

IDEA AND PERSPECTIVE

The ecology of differences: assessing community assembly with trait and evolutionary distances

Marc Cadotte,^{1,2†*} Cecile H. Albert^{3,4†} and Steve C. Walker^{5,†}

Abstract

Species enter and persist in local communities because of their ecological fit to local conditions, and recently, ecologists have moved from measuring diversity as species richness and evenness, to using measures that reflect species ecological differences. There are two principal approaches for quantifying species ecological differences: functional (trait-based) and phylogenetic pairwise distances between species. Both approaches have produced new ecological insights, yet at the same time methodological issues and assumptions limit them. **Traits and phylogeny may provide different, and perhaps complementary, information about species' differences. To adequately test assembly hypotheses, a framework integrating the information provided by traits and phylogenies is required.** We propose an intuitive measure for combining functional and phylogenetic pairwise distances, which provides a useful way to assess how functional and phylogenetic distances contribute to understanding patterns of community assembly. Here, we show that both traits and phylogeny inform community assembly patterns in alpine plant communities across an elevation gradient, because they represent complementary information. Differences in historical selection pressures have produced variation in the strength of the trait-phylogeny correlation, and as such, integrating traits and phylogeny can enhance the ability to detect assembly patterns across habitats or environmental gradients.

Keywords

Biodiversity, biodiversity–ecosystem function, community assembly, ecological gradients, functional diversity, null models, phylogenetic community ecology, phylogenetic diversity, trait divergence, trait-based ecology, traitgram.

Ecology Letters (2013) 16: 1234–1244

INTRODUCTION

Quantifying biodiversity is central to answering the most challenging questions in community ecology. Classic works sought to explain patterns of diversity in terms of the numbers and distributions of species (species diversity e.g. Andrewartha & Birch 1954; MacArthur & Wilson 1967). However, despite a long history of explaining ecological patterns and processes in terms of species ecological differences (Raunkiaer 1934; Grime 1979), the recognition that these differences constitute an important aspect of community diversity has emerged only recently (Walker *et al.* 1999; Webb 2000; Petchey & Gaston 2002). **Mechanisms influencing patterns of community assembly act on the ecological similarities (or redundancies) and differences (or complementarities) of organisms, and not on the number of species** (Weiher & Keddy 1995; Diaz & Cabido 2001; McGill *et al.* 2006). In the quest to understand species coexistence and community assembly, and to address the ecological consequences of anthropogenic changes, ecologists have moved from counting species to accounting for species.

Following this recognition that species ecological differences (or similarities) matter for community assembly has been an emerging focus on the challenges in measuring species differences, both conceptually and methodologically (e.g. Petchey *et al.* 2004; Poos *et al.* 2009). There have been two major approaches developed that quantify species ecological differences: functional (or trait based) and phylogenetic (or the amount of evolutionary divergence). Both approaches to measuring species differences can be aggregated at the community level to summarise the degree to which the constituent species differ in terms of their function, niche or evolutionary history. Both approaches have led to new insights in community ecology (Webb 2000), yet both are limited by methodological issues and important assumptions.

Functional measures of species' differences

In the trait-based framework, species' ecological differences (or functional distances, FDist) are usually estimated as distances between species' attributes along a single trait axis (e.g. Garnier

¹Department of Biological Sciences, University of Toronto - Scarborough, 1265 Military trail, Toronto, ON, Canada M1C 1A4,

²Department of Ecology and Evolutionary Biology, University of Toronto, 25 Wilcocks St., Toronto, ON, M5S 3B2, Canada

³Laboratoire d'Ecologie Alpine, UMR CNRS 5553, CNRS, Université Joseph Fourier, BP 53, 38041, Grenoble Cedex 9, France

⁴Department of Biology, McGill University, 1205 Dr. Penfield Avenue, Montreal, QC, Canada H3A 1B1,

⁵Département de Sciences Biologiques, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montreal, QC, Canada H3C 3J7

*Correspondence: E-mail: mcadotte@utsc.utoronto.ca

†All authors contributed equally to the writing of this article.

