

IS PHYLOGENETIC AND FUNCTIONAL TRAIT DIVERSITY A DRIVER OR CONSEQUENCE OF GRASSLAND COMMUNITY ASSEMBLY?

Do traits and phylogeny support congruent community diversity patterns and assembly inferences?

Marc W. Cadotte^{1,2}  | Marta Carboni¹ | Xingfeng Si^{1,3}  | Shinichi Tatsumi^{1,4} ¹Department of Biological Sciences, University of Toronto-Scarborough, Toronto, ON, Canada²Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada³Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China⁴Hokkaido Research Center, Forestry and Forest Products Research Institute, Sapporo, Japan

Correspondence

Marc W. Cadotte
Email: mcadotte@utsc.utoronto.ca

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Abstract

1. It is now commonplace in community ecology to assess patterns of phylogenetic or functional diversity in order to inform our understanding of the assembly mechanisms that structure communities. While both phylogenetic and functional approaches have been used in conceptually similar ways, it is not clear if they both in fact reveal similar community diversity patterns or support similar inferences. We review studies that use both measures to determine the degree to which they support congruent patterns and inferences about communities.
2. We performed a literature review with 188 analyses from 79 published papers that compared some facet of phylogenetic (PD) and functional diversity (FD) in community ecology. These studies generally report four main cases in which phylogenetic and functional information are used together in community analyses, to determine if: (a) there were phylogenetic signals in the measured traits in communities; (b) PD and FD were correlated with one another; (c) standardized PD and FD measures similarly revealed patterns of community over- or under-dispersion; and (d) PD and FD were both related to other explanatory variables (e.g. elevation) similarly.
3. We found that the vast majority of studies found both strong phylogenetic signals in their traits and positive correlations of PD and FD measures across sites. However, and surprisingly, we found substantial incongruencies for the other tests. Phylogenetic and functional dispersion patterns were congruent only about half the time. Specifically, when communities were phylogenetically over-dispersed, these same communities were more likely to be functionally under-dispersed. Similarly, we found that phylogenetic and functional relationships with independent predictors were incongruent in about half of the analyses.
4. *Synthesis.* Phylogenetic signal tests and PD–FD correlations appear to strongly support the congruence between traits and phylogeny. It is surprising that strong phylogenetic signals appeared so ubiquitous given that ecological studies often analyse phylogenetically incomplete sets of species that have undergone ecological sorting. Despite the largely congruent findings based on phylogenetic signal tests and PD–FD correlations, we found substantial incongruencies when researchers assessed either dispersion patterns or relationships with independent predictors. We discuss a number of potential ecological, evolutionary and

methodological reasons for these incongruencies. Phylogenetic and functional information might reflect species ecological differences unequally with phylogenies better reflecting multivariate conserved elements of ecological similarity, and single traits better able to capture recent divergence, and both elements influence ecological patterns.

KEYWORDS

biodiversity, community assembly, evolutionary history, functional traits, meta-analysis, phylogenetic community ecology

1 | INTRODUCTION

Over the past two decades, community ecology has gone through a fundamental shift in how community diversity is measured and how diversity is aligned with ecological theories and the mechanisms believed to control community assembly. Both phylogenetic and functional (or trait-based) information provides quantitative estimates of species' dissimilarity that can reflect ecological selection of species based on biotic and abiotic influences on population growth and performance (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Laughlin, 2014; McGill, Enquist, Weiher, & Westoby, 2006; Webb, Ackerly, McPeck, & Donoghue, 2002). For example, phenotypically similar species (or species with a recent common evolutionary history) will likely share similar environmental constraints and strategies for the use of resources, but will also inevitably compete more strongly for those same resources (Kraft, Godoy, & Levine, 2015; Laughlin, 2014). Therefore, diversity is now routinely quantified using a plethora of phylogenetic and functional diversity measures that rely on the dissimilarity among or summation of distances across co-occurring species within a community (Pavoine, Bonsall, Dupaix, Jacob, & Ricotta, 2017; Tucker et al., 2017).

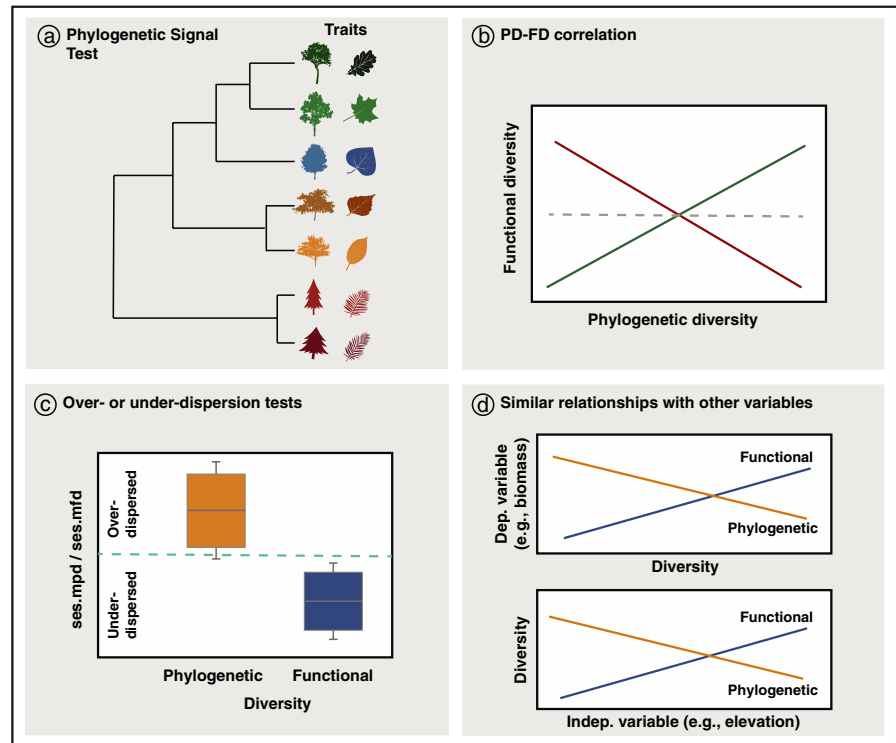
While measures of phylogenetic (PD) and functional diversity (FD) have provided important insights into community assembly (Helmus et al., 2010; Kraft & Ackerly, 2010), each approach comes with important assumptions and limitations that impact their usefulness and interpretability (Cadotte, Albert, & Walker, 2013; Funk et al., 2017; Gerhold et al., 2015). Phylogenies are often built from neutral genetic sequences that do not capture selection-driven change and there is therefore no direct mechanistic link between phylogenetic distances and ecological processes. Phylogenetic patterns could then be misleading without mechanistic evidence, and therefore traits might lead to alternative interpretations compared to inferences derived from phylogenetic patterns (Gerhold et al., 2015; Mayfield & Levine, 2010). It is difficult to infer competitive processes from either phylogenetic distances or functional traits because competition and coexistence are two processes that are complex and depend on the number of resource axes species compete for and the number of traits that separately influence species reproductive responses to environmental gradients and niche differences (Kraft et al., 2015). Using only a few traits to calculate trait dissimilarity

