displacement of any two taxa is more appropriately represented as a linear function of time's square root.
3. In light of this mismatch between theory and methodology, we argue that current methods at the interface of ecology and evolutionary biology often greatly overweight deep time relative to recent time.
4. An easy solution to this weighting problem is a square root transformation of the phylogenetic distance matrix. Using simulated models of trait evolution and community assembly, we show that this transformation yields considerably higher statistical power, with improvements in 92% of trials. This methodological update is likely to improve our understanding of the connection between evolutionary relatedness and contemporary ecological processes.

Key-words: trait evolution, phylogenetic distance, community phylogenetics, community assembly, comparative methods, functional traits

Introduction

With increasingly precise estimates of the most common ancestor among interacting species, modern phylogenetics offers the promise of a synthesis of contemporary ecology and evolutionary history (Webb *et al.* 2002; Johnson & Stinchcombe 2007; Cavander-Bares *et al.* 2009; Cadotte, Albert & Walker 2013; Swenson, 2013). Following on this, the last 10–15 years have seen a precipitous rise in the number of studies examining ecological patterns and processes through the lens of evolutionary relatedness. While this integrative approach has undoubtedly yielded new insights, much of the foregoing research has proved inconclusive; contemporary ecological interactions often appear, using conventional methods, to be unrelated to evolutionary history (Cahill *et al.* 2008; Bennett *et al.* 2013; Narwani *et al.* 2013; Fritschie *et al.* 2014). In this comment, we offer one explanation for the poor performance of the phylogenetic metrics used in contemporary ecology, as well as a partial solution.

From the beginning of the phylogeny–ecology synthesis, evolutionary relatedness has often been used a proxy for the

traits mediating species' interactions with each other and their environment. It is impossible to measure all the relevant traits for complex ecological interactions, but because evolution is a conservative branching process and traits are on average more conserved than random, phylogenies have the potential to provide an integrative measure across all traits (Webb 2000). It follows that the strength of this inference is contingent on an accurate model of how phylogenetic and functional distance covary. There is a widespread assumption in the literature (see Fig. 1b of Cadotte, Albert & Walker 2013) that phylogenetic and functional distance scale linearly. This assumption is implicit in many of the conventional metrics for assessing phylogenetic community structure and phylogenetic diversity (Vellend *et al.* 2010). Below, we consider this assumption critically, using current theory on trait evolution.

The classic, 'default' model for trait evolution is Brownian motion (Fig. 1b and Felsenstein 1985). The diffusion equation for Brownian motion (Einstein 1905) has the form:

$$\frac{\partial \rho}{\partial t} = \sigma^2 \frac{\partial^2 \rho}{\partial x^2} \quad \text{eqn 1}$$

where σ^2 is the diffusion constant, t is time, ρ is density and x is position in space. That equation has the solution:

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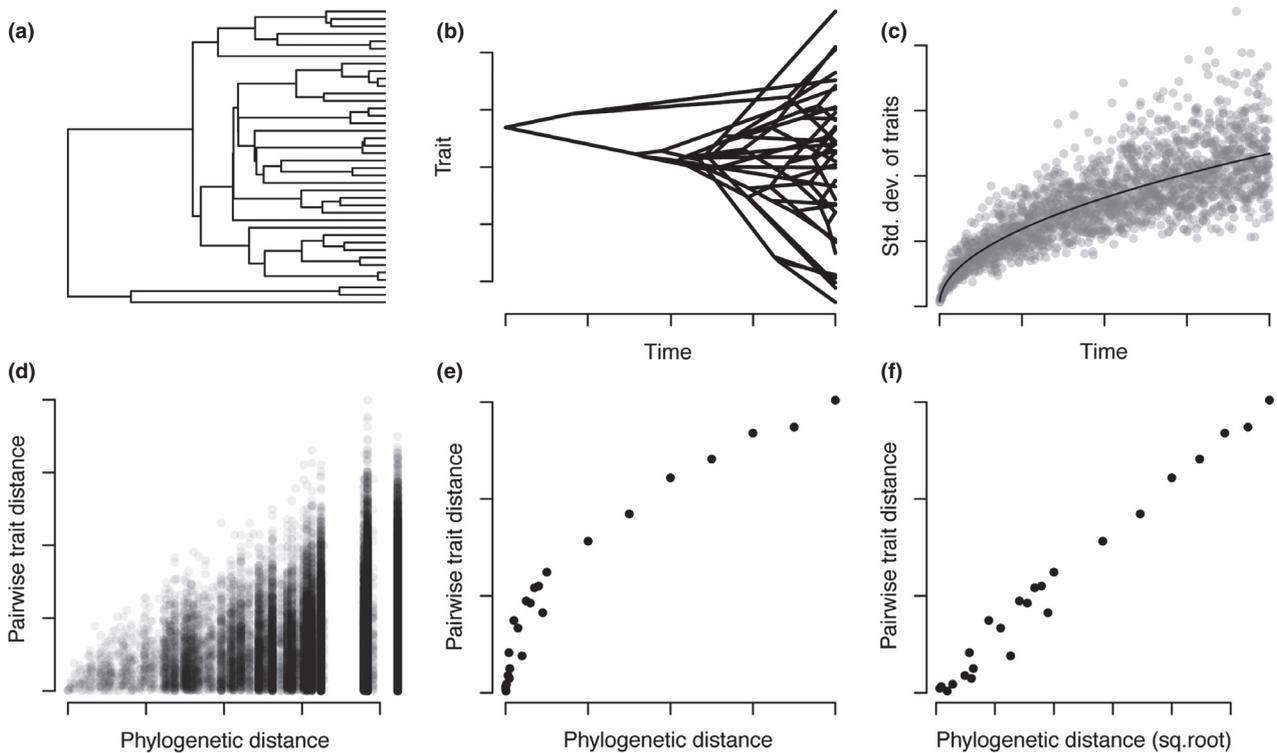