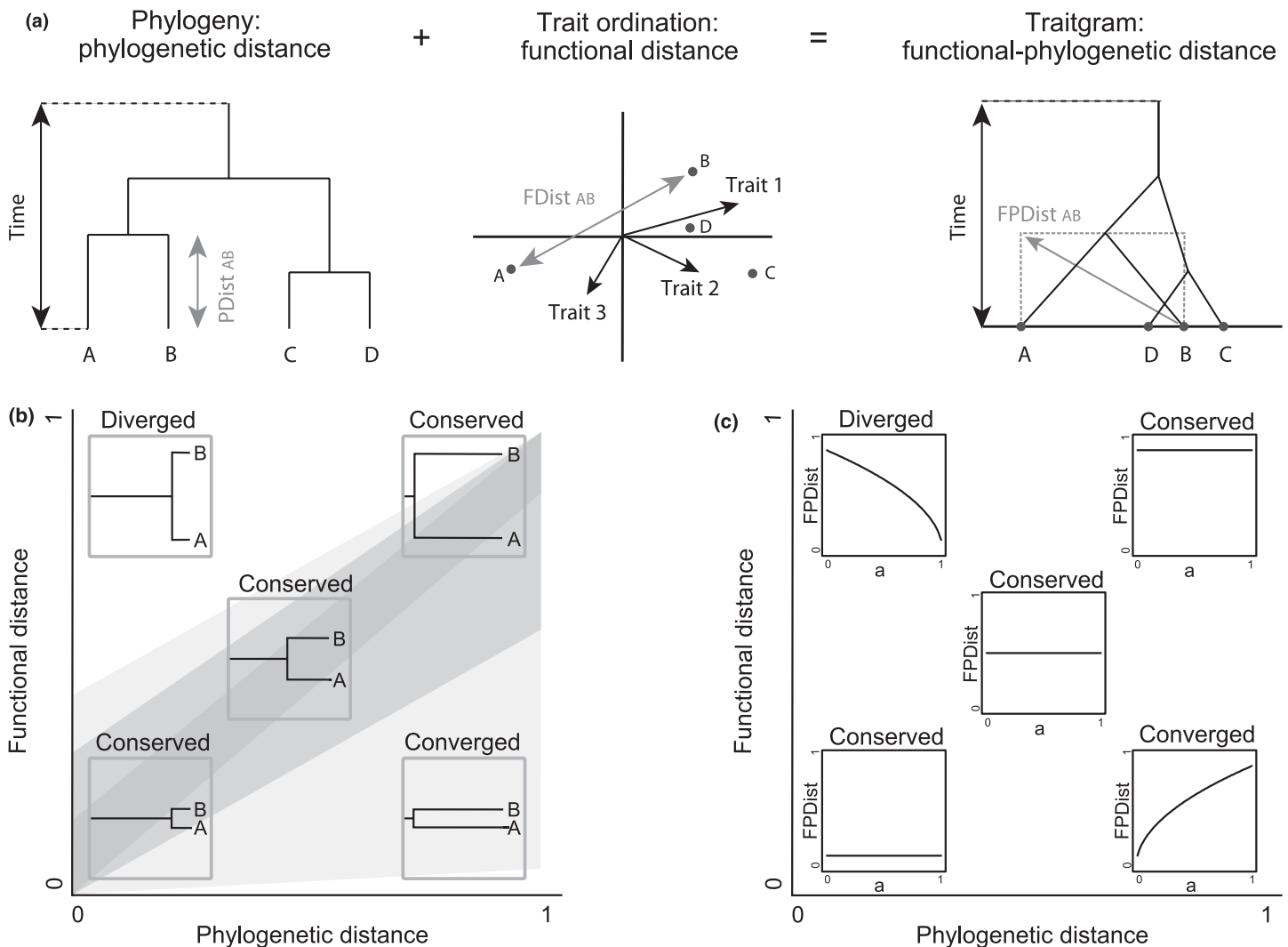


Figure 1 Combining functional and phylogenetic distances at the species level. (a) Traitgrams combine phylogenetic trees and functional trait space. Functional-phylogenetic distances in traitgram space are calculated as follows: $FPDist = (aPDist^p + (1 - a)FDist^p)^{1/p}$ ($p = 2$), which includes trait convergence and divergence into phylogenetic distances. (b) Traitgrams illustrate the possible kinds of pairwise relationships for different levels of functional and phylogenetic distances. The shading in the background indicates the relationships expected under Brownian motion for 1 (wide region), 5 and 20 (narrow region) traits. (c) The curves obtained by varying the phylogenetic-weighting parameter, a , provide signatures of whether pairwise evolutionary relationships are conserved (flat curves), divergent (decreasing curve) or convergent (increasing curve).

