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LETTER

Phylogeny structures species' interactions in experimental ecological communities

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Abstract

Species' traits and interactions are products of evolutionary history. Despite the long-standing hypothesis that closely related species possess similar traits, and thus experience stronger competition, measuring the effect of evolutionary history on the ecology of natural communities remains challenging. We propose a novel framework to test whether phylogeny influences patterns of coexistence and abundance of species assemblages. In our approach, phylogenetic trees are used to parameterize species' interactions, which in turn determine the abundance of species in a given assemblage. We use likelihoods to score models parameterized with a given phylogeny, and contrast them with models built using random trees, allowing us to test whether phylogenetic information helps to predict species' abundances. Our statistical framework reveals that interactions are indeed structured by phylogeny in a large set of experimental plant communities. Our results confirm that evolutionary history can help predict, and potentially manage or conserve, the structure and function of complex ecological communities.

KEYWORDS

coexistence, community phylogenetics, community structure, competition, interaction strength, phylogenetic trees

INTRODUCTION

Interactions between species are the essential building blocks that shape ecological community structure, influencing not only which species are present in a community but also their biomass and abundance. To make sense of the myriad possible interactions in species-rich communities, ecologists have long sought principles that organize species' interactions, and can help to understand and predict them. For example, simple models based on body size and other allometric constraints can explain many aspects of food web structure (Petchey et al., 2008; Stouffer et al., 2011), and (mis)matching between key traits is thought to organize interactions in plant-pollinator networks (Bergamo et al., 2018; Rosas-Guerrero et al., 2014). Competitive interactions can be related to similarity in functional traits (McGill et al., 2006; Navas & Violle, 2009), such as resource use overlap (MacArthur, 1970), but identifying and measuring relevant traits is challenging and provides limited insight across distinct communities.

Evolutionary relatedness is hypothesized to be one general principle that may structure ecological interactions (Gómez et al., 2010) and in particular competition (Cahill Jr et al., 2008; Cavender-Bares et al., 2009; Davies, 2021; Mouquet et al., 2012; Webb et al., 2002). The logic of this hypothesis is that more closely related species tend to possess more similar traits—a pattern known as phylogenetic signal (Freckleton et al., 2002; Losos, 2008; Srivastava et al., 2012)—and higher trait similarity produces greater niche overlap and stronger competition (Cavender-Bares et al., 2009; Mouquet et al., 2012). The

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essential elements of this hypothesis were already laid out by Darwin: ‘As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera’ (Darwin, 1859).

With the rapid development of molecular phylogenetics at the end of the twentieth century, interest in this ‘competition-relatedness’ hypothesis blossomed (Cahill Jr et al., 2008). Phylogenetic distance (relatedness) between species, which can be measured with relative ease and in a standardized way across different ecosystems, provides an enticing proxy for trait similarity and potentially for competitive interaction strengths (Cadotte et al., 2008; Mouquet et al., 2012; Srivastava et al., 2012). In the absence of detailed information on species' functional traits and interactions, many researchers have even suggested that phylogenetic diversity should be used to inform conservation and restoration decisions, under the hypothesis that communities with more phylogenetic diversity incorporate more functional diversity and thus weaker competitive interactions that should lead to higher community productivity (Campbell et al., 2019; Kettenring et al., 2014; Mazel et al., 2017; Mouquet et al., 2012; Srivastava et al., 2012).

However, it has proved challenging to test the competition-relatedness hypothesis, and it remains unclear whether phylogeny consistently structures species' interactions in competitive communities. There is a large literature on phylogenetic signal in traits, which underpins this hypothesis, and good evidence that at least some ecologically relevant traits show a phylogenetic signal in at least some clades (Burns & Strauss, 2011; Freckleton et al., 2002; Srivastava et al., 2012), although this pattern varies by trait, lineage and system (Losos, 2008; Lososová et al., 2016). This type of evidence is ultimately insufficient to evaluate the competition-relatedness hypothesis, though, without knowing how many and which traits are relevant for competitive interactions. Clear phylogenetic signal may only emerge when considering many traits in aggregate (Cadotte et al., 2017), and conversely, phylogenetic signal in a small number of traits may not indicate the same signal in other traits that matter more for shaping interactions. Therefore tests of the competition-relatedness hypothesis must relate phylogenetic information all the way to interactions and their outcomes.

Many studies have sought to evaluate the link between phylogeny and interaction strengths indirectly, by searching for patterns implied by a positive competition-relatedness relationship. For example, early studies (Elton, 1946; Simberloff, 1970) used species-to-genus ratios as proxy for the strength of competitive interactions, drawing on the logic of Darwin's hypothesis. Later, many studies under the umbrella of ‘community phylogenetics’ sought to detect the influence of competition in the assembly of ecological communities by comparing the phylogenies of local communities to those of regional species pools (Cavender-Bares et al., 2004, 2009; Graham et al., 2009; Webb, 2000; Webb et al., 2002). Under the assumption that strong competitive interactions between closely related species would result in competitive exclusions, one might find higher phylogenetic diversity than expected by chance (‘phylogenetic over-dispersion’) in communities shaped by competition (Cavender-Bares et al., 2009; Webb et al., 2002). However, numerous studies have challenged the idea that phylogenetic patterns can be used to infer community assembly processes and the structure of ecological interactions (Bennett et al., 2013; Cavender-Bares et al., 2006; Davies, 2021; Gerhold et al., 2015; Mayfield & Levine, 2010). In particular, relationships between phylogeny and co-occurrence provide a poor test of the underlying competition-relatedness hypothesis, as, for example, the absence of phylogenetic over-dispersion could be due to other factors, such as environmental filtering (Cavender-Bares et al., 2006; Webb et al., 2002) or dispersal limitation (Baeten et al., 2015; Keck & Kahlert, 2019; Liu et al., 2013), masking the effects of competition; conflicting effects of phylogeny on interaction strengths (Godoy et al., 2014; Mayfield & Levine, 2010); or a lack of any competition-relatedness relationship altogether.