Fig. 1. Panel (a) shows a Yule phylogeny. Panel (b) shows a ‘traitgram’ with one Brownian motion simulation with the trait value on the y-axis. Panel (c) shows the effect of time on the standard deviation of trait values at the tips for 2000 simulations with the same Brownian motion rate parameter; each point represents the standard deviation of the trait values of extant species within a separate simulation. Panel (d) shows the pairwise trait differences for 50 000 simulations plotted against phylogenetic distance. Panel (e) simply takes the data from panel (d) and places them in bins, to show the statistical expectation at a given relatedness. Panel (f) shows the effect of taking the square root of the phylogenetic distance matrix on the relationship between the phylogenetic distance and the expected trait difference. Note that the expectation for the trait standard deviation and the pairwise difference is linear with respect to the square root of time as shown analytically in the text. All simulations use code from FitzJohn (2012) and Revell (2012).

$$\rho(x, t) = \frac{\rho_0}{\sqrt{4\pi\sigma^2 t}} e^{-\frac{x^2}{4\sigma^2 t}} \quad \text{eqn 2}$$

which implies that the second moment of the distribution is:

$$\overline{x^2} = 2\sigma^2 t. \quad \text{eqn 3}$$

In other words, the variance goes up linearly with time, and the standard deviation rises with time’s square root, or as Einstein put it: ‘the mean displacement is therefore proportional to the square root of the time’. Applied in a phylogenetic context, this means that while among species variance in trait values goes up linearly with time (Felsenstein 1985), the expected displacement of any two taxa in trait space does not increase linearly with time, but rather with time’s square root (Fig. 1). This nonlinearity is true both for one trait and for Euclidean distance in n -dimensional trait space. Indeed, there is no plausible model for expected trait dissimilarity to be linearly related to evolutionary time. For there to be a linear relationship, after a speciation event, the functional distance between two lineages would increase constantly and continuously as their traits evolve away from each other. It is difficult to imagine a scenario where that would be the case.

While this technical point is well understood in parts of the comparative methods literature (Hardy & Pavoine 2012), the implications for many ecological applications have gone largely unnoticed. If evolutionary relatedness is used as a proxy for functional distance, the nonlinearity of their scaling relationship means that more recent evolution should have a disproportional influence on contemporary ecology. Current methods used in community phylogenetics (see review of methods in Vellend *et al.* 2010) typically treat evolutionary relatedness linearly; 1 and 6 million year relatedness difference is treated as having the same expected effect as a 101 and 106 million year relatedness difference. All evolutionary time is considered equal, whether that time occurred over the last 5 million years or more than 100 million years ago. Combined with imbalanced trees, this creates a problem that is well known in empirical investigations: the statistical over-weighting of early diverged, low diversity clades (Kembel & Hubbell 2006). When those clades are included in the sample (or in a randomization), they have a disproportionate weight on the test statistic, a weight that is highly disproportionate to the expected trait difference under a Brownian model.