et al. 2001) or within a multivariate space (e.g. Fig. 1, Diaz *et al.* 2004). Within a community, functional diversity may include the kind, range and relative abundance of trait values (Diaz & Cabido 2001; Mason *et al.* 2005). Even though for some groups of species, functional traits have been studied extensively, providing links between traits and environmental gradients, species' niches and ecosystem function, in particular through the recognition of the plant economics spectrum (e.g. Lavorel & Garnier 2002; Westoby *et al.* 2002; Wright *et al.* 2004), we lack sufficient information linking traits to community assembly for large numbers of species. Because multiple traits may affect ecological differentiation, a given trait may affect multiple axes of niche differentiation and not all ecological attributes will be mediated by the same set of traits (Cornelissen *et al.* 2003). Given these complexities, potentially important traits could easily be overlooked, or uninformative traits included in analyses, thus diminishing our ability to adequately

explain patterns of community assembly. These limitations on the use of trait-based measures were the impetus for using phylogenetic measures; specifically, it has been assumed that a phylogeny may represent unmeasured or complex traits better than a limited number of measured traits (Helmus *et al.* 2007; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012).

Phylogenetic measures of species' differences

The use of phylogenetic distances (PDist) in community ecology relies on the assumption that potential species ecological differences are proportional to the amount of time since they diverged from a common ancestor, often according to a Brownian motion model of evolution – which assumes homogeneous rates of trait evolution across the tree (Harvey & Pagel 1991; Webb *et al.* 2002). While studies that examine the evolution of complex characters tend to

support a Brownian motion model (Cooper & Purvis 2010; Harmon *et al.* 2010), it is also well known that ecological differences in sympatric species can rapidly increase (e.g. Urban & Skelly 2006), violating the Brownian model. For example, silverswords in Hawaii (Baldwin & Sanderson 1998), cichlids in the African Great Lakes (Seehausen 2006), anoles on Caribbean islands (Losos *et al.* 1997) and proteas in South Africa (Valente *et al.* 2009) are all classic examples of rapid diversification taking advantage of ecological opportunity. Conversely, it has also been often shown that distantly related lineages can converge on similar traits or strategies (e.g. homoplasy), such as the synonymous adaptations to arid environments in the Cactaceae and Euphorbiaceae. **Given that there could be very different models of evolutionary change for different groups of organisms in different systems, a single model leading to a systematic phylogenetic signal should not be assumed for all systems** (Losos 2008). An additional limitation of using phylogenies in community ecology is that one must assume that they correctly represent evolutionary history, which is similar to the assumption that measured traits correctly represent functional information. However, this assumption of phylogenetic correctness depends on a suite of methodological choices for reconstructing evolutionary history, including gene selection, estimation of evolutionary models and calibration of branch lengths.

The way forward

These concerns about trait-based and phylogenetic approaches suggest that there is a need to consider both sources of information in a complementary fashion in order to get ecologically meaningful estimates of species' pairwise differences, while coping with the limitations of both sources of information. We see two major ways forward, and study one of these two ways in detail here. The first approach, which we will not pursue in depth, involves **developing methods for scaling branch lengths** (e.g. Blomberg *et al.* 2003) **such that phylogenies provide better estimates of the ecological differences between species**. Such an approach would effectively remove the (often implicit) assumption in ecophylogenetics that trait evolution follows a Brownian motion model. If successful, such methods would enhance the ecological relevance of phylogenetic trees. Nevertheless, phylogenetic trees, however they are constructed, often contain information about species' ecological differences that can complement information provided by functional traits. Here, we develop a conceptual and methodological framework for exploring this potential complementarity.

Previous work in this area has set the stage for our synthesis. Certainly, studies have compared and contrasted the relative abilities of phylogenetic and trait-based measures to explain ecological phenomena (Cavender-Bares *et al.* 2006; Cadotte *et al.* 2009; Flynn *et al.* 2011), which is an important exercise. If the measured traits are the product of evolution (as opposed to non-genetic phenotypic plasticity), and are relatively conserved through time, they may correspond to a phylogeny quite well, meaning that measured traits and phylogeny explain ecological patterns similarly. In this case, measuring the traits directly is more meaningful since they invoke or point to candidate mechanisms (McGill *et al.* 2006). Conversely, if traits have been strongly selected under environmental or biotic pressures, then much adaptive change may have occurred after species have diverged from common ancestors. Further, different traits may show differing amounts of conservatism

and convergence/divergence along phylogenies (Blomberg *et al.* 2003; Cavender-Bares *et al.* 2006). Given this, phylogenies and measured traits may represent different aspects of species' ecology. If this is true, then it is not clear what a statistical comparison of their power to explain ecological variation means. One way forward is to integrate phylogeny and traits so that these complex patterns of evolutionary change and time can be used in hypothesis tests and predictive models.