might provide misleading information about competitive outcomes because of the hierarchical nature of competition, especially if competitive interactions are intransitive (Gallien, 2017). Further complicating things is the fact that multiple traits might influence the same processes or multiple processes might be influenced by the same trait(s) (Münkemüller, et al., 2012a). Finally, there are numerous under-appreciated methodological issues that need to be considered when using traits (Cadotte et al., 2013; Funk et al., 2017; Poff et al., 2006), including how to select relevant traits, how those traits relate, statistically or mechanistically, to ecosystem level patterns and processes, how to incorporate intraspecific variation and how or whether to combine multiple traits into composite measures, all of which will influence ecological interpretations.

Specifically, researchers often want to know if phylogenetic information, which is easier to obtain and compute, serves as a reliable proxy for functional diversity (e.g. de Bello et al., 2017; Cadotte et al., 2013; Kraft & Ackerly, 2010; Parrent et al., 2010; Pavoine, Gasc, Bonsall, & Mason, 2013; Prinzing, 2016). Kraft and Ackerly (2010) provide one of the first explicit attempts to assess insights from phylogenetic and functional diversity measures on inferences of community assembly. They found congruent dispersion patterns in their tropical forest plots but showed that their functional traits provided additional information about the even spacing of species in trait space, which their phylogenetic measures could not detect. There are reasons to be skeptical that phylogenetic diversity should normally serve as a proxy for functional diversity because methodological, evolutionary and ecological processes can bias this relationship (Cadotte, Davies, & Peres-Neto, 2017; Gerhold et al., 2015; Prinzing, 2016). The size of plot used, number of species included and number of traits measured might also influence the relationship between phylogenetic and functional diversity (Cadotte, Davies, et al., 2017; Tucker, Davies, Cadotte, & Pearse, 2018). Overall, there are four main ways in which researchers have incorporated phylogenetic and functional information together in community ecology analyses (Figure 1): (a) phylogenetic signal test, (b) PD-FD correlation, (c) dispersion tests, and (d) relationships with other variables.

First, to assess the ecological value of phylogenetic measures in community analyses, there have been several calls (e.g. Cavender-Bares et al., 2009; Parrent et al., 2010; Pavoine et al., 2013) to better understand whether ecologically relevant traits are conserved along

FIGURE 1 The four main ways in which researchers have incorporated phylogenetic and functional information together in community ecology analyses to determine whether: (a) there are phylogenetic signals by evaluating whether closely related taxa share more similar traits than expected by chance; (b) phylogenetic and functional diversity are correlated with one another across multiple sites; (c) communities show similar phylogenetic and functional dispersion patterns; and d) phylogenetic and functional diversity respond similarly to underlying environmental gradients (diversity as dependent variable) or similarly predict another variable like biomass production (diversity as independent variable). However, 'ses.mpd' and 'ses.mfd' indicate standardized effect size of mean pairwise distance and mean functional distance, respectively



the phylogeny or not, i.e. whether or not phylogenetic signals exist in the functional traits important for co-existence (Figure 1a). To do this, **phylogenetic signal is typically assessed by testing if closely related taxa share more similar traits than expected by chance** (Pagel, 1999). Nevertheless, there are several reasons to doubt the ubiquity of phylogenetic signals in community ecology datasets. First, spurious signals just might stem from methodological reasons (such as branch length estimation in phylogeny reconstruction) that impact the robustness of signal tests (Molina-Venegas & Rodríguez, 2017). Secondly, community datasets used in testing the phylogenetic signal, depending on sampling scale, contain relatively few species or only subsets of communities, and phylogenetic signal tests can be sensitive to the number of taxa (Blomberg, Garland, & Ives, 2003). Finally, signal tests are frequently performed on regional species pools which are subsets of the true phylogeny, often lacking sister taxa. These species pools are likely the result of ecological processes that non-randomly select species and so could be biased towards species that are functionally similar or dissimilar from one another depending on the dominant ecological processes selecting species, and we should expect then that phylogenetic signal tests are weaker than for full clades (Prinzing, 2016).

The second major question researchers often assess is whether phylogenetic and functional diversities are correlated with one another across multiple sites (Figure 1b). Mathematically, we should expect that phylogenetic and functional diversities are correlated (Pavoine et al., 2013), seemingly questioning the utility of this type of analysis. However, there are two reasons why researchers choose to examine correlations. First is that they might be examining phylogenetic and functional diversity metrics that differ in whether they

are correlated with species richness (Tucker et al., 2017) and differences in correlations could provide insights into the nature of how functional and phylogenetic diversities are distributed. Secondly, researchers could be concerned about the degree of correlation if they wish to include both forms of diversity into statistical models and are concerned about covariance among predictor variables. Finally, PD and FD metrics might be correlated beyond what would be expected from their common dependency on species richness, an issue which is typically addressed by calculating expected values (Rodrigues, Brooks, & Gaston, 2005) or through the use of null models to calculate metrics that capture dispersion patterns independent of species richness (Webb et al., 2002).

Then, the third important question that is commonly assessed with both sources of information is whether communities show similar phylogenetic and functional dispersion patterns (Figure 1c). Community dispersion tests compare observed phylogenetic or functional distances among species in a community to equally sized randomizations and calculate standardized effect sizes (Webb et al., 2002). The output of this type of analysis allows researchers to determine if assemblages contain more similar or dissimilar species than expected by chance, and specifically in our case, whether phylogeny and traits support the same conclusion (for example, Li et al., 2015).