The root of this problem is in the distribution of pairwise phylogenetic distances. In the basic simulated birth–death

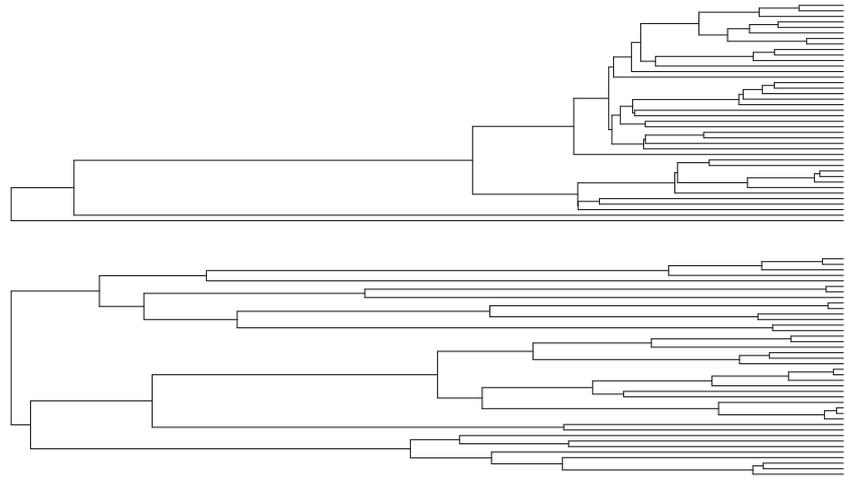


Fig. 2. Example of a real tree (top), obtained by randomly selecting taxa from the Zanne *et al.* (2014) tree, compared with a homogeneous birth–death simulation tree (bottom).

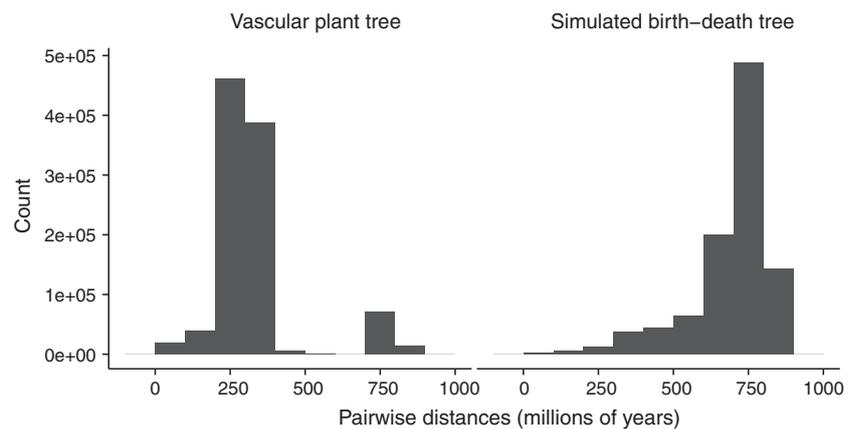


Fig. 3. The pairwise phylogenetic distances from a recent phylogeny of vascular plants by Zanne *et al.* (2014) and a simulated phylogeny of the same age and number of extant species.

trees, there is an equal probability at every time step for every branch of either a speciation or an extinction event. This creates what are known as balanced trees (Heard 1997, also Fig. 2). Balanced trees are rare in empirical studies, as heterogeneity in net diversification (Alfaro *et al.* 2009) creates trees that are imbalanced (Mooers 1995) and have peculiar distributions of pairwise distances (e.g. the vascular plant tree from Zanne *et al.* (2014) in Fig. 3).

Drawing from theory on Brownian motion reveals a simple solution to the weighting problem: a square root transform of the phylogenetic distance matrix. For example, the mean pairwise distance (sensu Webb 2000):

$$MPD = \frac{2 \sum_{i=1}^{n-1} \sum_{j=i+1}^n d_{i,j}}{(n)(n-1)} \quad \text{eqn 4}$$

can be redefined as the mean of the square root-transformed pairwise distances:

$$MPD^* = \frac{2 \sum_{i=1}^{n-1} \sum_{j=i+1}^n \sqrt{d_{i,j}}}{(n)(n-1)} \quad \text{eqn 5}$$

where n is the number of taxa and $d_{i,j}$ is the pairwise phylogenetic distance between species i and species j . This quantity MPD^* is proportional to the mean of the expected pairwise differences for traits evolving under a Brownian model, for both one trait in one dimension and for m traits in m

dimensional space. This equation is provided as an example: very similar adjustments are possible to most of the common community phylogenetics statistics (see definitions within Velend *et al.* 2010), simply via a square root transform of the distance matrix.