A related approach has been to examine the relationship between phylogenetic diversity and productivity in experimental communities. Under the competition-relatedness hypothesis, it is often expected that—controlling for species richness—less phylogenetically diverse communities experience higher niche overlap, resulting in strong competitive interactions that suppress community productivity (e.g. biomass), while more phylogenetically diverse communities experience weaker interactions and greater niche complementarity (Davies et al., 2016; Srivastava et al., 2012). This idea has been tested in biodiversity ecosystem and functioning (BEF) experiments, where species composition is manipulated in a range of experimental communities to generate a gradient of diversity and productivity is measured after some time. Typically, in these tests the evolutionary history of each community is summarized by some measure of phylogenetic diversity, such as the average relatedness between all pairs of species, and compared to the productivity (total biomass) of the community. Analyses of BEF experiments have often found positive relationships between phylogenetic diversity and productivity, consistent with the competition-relatedness hypothesis (Cadotte, 2013; Cadotte et al., 2008; Connolly et al., 2011; Flynn et al., 2011; Maherali & Klironomos, 2007; Steudel et al., 2016). However, careful re-analysis of these data has resulted in more mixed conclusions (Cadotte, 2015; Cardinale et al., 2015; Huang et al., 2020; Venail et al., 2015). In most BEF experiments, phylogenetic diversity is strongly confounded with species richness, leaving weak evidence that relatedness affects productivity independently of richness (Cardinale et al., 2015; Steudel et al., 2016; Venail et al., 2015). Additionally, BEF analyses rely on summary statistics (phylogenetic diversity as a predictor and community productivity as a response) that lose or obscure most information about a community's evolutionary history as well as its composition (Molina-Venegas et al., 2019; Yguel et al., 2016). Thus, despite the impressive scale of many BEF studies, the analysis of BEF data by simply regressing community productivity against phylogenetic diversity has limited ability to resolve relationships between relatedness and pairwise interaction strengths.

The relationship between competition and relatedness can be tested more directly in experiments designed to measure pairwise species' interactions. Results from these studies have also been mixed (Cahill Jr et al., 2008; Venail et al., 2014). Studies of freshwater protists, for example, have found a positive relationship between relatedness, measured as time since a last common ancestor, and competition strength in species pairs (Jiang et al., 2010; Violle et al., 2011). Similarly, another experiment found that priority effects, a signal of strong and relatively symmetric competition, were more likely between more closely related yeast species (Peay et al., 2012). On the other hand, experiments with freshwater algae have yielded no clear relationship between relatedness and competition strength (Alexandrou et al., 2015; Fritschie et al., 2014; Venail et al., 2014), and experiments with plants have shown weak relationships (Cahill Jr et al., 2008) or relationships that differ from the prediction of increased competition between closely related species (Godoy et al., 2014). While these studies allow direct comparison of interaction strengths against relatedness, they are logistically demanding, requiring a number of co-culture experiments that scales quadratically with the number of species used (Cahill Jr et al., 2008). For this reason, few such experiments have been conducted, and most have been limited to microbes or fast-growing plants.

Another, more fundamental, limitation applies to both BEF and pairwise competition experiments. By comparing interaction strengths (or total community biomass, as a proxy) directly against phylogenetic distances inferred from genetic sequence data, these analyses test the strong assumption that intensity of competition is linearly related to evolutionary divergence times. However, even in a simple scenario of neutral trait evolution, the relationship between phylogenetic distance and ecological trait dissimilarity is expected to be non-linear (Letten & Cornwell, 2015) and potentially heterogeneous (Cadotte et al., 2017), with substantial variation in the interaction strengths between distantly related species. If a small number of traits control the strength of competition, it is especially unlikely that competition will increase straightforwardly with phylogenetic distance (Cadotte et al., 2017). Additionally, it is probable that key functional traits relevant for species' interactions may be under strong selection, with disruptive and stabilizing selection acting to respectively accelerate or decelerate the rate of change of ecological similarity with respect to phylogenetic distances (Burin et al., 2024; Letten & Cornwell, 2015; Louw et al., 2024). Even if the competition-relatedness hypothesis holds and competition tends to increase with relatedness, many factors may influence the *rate* at which evolutionary divergence translates into weakened competition across time, clades and even across the genomes of individual species (Ackerly, 2009; Cadotte et al., 2017; Letten & Cornwell, 2015; Louw et al., 2024).

The main goal of this work is to test whether and how phylogeny maps into interactions between species using a new methodology that allows us to overcome many of the challenges outlined above. We re-analyse three large BEF data sets (Cadotte, 2013; Tilman et al., 2001; van Ruijven & Berendse, 2010) by resolving individual species' interactions and relating them directly to species' phylogenetic relationships, rather than relying on summary statistics. Furthermore, we incorporate a flexible link between phylogenetic distances and interaction strengths that allows us to test whether competition increases with relatedness without making additional assumptions about the form of this relationship.

We achieve this by building on recent methods for inferring species' interactions and predicting their outcomes in experimental communities (Maynard et al., 2020; Skwara et al., 2023). Using the phylogenetic topology for a given set of species, we parameterize a simple model of species' interactions in a manner consistent with the competition-relatedness hypothesis (Serván et al., 2023), such that, for any three species, the two that share the most recent common ancestor must compete more strongly. We then fit this model using the experimental data, and test whether phylogeny structures species' interactions by comparing the quality of fit against null model fits using a large number of randomized phylogenetic trees. This basic procedure yields a rigorous test of the competition-relatedness hypothesis while also revealing, rather than assuming, how interaction strengths change with phylogenetic distance.