The final comparison that is frequently made is to determine whether phylogenetic and functional diversities respond similarly to underlying environmental gradients (diversity as dependent variable) or similarly predict another variable like biomass production (diversity as independent variable) (Figure 1d). This research question, more than the first three, tries to answer fundamental questions

about what structures biodiversity and how biodiversity matters for other processes. When researchers compare phylogeny and traits, they are essentially asking how biodiversity, however it is measured, reflects the outcome of ecological structuring mechanisms.

In order to assess if phylogeny and traits provide congruent inferences to these four research questions, we compiled published empirical studies that used both sources of information to examine community ecology patterns focusing on within-community diversity (alpha diversity). If traits and phylogeny patterns similarly reflect common descent and underlying ecological processes, then we expect that all four tests should indicate congruence. Beyond assessing whether or not the measures provided congruent inferences, we also assessed whether methodological decisions or constraints, such as plot size, number of taxa, etc., influenced this congruency.

2 | MATERIALS AND METHODS

To assess patterns of usage for phylogenetic and functional approaches in community ecology, and to identify studies for inclusion in our analyses, we performed three searches using the Web of Science article database (Clarivate Analytics). For all searches, we set dates of articles as those published between 2000 and 2017 and we performed all searches on June 15th, 2018. The three searches were as follows: (a) '(functional diversity) and (community assembly)', which returned 1,057 publications; (b) 'phylogen*' and (community assembly)', which returned 1,059 publications; and (c) 'phylogen*' and (community assembly) and (functional diversity)', which returned 341 publications.

We downloaded all references from the three searches above. We then excluded studies that: (a) were not primary research papers (e.g. reviews and commentaries); (b) did not examine within-community (i.e. alpha) diversity patterns (e.g. turnover studies); (c) did not measure and report findings/analyses of both phylogenetic and functional diversity; and 4) were not based on field or experiment data (e.g. simulations). This left us with 79 papers that examined some element of analyses that included both phylogenetic and trait information (list available in the Supplemental Material). During this elimination process, we observed that virtually all microbial studies were excluded because analyses compared taxonomic and phylogenetic diversity, and only measured functional consequences as dependent variable, enzymatic activity, for example (Shafquat, Joice, Simmons, & Huttenhower, 2014).

From the papers that fit our criteria for inclusion, we not only collected information on phylogenetic and functional diversity, but also study variables including: geographic location, major taxonomic grouping (e.g. birds, plants), habitat type (e.g. wetlands, forests), number of plots or sampling units assessed (median = 717, range = 1 to 51,051), plot size (median = 200 m², range = 0.006 m² to global), number of species (or OTUs) included (median = 146, range = 13 to 4,536), number of traits used (median = 7, range = 1 to 29) and type of phylogenetic tree (e.g. supertree, $n = 67$; molecular tree, $n = 56$; Phylomatic, $n = 29$).

To test the phylogenetic and functional congruency for the four research questions shown in Figure 1, we either recorded values or indicated yes/no or significant/non-significant results. For the assessment of phylogenetic signal, we recorded Blomberg's K (Blomberg et al., 2003), Pagel's λ (Pagel, 1999) and Fritz and Purvis' D for binary traits (Fritz & Purvis, 2010), all of which are commonly employed measures of phylogenetic signal. However, we only show results for the first two measures since there were too few studies reporting D values within the context of community ecology analyses. For the second research question, we recorded the correlation coefficient between phylogenetic and functional diversity measures and whether the correlation was significant/non-significant, and if significant, the direction of the relationship (i.e. positive or negative). We labelled some results as 'mixed' if multiple phylogenetic and functional diversity measures were employed and correlated with varying results. For the third research question on congruent dispersion, we recorded whether or not phylogenetic and functional dispersion patterns were the same (e.g. both significantly over-dispersed). Further, for each dispersion measure, we recorded if it was significantly over-dispersed, significantly under-dispersed, or no different than random (i.e. non-significant). If the study did not report significance, we used standardized effect size values (Z -value) of greater than 2.0 or less than -2.0 as indicating significantly over-dispersed or under-dispersed, respectively. For the final question about similar relationships with other variables, we recorded whether or not phylogenetic and functional diversity showed a similar relationship with a predictor (e.g. both significantly positively related to predictor) or the response variable. We further recorded if the individual relationships were significantly positive, negative or non-significant.

All analyses and graphing were carried out using the R programming language version 3.5.0 (R Core Team, 2018).

3 | RESULTS

Our literature searches revealed that the number of studies employing either functional or phylogenetic diversity has been increasing exponentially over time and that the number of studies has been remarkably similar with these two approaches (Figure 2). Yet there seems to be a divergence in the number of studies using these two approaches since 2015 (Figure 2). The number of studies using both phylogenetic and functional approaches has also increased over time, though not as dramatically as for the individual approaches.

We collated the results from 188 unique PD–FD comparisons from 79 papers. The majority of these comparisons were done with plants (51.6%) and from forest ecosystems (51.1%) (Figure S1). These studies were from systems around the world with a global distribution (Figure S2). The comparisons of PD and FD included a diverse array of metrics, from distinct metric families (*sensu*: Mouchet, Villéger, Mason, & Mouillot, 2010; Tucker et al., 2017). These comparisons included richness-based metrics (PD, FD, functional

richness), distance-based pairwise measures (e.g. mean pairwise distance, MPD; mean nearest taxon distance, MNTD; mean functional distance, MFD; mean nearest functional distance, MNFD) and ones that were calculations of standardized effect sizes based on randomization tests (e.g. ses.MPD; net relatedness index, NRI;

trait relatedness index, TRI) (Figure S3). The standardized measures were the most frequently employed (Figure S3) and we note that these metrics are in some cases not independent of one another (e.g. NRI and SES.MPD), but we report what studies chose to analyse. Reassuringly very few studies compared divergent measures from different metric families (e.g. MPD with FD).