With this transformation, long-ago time is down-weighted compared to recent time. As such, the effect of the presence or absence of a species on MPD is weighted in proportion to the mean pairwise expected trait difference to all other species under a Brownian model. In practical terms, this re-scaling can be accomplished exceedingly easily with one additional line of code in combination with the tools in widely available statistical packages (Kembel *et al.* 2010).

Simulations

To explore the empirical implications of this idea, we conducted simulations applying a similar framework to that described by Kraft *et al.* (2007) in this case repeating the ‘filtering-derived’ and ‘neutral assembly’ algorithms). We simulated trait evolution by Brownian motion on both a real tree and a homogenous birth–death simulated tree (Fig. 2). To keep the pool size (number of tree tips) consistent across the real and simulated trees, the real tree was randomly pruned down to 200 taxa. In each run, we ‘evolved’ a trait across the phylogeny

and then applied one of two community assembly filters to obtain a final community of 40 taxa. Under the ‘filtering-derived’ assembly filter, the most derived (extreme) trait value was treated as the optimum, with the remaining 39 places in the community selected from taxa having the nearest trait values to that optimum. This process simulated community assembly via habitat filtering (Diaz, Cabido & Casanoves 1998), whereby the abiotic environment sets some threshold on the range of strategies (and thereby trait values) that are able to sustain a positive population growth rate (e.g. tolerance of inundation along a hydrological gradient). In contrast with the deterministic nature of the ‘filtering-derived’ algorithm, under the ‘neutral assembly’ algorithm, the community was obtained by randomly selecting 40 species independent of their trait values. One thousand runs were conducted for each community assembly algorithm on each of the real and simulated phylogenies. Finally, we quantified the effect of the filter using conventional community phylogenetics methods (MPD and MNTD – mean nearest taxon distance) and compared the standard approach with that of a square root transform of the phylogenetic distance matrix (all code to perform replicate simulations is provided in the supplementary material).

Simulation results indicate the transformed test has considerably higher statistical power (Fig. 4) for detecting the signal of community assembly. Using the square root transform improved 92% of trials for both MPD and MNTD. Using the standardized effect size metric developed by Webb (2000), whereby:

$$\text{SES}_{\text{METRIC}} = \frac{\text{METRIC}_{\text{observed}} - \text{mean}(\text{METRIC}_{\text{null}})}{\text{sd}(\text{METRIC}_{\text{null}})}$$

the median improvement in standardized effect size was 0.64 for MPD and 0.43 for MNTD (simulated and real trees combined). This is a comparatively large increase in effect size from a simple statistical adjustment. The improvement was similar for real and simulated trees, but may be more crucial in the real case because the general power of community phylogenetics is lower for the real tree (Kembel & Hubbell 2006). While a comprehensive exploration of the effect of the transformation on type 1 error rates is beyond the scope of this paper (Kraft *et al.* 2007), simulations indicated that the expected reduction in type 2 error rate is in the order of 5–25%

(depending on the community to pool size ratio and other factors).

Other models of trait evolution

While a highly useful ‘default’ model, we do not expect that a Brownian motion model will prove to be a fully adequate model for trait evolution at large scales. In general, the current evidence suggests that actually, the square root transform does not go far enough towards down-weighting long-ago evolution compared to recent evolution in many cases (Butler & King 2004; Harmon *et al.* 2010; Smith *et al.* 2010). In the event that there are bounding or mean-reverting processes (e.g. Ornstein–Uhlenbeck (OU) Butler & King 2004), phylogenetic signal will be less strong than under a Brownian model. Under these alternative models, the effect of evolutionary relatedness decays more rapidly, a phenomenon defined as ‘phylogenetic half-life’ by Hansen, Pienaar & Orzack (2008). If trait evolution typically includes this type of process, the problem we describe here will be even more extreme. In this case (see Kelly, Grenyer & Scotland 2014), the square root transformation will not go far enough. For the alternatives to Brownian motion, such as OU and heterogeneous models where rates of evolution vary among clades (Beaulieu *et al.* 2012), there are analogous tree scaling approaches (Pearse, Jones & Purvis 2013), but these, unlike the square root transformation, require *a priori* information about trait evolution in the relevant clade.

Conclusion

We recommend a square root transform of the phylogenetic distance matrix for all uses where phylogenetic relatedness is used as a proxy for current-day functional disparity. There are some cases where the number of years of evolutionary history in a place may be an interesting quantity in and of itself (Purvis & Hector 2000). In those cases, linear relatedness may still be of interest; however, many ecological studies use evolutionary relatedness as a proxy for trait dissimilarity, and in these cases, using relatedness linearly will decrease the power of the investigation.