Our method departs considerably from previous approaches to testing for phylogenetic effects in the same data sets (Cadotte, 2013; Connolly et al., 2011, 2013; Venail et al., 2015). Here, we are not focused on the relationship between phylogenetic diversity and productivity; rather, we take advantage of BEF experiments because they offer large data sets with unique control over the composition of communities. Unlike previous studies, we make use of the biomasses recorded for individual species, rather than the total biomass per plot—thereby gaining statistical power and resolution. We also relate the phylogenetic tree structure for each community directly to species' interactions and then to biomasses via a model consistent with population dynamics, rather than using phylogenetic diversity as a covariate in a regression model. As described above, most prior approaches to studying phylogenetic structure in these data use summary statistics (e.g. phylogenetic diversity, Cadotte et al. 2008; Flynn et al. 2011) to characterize evolutionary history; these approaches extract quantitative information (i.e. branch lengths) from trees but are insensitive to the specific tree topology [but see Yguel et al. (2016), Davies et al. (2016) and Molina-Venegas et al. (2019) for related approaches that incorporate topology]. However, tree topology encodes fundamental similarity relationships between species (Molina-Venegas et al., 2019; Yguel et al., 2016), while branch lengths inferred from genetic data may not be closely related to the similarity of functional traits relevant to species' interactions. Thus, we take essentially the opposite approach here: we fit models that are structured by the topology of community phylogenies, but we fit branch length parameters to the ecological (not molecular) data.

Overall, our approach reveals strong evidence for phylogenetic structure that increases competition between more closely related species. The probability that a model parameterized with a random tree fits the empirical data better than a model based on the actual community phylogeny is typically small, an outcome that is consistent across three different experimental settings, comprising a total of 19 distinct data sets. Additionally, we connect the high performance of biologically informed trees to specific features of the community phylogenies by identifying which clades are most important for accurately predicting final biomasses. Finally, we discuss how our framework may be extended and used to test other hypotheses about factors that structure interactions in ecological communities.

METHOD OVERVIEW AND RESULTS

To test whether and how evolutionary relationships structures species' interactions, we introduce a framework in which, first, phylogenetic information is used to parameterize a model of interactions among a pool of n species; second, species' interactions are used to predict species-level biomasses for different assemblages that can be formed from the pool (Maynard et al., 2020); and third, predictions are scored against experimental data from BEF experiments (Cadotte, 2013; Tilman et al., 2001; van Ruijven & Berendse, 2010). We repeat this procedure many times, using both the 'true' (molecular) phylogenetic topology for a given community, as well as randomized trees. By comparing the resulting likelihoods, we assess whether the true phylogeny allows superior prediction of the ecological data, which would indicate that interactions are structured by phylogeny.

We analyse data from three BEF experiments, with a total of 19 unique data sets [one for Cadotte (2013), 9 years for the Biodiversity II experiment from Tilman et al. (2001) and another 9 years for the Wageningen Biodiversity experiment from van Ruijven and Berendse (2010)] in which plants selected from a pool of n species are grown together in many different combinations. These data sets include the recorded biomass of each species i across different plots in which it was grown along with other species. We use $\tilde{x}_i^{(k,r)}$ to denote the biomass of species i when growing in the assemblage k (corresponding to the set of extant species in the plot) and replicate r (as the same assemblage may occur in different plots). For each data set, we build a matrix of species' interactions reflecting the topology of the corresponding phylogenetic tree for the species pool. We then use this matrix of interactions to compute the expected biomass of each species i in assemblage k, $x_i^{(k)}$, and, by relating the expected and observed values via a likelihood function, we can find the maximum likelihood estimates of the free parameters in the model. The model we consider relates phylogenetic structure to interactions based on the competition-relatedness hypothesis, that is, competition between species is expected to increase with the amount of shared evolutionary history. In other words, niche overlap is determined by trait similarity, which in turn reflects shared branch lengths between species in the phylogeny.

Model fitting is accomplished in three steps. First, the phylogenetic tree topology is combined with free parameters representing branch lengths in the phylogeny to produce a matrix of competitive interactions constrained by phylogenetic relationships. These constraints ensure that, for any three species, the two that are most closely related must compete more strongly with one another than with the third. Our paramerization can be derived from models for consumer-resource dynamics [Supplementary Material; see also Serván et al. (2023)], where more closely related species are assumed to require and use more similar sets of resources. This model has $2n-1$ free parameters, $\lambda_\ell \geq 0$, which are associated with the branches of the phylogenetic tree. We refer to $\lambda_\ell \geq 0$ as the length parameter for branch ℓ. For any pair of species i and j, the competition coefficient A_{ij} describing their interaction strength is given by the sum of all λ_ℓ corresponding to branches ℓ shared by i and j in the phylogeny. Thus, larger values of λ_ℓ result in stronger competition between species in the clade subtended by branch ℓ. More complex versions of this basic model are also possible, sharing the same underlying relationship between branch length parameters and competition strength, but with additional parameters (up to $4n-3$ total parameters) accounting for potential variation in species competitive abilities unrelated to phylogeny. We consider these more complex models, which yield similar conclusions, in the Supplementary Material.

Second, we use the matrix of interactions to compute the expected biomass of each species in every assemblage, following the approach of Maynard et al. (2020) and Skwara et al. (2023) (further details of the modelling approach are provided in the Supplementary Material). Thus, for each species in each assemblage, we obtain a prediction, influenced by both the structure of the tree and the tunable branch length parameters. Finally, we specify a statistical model describing how experimental data are distributed around these predicted means (requiring an extra parameter to control the shape of this distribution). This allows us to compute an overall likelihood for the branch length parameters given a specific tree, data set and model formulation. We perform numerical optimization to search for the maximum likelihood estimates for these free parameters (Supplementary Material), ultimately allowing us to associate a (maximum) likelihood with each tree topology. Figure 1 represents these steps graphically, and the Detailed Methods section in the Supplementary Material contains mathematical and statistical details.

Results for three selected data sets [year 2008 of Biodiversity II experiment by Tilman et al. (2001); data from Cadotte (2013); and year 2003 of the Wageningen experiment by van Ruijven and Berendse (2010)] are shown in Figure 2. For all of these data sets (including a total of 31 species, measured in 91 distinct communities, with 530 observations, including replicates), our model recapitulates the observed biomasses well. We find a correlation between the logarithm of the observed biomasses and the logarithm of the predicted biomasses of at least 83% for all three data sets (see Supplementary Material for additional years of the Biodiversity II and Wageningen experiments).