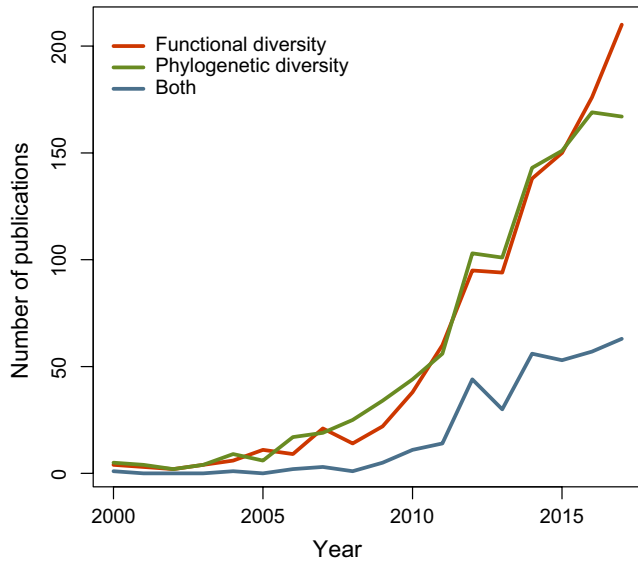


FIGURE 2 The increase in the number of community ecology publications that employ either functional diversity (red line), phylogenetic diversity (green) or both (blue) over time

3.1 | Phylogenetic signal tests

While we did record the results of phylogenetic signal assessments using a variety of tests, Blomberg's K and Pagel's λ were by far the most commonly used and what we report here. The overwhelming majority of phylogenetic signal tests (75.6%) find a significant phylogenetic signal (Figure 3a). Blomberg's K values, while being frequently significantly different than null expectations based on randomizations, tended towards very small values (Figure 3c), thus exhibiting phylogenetic signals that are substantially weaker than Brownian motion expectations (i.e. for a trait evolving along the phylogeny by sampling from a normal distribution). Conversely, and unexpectedly, Pagel's λ values tended to be at or near values expected by Brownian motion (Figure 3d). Evaluation of study variables (plot size, number of species, number of traits evaluated, number of plots, taxa grouping and habitat) showed that studies including a greater number of traits and a greater number of species tend to find lower Blomberg's K values on average (traits: $\beta_1 = -0.021$, $p < .001$, $R^2 = .085$; species number: $\beta_1 = -2.32 \times 10^{-4}$,

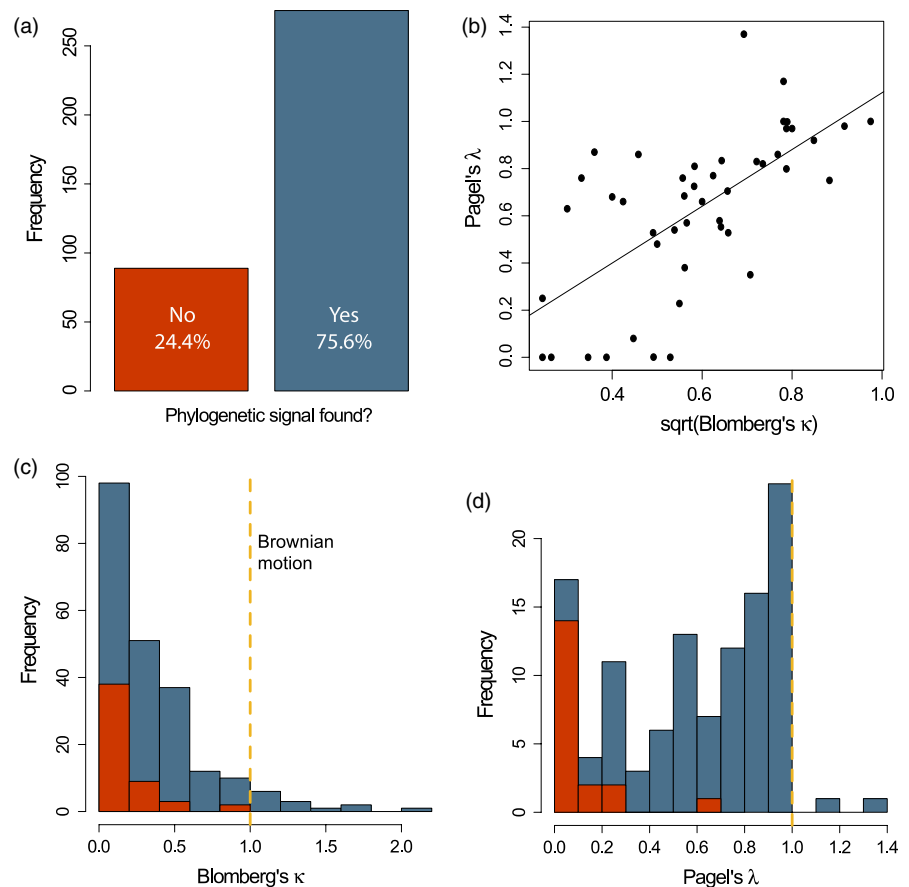


FIGURE 3 Summary of the phylogenetic signal tests in the ecological literature. (a) The vast majority of analyses find a statistically significant phylogenetic signal and (b) the two most commonly employed measures (Blomberg's K and Pagel's λ) are strongly correlated. However, these two measures show different patterns with (c) Blomberg's K being skewed towards weak signal ($K \approx 0$) and (d) Pagel's λ skewed towards signal values predicted by Brownian motion evolution ($\lambda = 1$). Red bars indicate phylogenetic signal values that were not significant

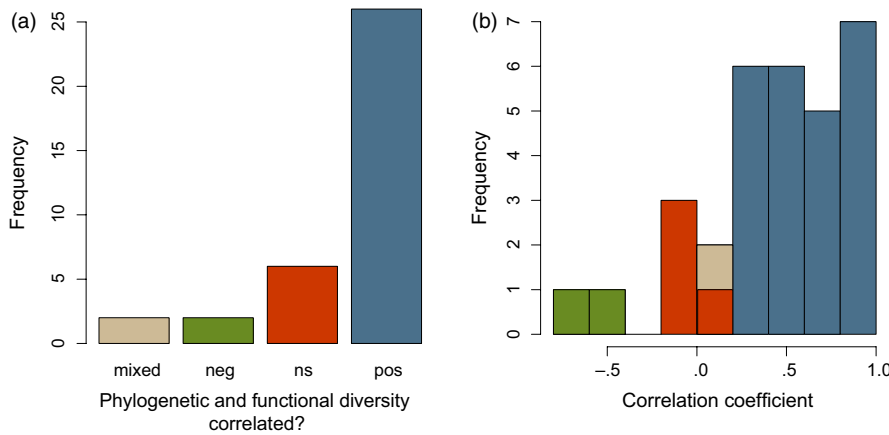


FIGURE 4 Summary of PD-FD correlation tests with (a) the majority of tests showing a positive and statistically significant correlation and (b) with relatively high correlation coefficients