While we have made a statistical argument above, in conclusion, we stress that this is actually a conceptual point. We argue

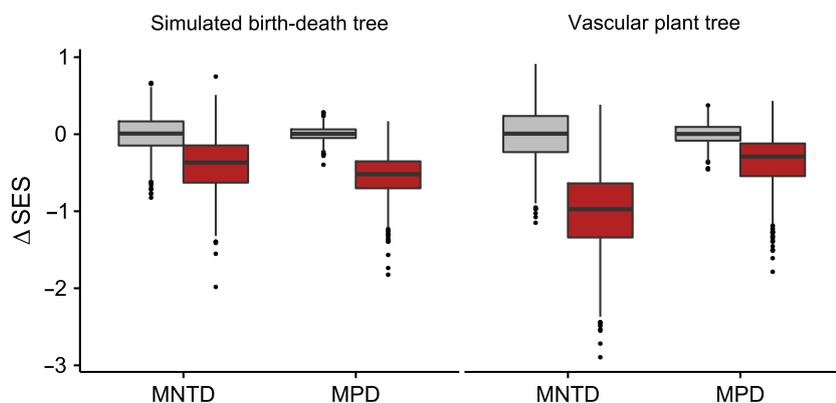


Fig. 4. Improved statistical power from down-weighting long-ago evolution: change in standardized effect size for mean pairwise distance (MPD) and mean nearest taxa distance (MNTD) using a square root-transformed phylogenetic distance matrix vs. the conventional approach. Box plots with grey-fill group communities assembled under a neutral (random sample) model; box plots with red-fill group communities assembled under a ‘habitat filter’ model.

that conventional approaches overweight long-ago evolutionary time and underweight recent evolution both conceptually and statistically, and in doing so inadvertently limit the statistical power and success of efforts to leverage phylogenetic information in ecological contexts. There are many other reasons why the mapping of ecological process to phylogenetic community patterns may be inconclusive (Mayfield & Levine 2010; Godoy, Kraft & Levine 2014); many of these issues are hard to address. Here, we have identified one problem – the weighting of evolutionary history – where a simple adjustment may help.

Of course, by using the square root transformation, we make the assumption that trait differences scale linearly with ecological fitness. While disentangling the ecological/evolutionary processes is somewhat intractable in this instance, this is at least a parsimonious assumption. Instead, justification for using more complex measures of functional distance (e.g. squared distance) in the context of ecological selection/assembly should be contingent on supporting theory. To our knowledge, none exists. The magnitude of fitness–trait relationships has received some attention (Kimball *et al.* 2011; Adler *et al.* 2013), but explicitly exploring their scaling properties could well prove an invaluable area of future research.

In general, there needs to be a more nuanced use of evolutionary relatedness within community ecology. By improving the connection between metrics within community phylogenetics and trait evolution, we can increase the power and utility of using evolutionary relatedness to ask ecological questions. This methodological update will not be a one-off: as our understanding of the processes and patterns in trait macro-evolution at large scales grows (O'Meara 2012; Pennell & Harmon 2013), the phylogenetic metrics used in contemporary ecology will need to be continually updated.

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Data accessibility

R code to reproduce simulations available as online supporting information.