While these results indicate that our phylogenetically structured model can describe the data adequately, they do not tell us if the particular tree topology is responsible for the quality of fit, or if other models of similar complexity would fit the data equally well. To answer this question, we compare the quality of fit, measured by the model's likelihood, against alternative models where the structure of the interaction matrix varies. First, as a natural reference point, we consider a model based on a 'star tree' topology, in which all species descend directly from the root of the tree (Tucker et al., 2018). This configuration can be obtained from any tree topology by setting the parameters λ_ℓ corresponding to internal branches to zero; therefore, the likelihood for the star tree provides a lower bound for the likelihood distribution across all trees (solid line in Figure 2b). In the star tree, phylogenetic relationships are disregarded and only the root branch and the tips of the tree are fitted; in ecological terms, this models mean-field competition between species (corresponding to the root branch) plus intraspecific competition

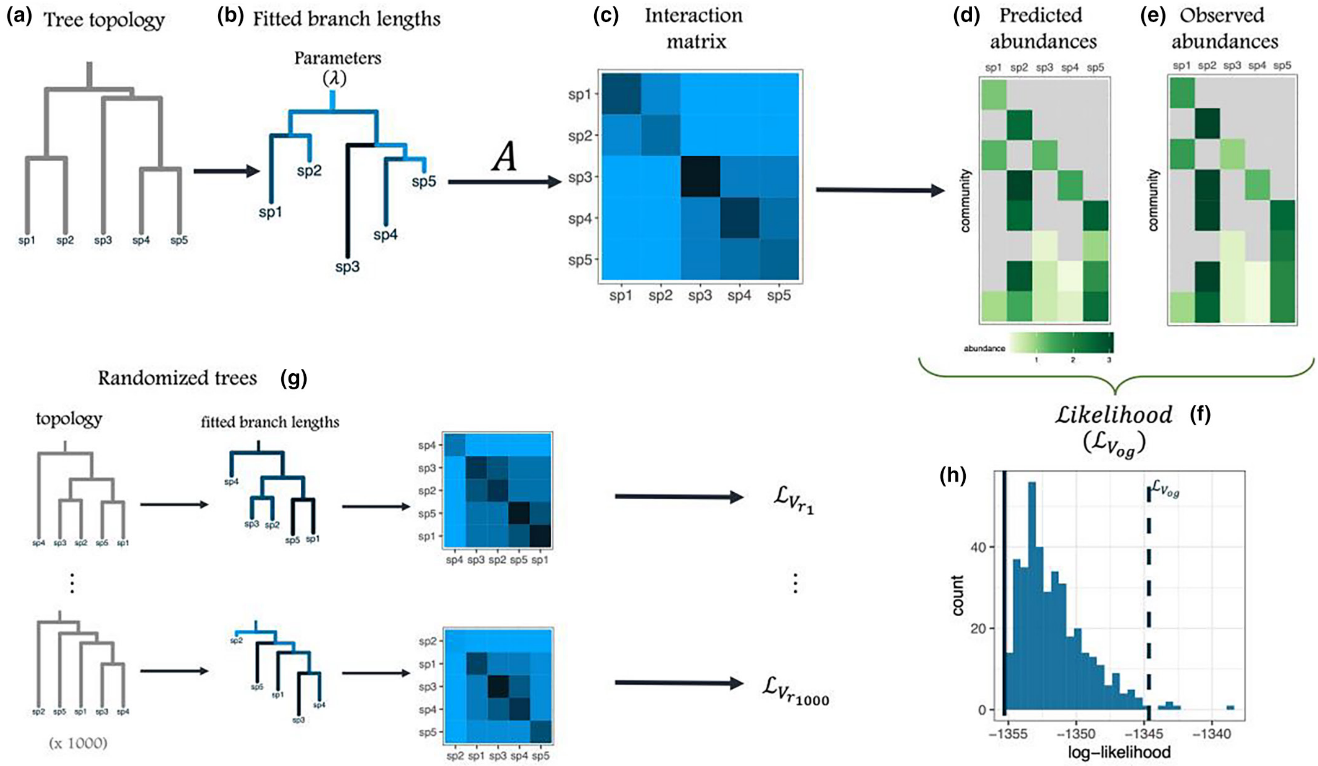

FIGURE 1 Diagram illustrating the steps of our approach. From the phylogenetic tree for a pool of species, we combine the tree topology (a) with a set of free parameters representing branch lengths of the tree (b). These parameters are translated into a matrix of interactions between all the species in the pool, with a structure corresponding to the tree topology (c). Using the matrix of interactions, we predict the biomasses of all species in each observed assemblage (d). These predicted biomasses are thus determined by the structure of the phylogenetic tree as well as the branch lengths. The predicted biomasses are contrasted with biomasses observed in experimental communities (e), allowing us to compute the likelihood of the parameters given the tree, data and model (f). We maximize the likelihood of the parameters under the fixed tree topology, obtaining a maximum likelihood score for that topology, and then contrast it with model fits using random trees (g). By repeating this procedure many times, we build a distribution of likelihoods over the set of random tree topologies. Finally, we compute a p-value which measures the probability of obtaining a better likelihood when using a random tree in place of the true phylogenetic tree (h).