$p = .012$, $R^2 = .023$; Figure S4). Further, Blomberg's K values significantly differed among the taxa and habitat type studied (taxa: $F_{3,221} = 17.08$, $p < .001$, $R^2 = .182$; habitat: $F_{3,217} = 5.106$, $p < .001$, $R^2 = .100$), and Blomberg's K values were lower for plants compared to other taxa and in urban and grassland habitats (Figure S4). The only study variables that significantly influenced Pagel's λ values were the taxa and habitat type studied (taxa: $F_{3,111} = 8.787$, $p < .001$, $R^2 = .170$; habitat: $F_{3,111} = 4.108$, $p = .008$, $R^2 = .076$), with Pagel's λ values lower within plants and fungi and in grassland habitats (Figure S5). Despite some of these important differences between Blomberg's K and Pagel's λ values, and the fact that Pagel's λ is reported only about half as frequently as Blomberg's K (115 vs. 225), these two measures were strongly correlated ($r = .639$, $p < .001$), with the best model using a square root transformation of Blomberg's K (Figure 3b).

3.2 | PD-FD correlation

Despite the fact that many studies articulated an interest in comparing phylogenetic and functional diversity, relatively few studies explicitly reported whether the phylogenetic and functional measures they used were correlated ($n = 36$ studies). The studies that did test for a correlation between the two measures overwhelmingly found that these measures were, unsurprisingly, correlated (Figure 4a). Reported correlation coefficients were positive and tended to high values ($r = .4$ to 1.0 , Figure 4b).

3.3 | Same dispersion patterns

A total of 99 comparisons evaluated the dispersion of both phylogenetic and functional diversity measures. Interestingly, phylogenetic and functional diversity showed similar dispersion patterns only about half of the time (Figure 5a). Both strong and weak incongruencies (opposing patterns vs. one measure being non-significant) underpin this incongruent result. When communities were observed to be phylogenetically over-dispersed, these same communities were more likely to be functionally under-dispersed, and the proportions of cases in the different FD dispersion classes were no different than random ($\chi^2_{df} = 3.0$, $p = .223$, Figure 5b). Conversely,

when communities were phylogenetically under-dispersed then they were also likely to be functionally under-dispersed ($\chi^2_{df} = 22.962$, $p < .001$, Figure 5c). Communities that were significantly functionally over or under-dispersed were largely congruent with phylogenetic dispersion, being more likely to be phylogenetically over or under-dispersed, respectively ($\chi^2_{df} = 9.6$, $p = .008$, $\chi^2_{df} = 6.0$, $p = .049$, respectively, Figure 5d,e).

It did not appear as though experimental design decisions influenced the probability that phylogenetic and functional diversity exhibited the same dispersion patterns. Using a logistic regression, none of number of samples, plot size, number of taxa recorded, or number of traits measured, significantly influenced the probability that phylogenetic and functional dispersion show congruent patterns or not ($p > .05$ for all).

3.4 | Same response to independent variable

Very few studies evaluated the effect of both phylogenetic and functional diversity on a dependent variable (e.g. biomass production) and so we do not evaluate congruent/incongruent patterns for phylogenetic and functional diversity as the independent variables. However, 108 comparisons did evaluate how both phylogenetic and functional diversity respond to independent variables. These studies evaluated a large variety of potential factors that might influence phylogenetic and functional diversity, but most commonly assessed was elevation (20%), followed by land use (7%), forest age (6%) and time (6%).

Similar to the assessment of dispersion congruency, it appears as though phylogenetic and functional diversity are similarly explained by an independent variable about half of the time (Figure 6a). However, unlike with dispersion, when either phylogenetic or functional diversity had a significant linear relationship with a predictor, the source of incongruency was not likely to be a strong opposing significant relationship with the independent variable for the other diversity measure. When phylogenetic diversity was positively associated with a predictor, then so was functional diversity ($\chi^2_{df} = 36.0$, $p < .001$, Figure 4b) and negative phylogenetic diversity correlations with a predictor were similarly associated with negative functional diversity associations with that predictor ($\chi^2_{df} = 7.125$, $p = .028$,

FIGURE 5 Summary of publications presenting phylogenetic and functional over-dispersion tests. (a) phylogenetic and functional over-dispersion are congruent only in about half of the comparisons. Most of the incongruence appears to be driven by (b) phylogenetically over-dispersed assemblages that also exhibit functional under-dispersion, while the other comparisons (c–e) are largely congruent