References

- Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. & Franco, M. (2013) Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 740–745.
- Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L., Carnevale, G. & Harmon, L.J. (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences*, **106**, 13410–13414.
- Beaulieu, J.M., Jhwueng, D.C., Boettiger, C. & O'Meara, B.C. (2012) Modeling stabilizing selection: expanding the ornstein-uhlenbeck model of adaptive evolution. *Evolution*, **66**, 2369–2383.
- Bennett, J.A., Lamb, E.G., Hall, J.C., Cardinal-McTeague, W.M. & Cahill, J.F. (2013) Increased competition does not lead to increased phylogenetic verdspersion in a native grassland. *Ecology Letters*, **16**, 1168–1176.
- Butler, M.A. & King, A.A. (2004) Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *The American Naturalist*, **164**, 683–695.
- Cadotte, M., Albert, C.H. & Walker, S.C. (2013) The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters*, **16**, 1234–1244.
- Cahill, J.F., Kembel, S.W., Lamb, E.G. & Keddy, P.A. (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 41–50.
- Cavander-Bares, J., Kozak, K.H., Fine, P.V. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.
- Diaz, S., Cabido, M. & Casanoves, F. (1998) Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, **9**, 113–122.
- Einstein, A. (1905) Über die von der molekularkinetischen Theorie der Wärme geforderte Bewegung von in ruhenden Flüssigkeiten suspendierten Teilchen. *Annalen der Physik*, **322**, 549–560.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.
- FitzJohn, R.G. (2012) Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol Evol*, **3**, 1084–1092.
- Fritschie, K.J., Cardinale, B.J., Alexandrou, M.A. & Oakley, T.H. (2014) Evolutionary history and the strength of species interactions: testing the phylogenetic limiting similarity hypothesis. *Ecology*, **95**, 1407–1417.
- Godoy, O., Kraft, N.J.B. & Levine, J.M. (2014) Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, **17**, 836–844.
- Hansen, T.F., Pienaar, J. & Orzack, S.H. (2008) A comparative method for studying adaptation to a randomly evolving environment. *Evolution*, **62**, 1965–1977.
- Hardy, O.J. & Pavoine, S. (2012) Assessing phylogenetic signal with measurement error: a comparison of Mantel tests, Blomberg *et al.*'s K, and phylogenetic distograms. *Evolution*, **66**, 2614–2621.
- Harmon, L.J., Losos, J.B., Jonathan Davies, T., Gillespie, R.G., Gittleman, J.L., Bryan Jennings, W. *et al.* (2010) Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, **64**, 2385–2396.
- Heard, S.B. (1997) Inferring evolutionary process from phylogenetic tree shape. *The Quarterly Review of Biology*, **72**, 31–54.
- Johnson, M.T. & Stinchcombe, J.R. (2007) An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology & Evolution*, **22**, 250–257.
- Kelly, S., Grenyer, R. & Scotland, R.W. (2014) Phylogenetic trees do not reliably predict feature diversity. *Diversity and Distributions*, **20**, 600–612.
- Kembel, S.W. & Hubbell, S.P. (2006) The phylogenetic structure of a neotropical forest tree community. *Ecology*, **87**, S86–S99.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
- Kimball, S., Gremer, J.R., Angert, A.L., Huxman, T.E. & Venable, D.L. (2011) Fitness and physiology in a variable environment. *Oecologia*, **169**, 319–329.
- Kraft, N.J., Cornwell, W.K., Webb, C.O. & Ackerly, D.D. (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist*, **170**, 271–283.
- Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.
- Mooers, A.O. (1995) Tree balance and tree completeness. *Evolution*, **49**, 379–384.
- Narwani, A., Alexandrou, M.A., Oakley, T.H., Carroll, I.T. & Cardinale, B.J. (2013) Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters*, **16**, 1373–1381.
- O'Meara, B.C. (2012) Evolutionary inferences from phylogenies: a review of methods. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 267–285.
- Pearse, W.D., Jones, F.A. & Purvis, A. (2013) Barro Colorado island's phylogenetic assemblage structure across fine spatial scales and among clades of different ages. *Ecology*, **94**, 2861–2872.
- Pennell, M.W. & Harmon, L.J. (2013) An integrative view of phylogenetic comparative methods: connections to population genetics, community ecology, and paleobiology. *Annals of the New York Academy of Sciences*, **1289**, 90–105.
- Purvis, A. & Hector, A. (2000) Getting the measure of biodiversity. *Nature*, **405**, 212–219.
- Revell, L.J. (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.
- Smith, F.A., Boyer, A.G., Brown, J.H., Costa, D.P., Dayan, T., Ernest, S.M. *et al.* (2010) The evolution of maximum body size of terrestrial mammals. *Science*, **330**, 1216–1219.
- Swenson, N.G. (2013) The assembly of tropical tree communities the advances and shortcomings of phylogenetic and functional trait analyses. *Ecography*, **36**, 264–276.

- Vellend, M., Cornwell, W.K., Magnuson-Ford, K. & Mooers, A.Ø. (2010) Measuring phylogenetic biodiversity. *Biological diversity frontiers in measurement and assessment* (eds A.E. Magurran & B.J. McGill), pp. 194–207. Oxford University Press, Oxford, UK.
- Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist*, **156**, 145–155.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Zanne, A., Tank, D., Cornwell, W., Eastman, J., Smith, S., FitzJohn, R. *et al.* (2014) Data from: Three keys to the radiation of angiosperms into freezing environments. *Nature*, **506**, 89–92. Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.63q27.2>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1. R code to reproduce simulations (Simulations.pdf).

Data S2. Simulation functions (power_funcs.r).