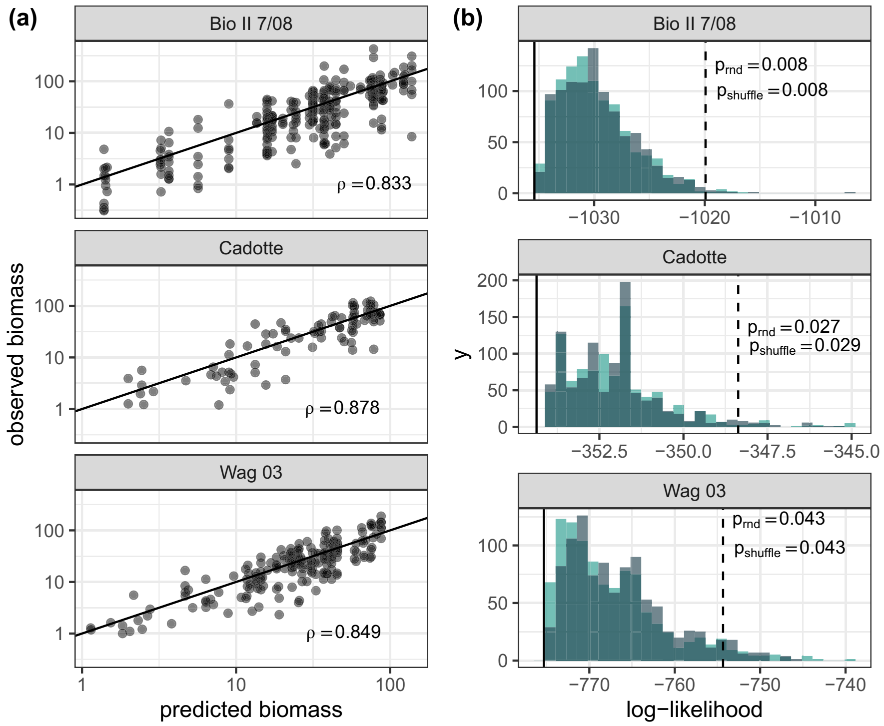

FIGURE 2 Predicted biomasses of experimental communities and distribution of log-likelihoods for three different data sets (Biodiversity II, year 2008, data from Cadotte, 2013 and year 2003 of Wageningen experiment). (a) Predicted versus observed biomasses. Each point corresponds to the biomass measured for a particular species in a particular plot. Each panel refers to one data set. Note that for replicated communities, the predicted value is necessarily the same. The correlation between the logarithm of the predicted and observed biomasses is reported in each panel. (b) Distribution of the likelihoods for each data set using random trees as input. Colours indicate whether the random trees were obtained from the Yule process (teal) or by shuffling the leaves of the original tree (grey). The vertical dashed line represents the likelihood using the true phylogenetic tree. The solid line represents the likelihood using a 'star' tree, which provides a lower bound for the distribution (see text). Approximate p-values obtained for one thousand randomizations are reported in the panels.

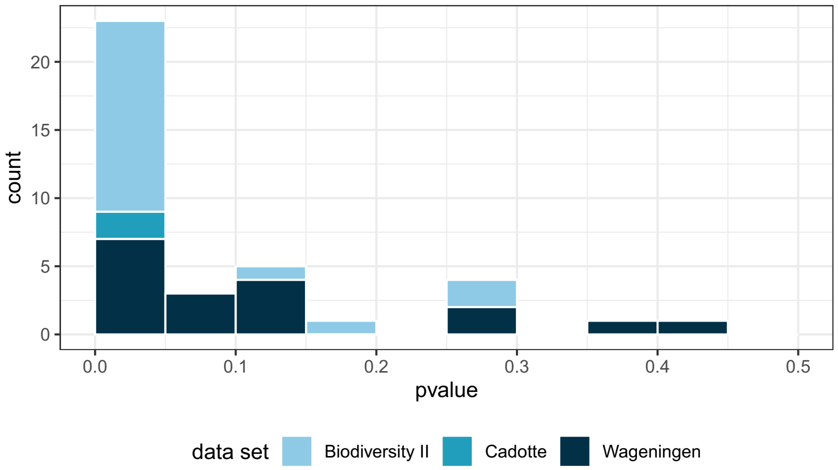

FIGURE 3 Distribution of p-values for all data sets. Pooled p-values obtained by testing for phylogenetic effects using two randomizations, and 19 data sets (38 p-values in total). We count the p-values falling in each bin of size 5% to build the histogram; colours indicate which of the three experiments each p-value corresponds to. The distribution of p-values is greatly enriched in low values, as expected when the null hypothesis of no phylogenetic effects (no difference between the true and random trees) can be rejected.

within each species (branch lengths associated with the tips of the tree). Next, we fit a large number of models using different random trees to structure interactions. We consider two ways to build random trees: generated via the Yule model (teal in Figure 2b) or randomized by shuffling species' identities but maintaining the true tree topology (grey in Figure 2b). Both approaches keep the number of free parameters fixed, and the second approach retains additional structure, such as the asymmetry of the tree. We generate 1000 distinct random trees for each type of randomization, and maximize the likelihood for each tree by fitting the tunable parameters (branch lengths) that control competition. From this ensemble of randomizations we compute a p-value, quantifying the fraction of random trees that yield a better likelihood than the true phylogeny. Intuitively, $1-p$ is the probability that using the true phylogenetic relationships for the community will improve the model fit.

Figure 2 shows that only a few a random trees perform better than the true tree (dashed black line) for each data set. All p-values are significant at the 0.05 level for both the shuffled and Yule trees, indicating strong support for phylogenetic effects in the data. When considering all data sets [i.e. additional years for the species-rich Biodiversity II experiments by Tilman et al. (2001) and for the Wageningen biodiversity experiment by van Ruijven and Berendse (2010) with a larger number of observations], we find substantial evidence for phylogenetic structure. In Figure 3, we summarize these results by plotting the distribution of p-values. This distribution is greatly enriched in low values. Out of a total of 38 tests (19 data sets and two randomizations), we find that 23 p-values are ≤ 0.05, while we would expect less than 2 by chance alone. Another 3 are below 0.1, and the remaining 12 are between 0.1 and 0.5 (we would expect more than 34 to be greater than 0.1 by chance). This pattern is evident across the three experimental settings. If we reduce the number of tests by pooling the results of the two randomizations (as the likelihood distributions for the two randomizations are very similar), we find 11 p-values ≤ 0.05 out of 19 tests (one test for each data set). All of the significant p-values remain below this threshold when they are adjusted according to the Bonferroni or Hommel corrections. We conclude that these data bear a strong signature of phylogenetic structure.