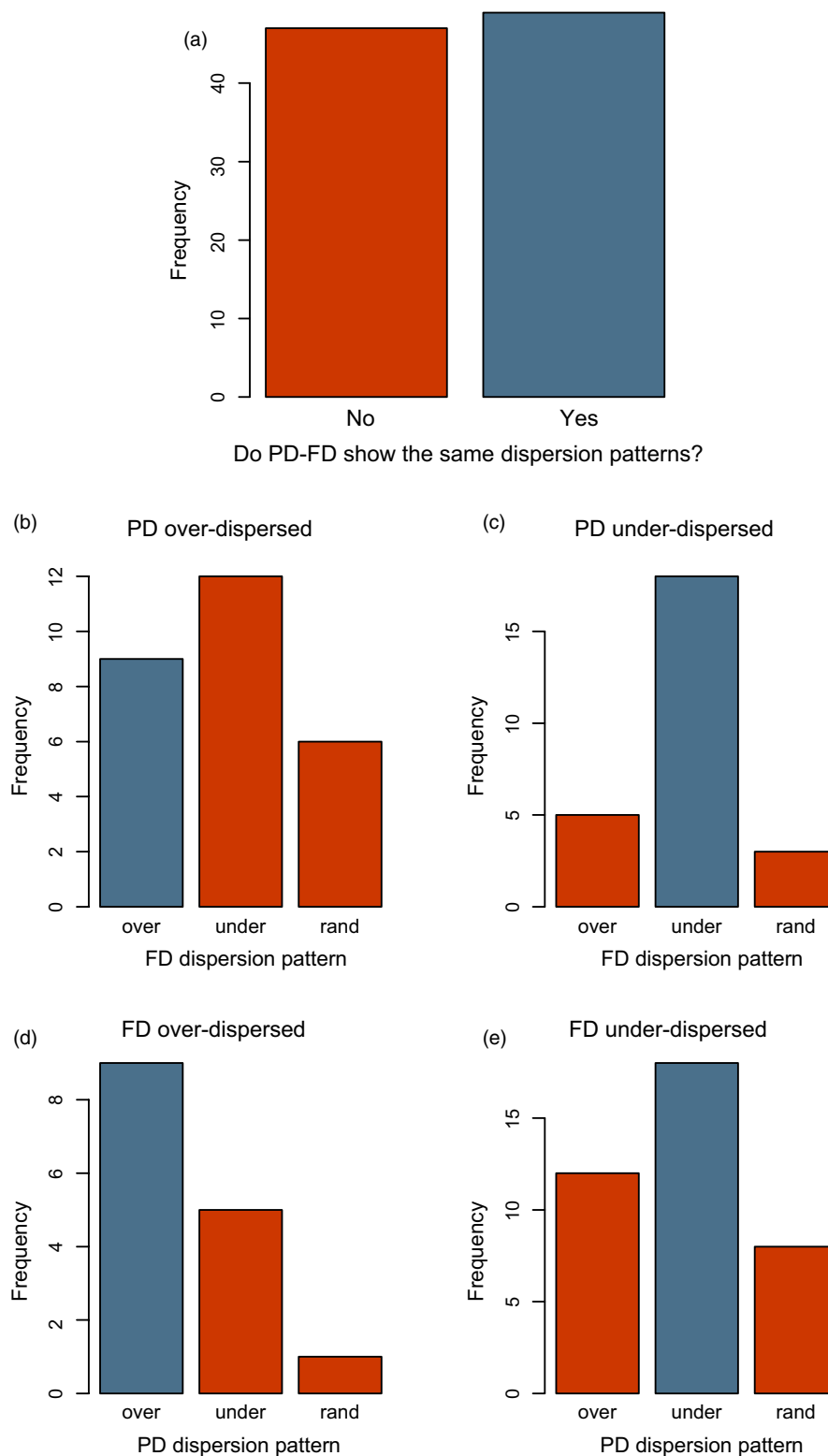


Figure 4c). Communities that were functionally positively or negatively correlated with a predictor variable were largely congruent with phylogenetic measures, being more likely to be phylogenetically positively or negatively correlated with the same predictor, respectively ($\chi^2_{df} = 46.295$, $p < .001$, $\chi^2_{df} = 7.32$, $p = .026$, respectively, Figure 6d,e).

It did not appear as though experimental design decisions influence the probability that FD and PD respond similarly to an independent predictor. Using a logistic regression, none of number of samples, plot size, number of taxa recorded, or number of traits measured significantly ($p > .05$ for all) influenced the probability that PD and FD show congruent patterns with a predictor variable.

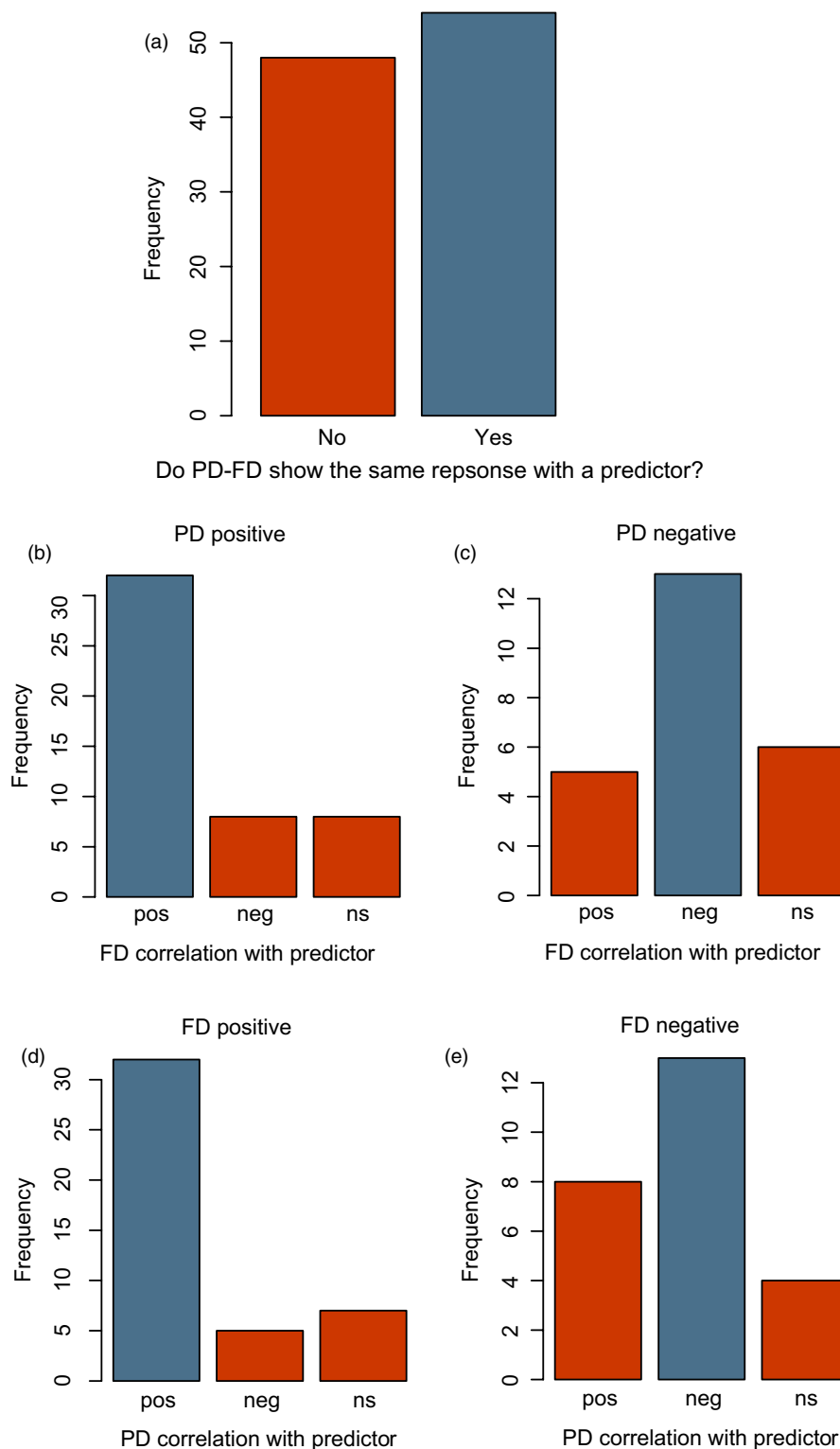


FIGURE 6 Summary of tests of phylogenetic and functional relationships with predictor variables. (a) phylogenetic and functional diversity show a congruent relationship with predictor variable only in about half of the comparisons. However, the direction of the relationships between phylogenetic and functional diversity and the predictor variable (b–e) are largely congruent