We can learn more about this structure by exploiting the fact that each ensemble of randomized trees contains topologies of varying similarity to the true phylogeny. When we quantify this similarity by measuring the distance between each random tree and the true tree (using a generalized Robinson-Foulds metric [Smith, 2020]), we find that for most of our data sets, there is a significant negative correlation between this distance and the model likelihood (33 negative correlations and 5 indistinguishable from zero; see Figure 6 in the Supplementary Material). In other words, trees that are more similar to the true phylogeny allow a better fit to the empirical data on average. Overall, the correlation between distance and likelihood is most negative for data sets where we also find a small p-value. However, we find weak but significant correlations even for several data sets where $p > 0.05$, indicating that some structural features of the phylogeny may be informative in those cases, too.

Our methodology makes it possible to probe even further and identify which specific features of the phylogeny contribute most to capturing the patterns in the empirical data. In our model formulation, each branch of the tree is associated with an increase in the strength of competition between the species in the corresponding clade. When species belonging to a certain clade do not experience increased competition with one another, relative to their interactions with species outside the clade, the maximum likelihood estimate of the corresponding branch length parameter will be small. If the interactions had no structure, or structure not corresponding to the input tree topology, all internal branches would shrink to near zero, as in the star tree, where only the branches associated with the root (encoding 'mean-field' interspecific competition) and the tips (intraspecific competition) have positive lengths. Thus, branches with positive values correspond to clades that help explain the structure of the data. Figure 4 represents this feature visually by plotting the inferred branch length parameters on the tree: branches that do not strongly affect the pattern of interaction strengths are short, while those that help explain the data are long.

For the data from Cadotte (2013), likelihood maximization singles out the clade of grasses (Poaceae, clade *b* in the phylogeny in Figure 4) and separates the only legume (*Desmodium canadense*) from the rest of the species (clade *a* in the figure). Likewise, the fit to the Wageningen data (van Ruijven & Berendse, 2010) (year 2003) highlights the key role of competition between the grasses (Poaceae, clade *a* in Figure 4) in this community, as well as between the two asters (Asteraceae, clade *b*). We confirm this visual interpretation by stratifying the random trees according to the presence of these highlighted clades and comparing likelihoods. For the data from Cadotte (2013), trees that group the grasses (clade *a*) perform slightly better than other random trees, those that retain clade *b* perform much better, and those retaining both *a* and *b* (as in the true tree) perform best of all. In fact, this last set of trees has likelihoods as higher or higher than the true tree (dashed line), indicating that these two partitions are the salient components of the phylogenetic structure for explaining the data. Similar results are found for the Wageningen experiment: trees clustering the grasses or asters perform better than those that do not, and trees retaining both clades yield a much higher likelihood. For more speciose trees, we also find evidence that a few clades contribute strongly to the quality of fit, although in this case sampling enough random trees to find all combinations of key clades would require a prohibitive number of randomizations. In the Biodiversity II experiment (year 2012), the model fit supports increased competition between the legumes (clade *a*), and all random trees clustering the legumes together yield high likelihood; the grasses

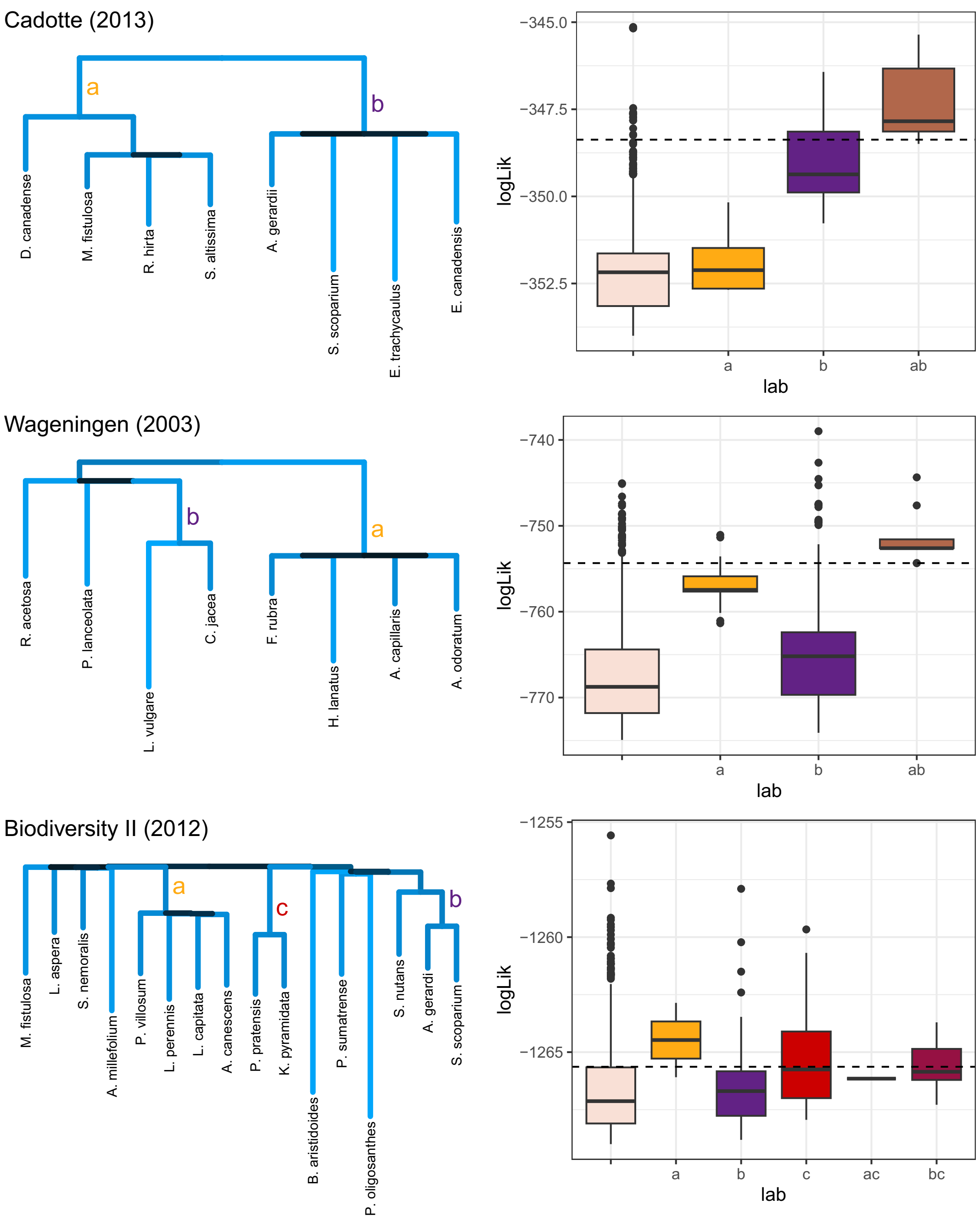

FIGURE 4 Best-fitting branch lengths and likelihood of trees retaining clade structure. Maximum likelihood trees for three selected data sets are shown on the left. The length and colour of the branches correspond to the strength of competition between the species subtended by the branch. Some branch lengths are close to zero, indicating that the species in these clades do not experience elevated competition with one another. In the data from Cadotte (2013), for example, the model does not support an increase in the strength of competition between *Rudbeckia hirta* and *Solidago altissima*, compared to their interactions with *Monarda fistulosa*, despite the additional evolutionary history shared by these two species. As a result, this clade collapses into a polytomy with three species. Clades highlighted by letters correspond to fitted branch lengths that are longer than the mean fitted branch lengths for that tree. Box-plots show the distribution of log-likelihoods for randomizations that retain these highlighted clades (indicated by letters; boxes without labels show randomizations where no labelled clades were retained). The dashed line indicates the log-likelihood of the original tree. Species genus are collapsed for visualization, see Supplementary Material for a list of full species' names.

are split into several distinct clades, with strong support for increased competition between two C4 grasses (clade *b*), and two C3 grasses (clade *c*). Again, randomized trees conserving these clades perform better on average than those that do not.

DISCUSSION

One of the oldest and most intuitively appealing hypotheses in ecology is that evolutionary relatedness structures competitive interactions (Cavender-Bares et al., 2009; Mouquet et al., 2012; Webb et al., 2002). But testing this hypothesis directly is challenging, and support for it is mixed. In this study, we introduced a new approach to assessing whether competition increases with relatedness in experimental communities, leveraging the statistical framework of Maynard et al. (2020) to parse pairwise species' interactions in BEF data sets and relate them directly to phylogenetic relationships. By fitting species' interaction models where competition reflects evolutionary relatedness, and comparing likelihoods against an ensemble of models based on randomized tree topologies, we obtain a simple and direct test to determine whether phylogeny structures species' interactions, and thus patterns of coexistence and abundance. Analysing 19 plant community data sets from three different experimental settings, we found substantial and consistent support for phylogenetic structure in species' interactions.

Our approach builds on recent methods to infer interactions from community 'endpoints'— snapshots of community biomass or abundance at a single point in time, usually at the end of a growing season, and spanning a range of community compositions (Ansari et al., 2021; Fort, 2018; Maynard et al., 2020; Skwara et al., 2023; Xiao et al., 2017). These methods are able resolve pairwise interactions in a manner consistent with models of population dynamics: if we were to simulate communities using the fitted interaction strengths as parameters of the generalized Lotka–Volterra model, we would find the abundances predicted by our statistical model as equilibria of the dynamics (Maynard et al., 2020). This allows us to investigate phylogenetic structure at the level of individual species' interactions in large BEF data sets, using species-level biomass measurements, whereas previous analyses of these data have focused only on relationships between total biomass and phylogenetic summary statistics (Cadotte, 2013; Connolly et al., 2011; Huang et al., 2020; Tilman et al., 2001).

Testing for phylogenetic structure at this more granular level is crucial, not only because it enables us to extract more information—and more statistical power—from these data sets, but because the competition-relatedness hypothesis fundamentally operates at this level. We are able to test the specific hypothesis that competition increases with relatedness by building this hypothesis into our species' interaction models, which then provide a coherent way to obtain predictions (biomass patterns) that can be compared against empirical data. To translate between a tree topology and a matrix of interaction strengths, we used a principled model that can be derived from consumer-resource dynamics (Supplementary Material) or random trait evolution (Serván et al., 2023). Ultimately, this model simply formalizes the intuition already clear to Darwin: pairs of species with more shared ancestry compete more strongly.

Our analysis differs perhaps most significantly from previous studies in that we otherwise make no assumption about precisely how competition increases with shared ancestry. Instead, we fit a free parameter associated to each branch of the phylogeny, allowing the implied relationship between molecular divergence and interaction strength to differ along each branch. This enables us to identify phylogenetic effects even if the underlying processes of trait evolution are variable across time, lineages or genes (Ackerly, 2009; Hansen & Martins, 1996; Louw et al., 2024; Nuismer & Harmon, 2015; Tucker et al., 2018). This flexibility is critical; in the Supplementary Material, we show that parameterizing species' interaction models directly based on phylogenetic (molecular) branch lengths from the empirical trees produces very poor biomass predictions. We also compared the branch length parameters that were fitted to the data against the corresponding molecular branch lengths from the empirical tree and found little agreement between them (Supplementary Material).

Phylogenetic signal in functional traits can cause closely related species to compete more strongly due to smaller niche differences between them, as hypothesized by Darwin, but can potentially also reduce fitness differences between closely related species, owing to similar competitive abilities (Mayfield & Levine, 2010). Mayfield and Levine (2010) noted that if the latter pattern dominates, then strong competitive effects, such as competitive exclusion, might actually be more likely between distantly related species (having large fitness differences) than between closely related ones. In contrast with this possibility, our results suggest that competition does increase with relatedness in the plant communities we study, but idiosyncratically.