4 | DISCUSSION

Phylogenetic and functional diversity offer important insights into community diversity patterns and assembly when analysing ecological communities. Both measures are frequently used, though functional diversity has increased substantially over phylogenetic diversity in the past few years (Figure 2), likely due to a

perceived inferential benefit from using traits and a greater recent availability of trait information contained in online trait databases (e.g., Kattge et al., 2011; Wilman et al., 2014). These two measures are often assessed independently, but an increasing number of studies evaluate both sources of information to determine if the two approaches provide synonymous or congruent insights into communities.

In our analyses, we showed that the vast majority of studies found a statistically significant phylogenetic signal for most assessed traits (Figure 3), despite the numerous potential methodological and ecological reasons that were expected to undermine the detection of a signal. Despite this strong pattern, we did find that Blomberg's K and Pagel's λ varied with study factors like the number of traits that studies assessed and the taxa and habitat type investigated (Figure S4). A likely explanation for the trait effect is that studies using few traits selected those that were known to be important with strong signals, while studies assessing more traits have a higher chance of including weaker traits. The influence of taxon and habitat likely reflect evolutionary and biogeographic factors that influence the mode and tempo of trait evolution. One unexpected result from the signal analyses was that the reported values of Pagel's λ were much larger, and closer to values expected from Brownian motion models, than for Blomberg's K values. The cause of this difference might be explained by the recent finding by Molina-Venegas & Rodríguez (2017) that Pagel's λ is often a more reliable measure of phylogenetic signal than Blomberg's K (see too: Münkemüller, Lavergne, et al., 2012b). Further, a square root transformation of Blomberg's K appeared to increase its similarity to Pagel's λ (Figure 3b), which agrees with the conclusion of Letten and Cornwell (2015) that square root transformations are needed to make phylogenetic distances equivalent with functional distances.

Of the vast diversity of metrics available (e.g. reviewed in Tucker et al., 2017), we note that only a relatively small number are frequently assessed in the community ecology literature. Regardless of the exact measure used, it should not be surprising that phylogenetic and functional diversity measures are correlated (Pavoine et al., 2013) as multiple forms of diversity should covary spatially. This is especially true for richness-based measures, but yet only about 30% of correlations used measures (e.g., PD and FD) that are known to be mathematically correlated with species richness (Pavoine et al., 2017, 2013; Tucker et al., 2017) and inferences do not change when they are removed ($r^- = 0.527$); 24 of 29 studies finding a significant positive correlation when Faith's PD and FD are removed). The explanation for strong positive correlations is either that, on average, places with more phylogenetically distinct species also contain species that are functionally distinct (as a consequence of the ubiquitous phylogenetic signal found for most traits), or that the presence of outlier species (those that are evolutionarily and functionally very distinct) drives this correlation. Given the breadth of taxa in this study, we could not assess the influence of phylogenetic depth.

Despite the largely congruent findings based on phylogenetic signal tests and correlations between diversity measures, we found substantial incongruencies between functional and phylogenetic diversity when researchers assessed either dispersion patterns (Figure 5) or relationships with independent predictors (Figure 6). Pavoine et al. (2013) showed that despite strong correlations between phylogenetic and functional diversity for plant communities, only functional diversity was significantly predicted by an underlying salinity gradient. They concluded that phylogenetic diversity was a poor stand-in for functional diversity (but see Purschke et al., 2013).

While the conclusion about stand-in value needs to be treated with caution since phylogenetic and functional information can provide very different insights that depend on how conserved functionally important traits are and the ecological processes influencing species, it is worth exploring why seemingly correlated diversity measures, or traits with phylogenetic signals, reveal differing inferences about community assembly and the mechanisms structuring local diversity (Bässler, Ernst, Cadotte, Heibl, & Müller, 2014; Mason & Pavoine, 2013; Sobral & Cianciaruso, 2016).

There are a number of potential ecological, evolutionary and methodological reasons for incongruencies. First and foremost, the implicit assumption when comparing functional and phylogenetic measures is that they scale similarly to one another and to the underlying ecological differences that matter for community assembly, calling into question whether parametric correlations are the best approach. A one-unit change in functional or phylogenetic diversity will not likely result in a one-unit change in, say, the amount of overlap in resource use among coexisting species. There are very likely complex nonlinearities (Letten & Cornwell, 2015) in these relationships that might be smoothed over when correlating across multiple sites, but this only addresses the relationship between PD and FD measures and not how they each reflect the ecological processes acting on species.

There is an inherent difference in how traits and phylogeny can be related to ecological processes that can, in part, be addressed by methodological choices. Perhaps more critically is explaining the fact that phylogenetically over-dispersed assemblages also appear to be functionally clustered about half the time. In this case, the logical explanation is that measured and unmeasured traits do not reflect ecological processes equivalently and that the phylogeny is reflecting complex multivariate traits that appears to better capture processes leading to over-dispersion (e.g. competition, pathogen sharing, facilitation, etc.) while conspicuous measured traits might better infer environmental influence and species filtering. Further, phylogeny is a singular measure and there is no consideration about how to combine multiple measures, in contrast to trait analyses, where researchers must explicitly deal with which traits to measure and how to combine them into multivariate measures. With phylogenies, one can use a number of differing evolutionary models or phylogenetic tree transformations to determine how evolutionary change influences current ecology (Cadotte, Livingstone, et al., 2017). In essence, these models can serve as a translation function, turning phylogenetic distances into ecological differences. For functional traits, unless there is a single trait that strongly influences ecological dynamics, how to handle multiple traits and how to relate these to ecological differences is not as obvious.

It is now becoming clear that different components of species interactions could be influenced by different numbers of traits. Competitive inequalities and the fitness differences determining these are likely influenced by relatively few traits, especially height in herbaceous plants (Kraft et al., 2015; Mayfield & Levine, 2010). At the same time, coexistence depends substantially on niche differences and complementary resource use, which appear to be

influenced by multiple traits simultaneously and in more statistically complex ways (Kraft et al., 2015). Beyond just competitive coexistence, niche and fitness differences might be important in determining the outcome of other species interactions structuring communities, such as facilitation, which again could rely on different numbers of traits than, say, fitness. Differences in the number of traits that influence ecological processes matter for phylogenetic and trait congruence. Functional diversity calculated from small numbers of traits can appear idiosyncratically or weakly related to phylogenetic diversity even when these traits evolve according to known evolutionary models because of the stochastic nature of evolutionary models (Cadotte, Davies, et al., 2017; Tucker et al., 2018). With single or few traits, the influence of rapid trait divergence or trait convergence between distantly related species will be very influential and this could explain why we see such a large number of cases where phylogenetically over-dispersed assemblages are simultaneously functionally under-dispersed (Figure 5b). However, when functional diversity is calculated from a larger number of traits, even with the exact same evolutionary models inferred for the few trait scenario above, it should be more congruent with phylogenetic diversity (Cadotte, Davies, et al., 2017; Tucker et al., 2018). This implies that if the dominant community assembly mechanism is driven by a few traits, then incongruent findings should not be surprising, and phylogenetic and functional diversity measures should be more congruent when mechanisms are influenced by large numbers of traits. However, we do not actually show that this is the case and more work needs to be done to assess how the number of traits with phylogenetic signal influence community assembly under different ecological scenarios (e.g. strong environmental filters vs. intense competition for limited resources).

Most studies that compare phylogenetic and functional diversity make a number of implicit assumptions about the independence, similar statistical behaviour and the consistent effect of spatial scale on these measures. However, these implicit assumptions need to be evaluated better. We know that traits and trait differences among species are not independent of relatedness, but this non-independence is further confounded by biogeographic history (Cavender-Bares, Ackerly, Hobbie, & Townsend, 2016; Davies, Meiri, Barraclough, & Gittleman, 2007). Specifically, co-occurring species that evolved in sympatry are very likely to show different phylogenetic distance and trait difference relationships than those that evolved allopatrically (Davies et al., 2007). Further, phylogenetic and trait distances among species differ in their statistical distributions, with phylogenetic distances often appearing left skewed (Cadotte, Davies, et al., 2017), while trait data are much more likely to be normally distributed. It is not clear how these distributional differences will influence comparisons across different numbers of species and communities. However, it is likely that spatial scale might influence how phylogenetic and functional diversity measures are distributed and related to one another. The ecological mechanisms structuring communities, like competition, are not independent of scale (Ricklefs & Schluter, 1993). For example, competitive mechanisms are especially important for coexistence of

spatially close individuals. Moreover, other important processes like facilitation and exploitation by other trophic levels are spatially and phylogenetically non-random (Parker et al., 2015; Valiente-Banuet & Verdu, 2013). As a consequence, at fine scales more overlaying processes will influence community assembly, resulting in more variation in both functional and phylogenetic diversity patterns (Chapman, Tobias, Edwards, & Davies, 2018), but more research on scale effects is needed (Perronne, Munoz, Borgya, Reboud, & Gaba, 2017). Finally, even though the studies included in our analyses all examined ecological communities, they invariably include only sub-components of communities and further likely incompletely sample the community investigated (e.g. biased towards abundant or conspicuous species in particular for the measurement of functional traits). It is not clear how incomplete sampling will influence the congruency between PD and FD, though there is evidence that inferences about assembly can be strongly influenced by non-random incomplete sampling of communities (Jarzyna & Jetz, 2016; Si et al., 2018).

The studies analysed here use a number of functional and phylogenetic diversity metrics and while we understand which measures should be correlated spatially (Pavoine et al., 2017, 2013; Tucker et al., 2017), we do not know how metric choice might indirectly influence how diversity links to ecological processes. It stands to reason that richness-based measures (PD and FD) will capture different components of community assembly (e.g. total resource availability) differently than divergence measures (e.g. mean pairwise distances). Researchers need to carefully choose which metrics to use and compare to ensure that they are in fact comparable (Mouchet et al., 2010; Tucker et al., 2017) and that they have the ability to detect processes (Aiba et al., 2013). Further, it is valuable to use complementary measures, for example, comparing both richness and divergence measures to see if both types of comparisons are in agreement (Liu, Guenard, Blanchard, Peng, & Economo, 2016).

4.1 | What we do not do

One way in which phylogenies have been used in trait-based ecology is by providing a way to control for the evolutionary non-independence of species (Harvey & Pagel, 1991). For example, we might wish to test the hypothesis that taller plants have larger geographic range sizes, but closely related species could have similar heights and environmental limits because of common descent, without any mechanistic link between the two. While such phylogenetic corrections for ecological inference has been controversial in the past (Ackerly & Donoghue, 1995; Fitter, 1995; Harvey, Read, & Nee, 1995a, 1995b; Westoby, Leishman, & Lord, 1995), there are research questions that require phylogenetic corrections and there is ongoing dialogue about the need to control for relatedness in analyses of functional diversity (de Bello et al., 2015). However, this use of phylogeny in functional ecology was not the focus of our analyses and we did not include papers using these methods.

Further, there are a substantial number of analyses that examine incongruencies between taxonomic diversity and either

phylogenetic or functional diversity (Li et al., 2015; Mori et al., 2015). While such analyses frequently report incongruencies, and the reasons for these are interesting, we did not include these comparisons in our analyses. The reasons are that the causes are mechanistically different than mismatches between phylogenetic and functional diversity, and further, the influence of metric choice is especially confounding for these comparisons (Tucker et al., 2017).

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AUTHORS' CONTRIBUTIONS

M.W.C., M.C., X.S. and S.T. all conceived of the study and designed methodology. M.W.C. collected data and led the analyses, with feedback from all authors. M.W.C. led the writing, and all authors contributed critically to manuscript preparation and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data used in this article are available from the Dryad Data Repository: <https://doi.org/10.5061/dryad.vr2f738> (Cadotte, Carboni, Si, & Tatsumi, 2019).

ORCID

Marc W. Cadotte  <https://orcid.org/0000-0002-5816-7693>

Xingfeng Si  <https://orcid.org/0000-0003-4465-2759>

Shinichi Tatsumi  <https://orcid.org/0000-0002-1789-1685>

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SUPPORTING INFORMATION

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