These results suggest it may be possible to make qualitative predictions about species' interactions from phylogenetic data, but not quantitative predictions. However, by learning effective branch lengths from ecological data, rather than predicting them from molecular data, our framework opens new possibilities for studying the empirical connection between evolutionary history and interaction strengths. For example, we found that inferred branch lengths were much more heterogeneous than those in the molecular phylogenies, with many internal branch length parameters near zero and a few much larger. This pattern is potentially consistent with abrupt shifts or bursts of trait evolution in a few ecologically relevant traits, rather than gradual evolution of a large number of traits (Cadotte et al., 2017). Further exploration of these patterns could shed new light on functional trait evolution from the perspective of species' interactions (Weber et al., 2017).

We were also able to identify branches in the phylogeny that are most important for accurately modelling species' interactions. These branches correspond to clades of species that experience elevated competition, and potentially to evolutionary events that strongly shaped species' interactions. While our observations regarding particular clades are highly tentative, based only on a few selected species in each clade, this type of analysis may provide a new tool to identify functional traits or corresponding functional groups with high potential for predicting and understanding species' interactions. This aspect of our analysis complements previous efforts to use network tools to identify important phylogenetic branches in experimental communities (Davies et al., 2016). Analysing the Biodiversity II data, as we did here, Davies et al. (2016) used this approach to detect an important effect of legumes on community function (total biomass). In agreement with their conclusions, we also found a key role for legumes in structuring these experimental communities (clade *a* in Biodiversity II, Figure 4).

Important considerations, both practical and theoretical, apply to our methodology. Practically, this approach is computationally very intensive, due to the challenge of searching for parameters over a rough likelihood surface for a large number of randomized models. More fundamentally, our framework requires the observation of a large number of distinct community compositions across a constant environmental background (Maynard et al., 2020; Skwara et al., 2023). This likely limits the application of our methodology to experimental communities, where composition can be manipulated, and even then only to experimental designs where the number of distinct community compositions is sufficiently large relative to the number of species. If this ratio becomes too small, there is a risk of model over-fitting, which may reduce our ability to detect phylogenetic structure and preclude interpretation of the fitted parameters. Due to these constraints, our model framework likely has limited applicability to observational data from natural systems. However, despite this limitation, our approach provides a powerful proof of concept for the assumptions underlying community assembly theory, such as relating the amount of shared evolutionary history between species to their resource requirements and hence degree of competition. Also, previous results from BEF experiments have proven to be consistent with patterns found in agriculture and prairie grasslands (Jochum et al., 2020) demonstrating that inferences from these experimental systems can be relevant for natural communities.

We found that many branch length parameters shrink to zero through likelihood maximization. This pattern indicates that even coarser models of community structure, with fewer free parameters, may provide a good approximation of species' interactions. The use of simpler models could reduce the data requirements needed for this approach, potentially expanding its applicability. To find sparser models, it might be possible to search over simplified tree topologies, where some branches are deleted from the tree, reducing the number of free parameters in the model. Beyond serving as a convenient model simplification this procedure could even be used to identify ecologically informed and phylogenetically consistent groupings of species. In fact, our approach could be used to test for other kinds of structure in species' interactions, even beyond phylogeny. In the models used here, phylogenetic topology is encoded in a binary matrix V (Supplementary Material), in which rows correspond to ancestral species, columns to extant species and $V_{ij} = 1$ whenever the row is an ancestor of the column (and zero otherwise). The same computational pipeline could be used to test for any other structure that can be encoded in a similar way, such as 'groups' of species with or without nested or overlapping membership. Such groups could be, for instance, functional groups hypothesized to influence community structure and species' interactions. While it would be computationally challenging at present, one could in principle even search for a maximum likelihood topology that best explains the data, effectively 'reverse-engineering' the traits or groups that structure interactions. Importantly, regardless of the structure of interest, the same randomization scheme can be used to compute a p-value that quantifies the value of using the chosen structure to constrain interactions, as compared to models that are equally complex, but biologically 'uninformed'.

Finally, we note that we have investigated a specific type of phylogenetic structure, manifest in strictly competitive interactions. In this case, the competition-relatedness hypothesis provides a clear conceptual model for how phylogeny is expected to shape interactions (Cahill Jr et al., 2008). However, this focus on competition is likely too limited, even for species at the same trophic level, such as the plant communities studied here. Facilitative interactions are present and possibly important in these communities (Wright et al., 2017), and other effects may be mediated by species at un-modelled trophic levels, such as herbivores or soil microbes (Frainer et al., 2018). There is evidence that phylogeny has explanatory power beyond the competition-relatedness hypothesis, for instance predicting interaction partners across different clades (Burin et al., 2024; Gómez et al., 2010; Nuismer & Harmon, 2015). Our general framework—fitting interaction models constrained by phylogenetic topology, and comparing fits across randomizations – may be extendable to consider other types of interactions. For example, characterizations of interspecific interactions between perennial crop plants showed a wide range of possible interactions beyond symmetric competition, including facilitative and neutral interactions (Halty et al., 2017). These interactions could be included straightforwardly in our models by allowing branch length parameters (λ_ℓ) to take any sign. However, in the absence of a clear expectation for how the strength of facilitation should be related to shared evolutionary history, we chose to exclude this possibility. In general, our methodology provides a platform that might be used to investigate other hypotheses about how evolutionary history translates into ecological interactions—positive or negative—whenever they can be formulated as a set of constraints on species' interactions.

AUTHOR CONTRIBUTIONS

PL-C and ZRM share first authorship. *Conceptualization*: SA. *Methodology*: PL-C, ZRM and SA. *Investigation*: PL-C, ZRM and SA. *Visualization*: PLC, ZRM and SA. *Funding acquisition*: SA. *Supervision*: SA. *Writing—original draft*: PL-C and SA. *Writing—review and editing*: PL-C, ZRM and SA.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The code, raw and organized data, and results are available at github.com/paulinhalemos/lemos-costa_2024 as well as in the curated repository https://figshare.com/articles/software/lemos-costa_2024/26084626.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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