REPRESENTING TRAITS AND EVOLUTION: THE TRAITGRAM

Distances at species-pairwise level

Recently, several authors have independently introduced a new method to visualise trait evolution by having tips of a phylogeny positioned along a trait axis with internal nodes positioned according to ancestor trait reconstruction (Ackerly 2009; Evans *et al.* 2009; Fig. 1). Traditionally, **a phylogenetic tree is one-dimensional, that is, the only meaningful distance is the measure of evolutionary distance (usually time or genetic distance) while species and nodes are evenly and arbitrarily spaced along the other axis** (Fig. 1). This second axis need not be arbitrary, rather it can be used to position species nodes according to trait, niche dimension, ecological, spatial or environmental distances (Fig. 1; here, we will stick to trait-based distance, for clarity).

Just as we can measure species differences as distances between species in phylogenetic-space only (phylogenetic distance, PDist, Fig. 1a) and in trait-space only (functional distance, FDist, Fig. 1a), we can also **measure them as distances between species in this new 'traitgram-space'** (functional-phylogenetic distance, FPDist, Fig. 1a). This can be done by weighting the independent contributions of FDist and PDist to FPDist (a) and combining them nonlinearly (p) following:

$$FPDist = (aPDist^p + (1 - a)FDist^p)^{1/p} \quad (1)$$

Functional-phylogenetic distance is a p -norm distance and satisfies all mathematical requirements of a distance metric (*non-negativity, identity of indiscernibles, symmetry and triangle inequality*), when $p \geq 1$ and when both PDist and FDist are themselves proper distance metrics (i.e. they need to be positive values). Functional distance can be based on a single trait, a single axis of a multivariate measure or can itself be a linear combination of multiple traits. For the remainder of this article, we will assume FDist is a single measure (i.e. single trait or single multivariate dimension) and use $p = 2$ to obtain a Euclidean distance from the combined functional and phylogenetic distances, but any choice for which $p \geq 1$ is possible.

Functional-phylogenetic distances, FPDist, can be thought of as **phylogenetic distances that take trait convergence and divergence into account, or as functional distances that account for information from unmeasured, phylogenetically correlated traits**. It is thus expected to be a better estimate of overall species functional differences, which are what drives ecological processes. Here, we refer to conserved traits generically as the tendency for close relatives to be more similar to one another compared to distant relatives without relying on a specific test of conservatism (e.g. Wiens 2008). For example, species A and B in the traitgram in Fig. 1a show divergent evolution. This divergence stretches the branch lengths connecting

them to their common ancestor along the FDist axis. When $FDist_{i,j} > PDist_{i,j}$ (top left of Fig. 1b), species traits are likely the product of divergent selection and when $FDist_{i,j} < PDist_{i,j}$ (e.g. species B and D of Fig. 1a; and bottom right of Fig. 1b), traits are likely constrained or positioned on a fitness peak, resulting in conserved traits (Losos 2008; Futuyma 2010). Whether traits show convergence and divergence will be reflected in the new FPDist dissimilarity measure. When species are both functionally and phylogenetically similar (i.e. FDist and PDist are both small), then FPDist will also be small, reflecting the overall similarity between species (bottom left of Fig. 1c). When species are both functionally and phylogenetically dissimilar, then FPDist will also be large, reflecting the overall dissimilarity between them (top right of Fig. 1c). However, when species have diverged (top left of Fig. 1b,c) or converged (bottom right of Fig. 1b,c), FPDist values will be intermediate to the two components (PDist and FDist), for intermediate values of a (a different from 0 and 1). Distances in traitgram-space then have the potential to differentiate pairs of species that appear similar by either functional or phylogenetic distances only, meaning that traitgrams can reveal different facets of species differences. Unlike the traitgram graphical representation (Fig. 1a), the combined measure does not need to assume any given model of ancestral trait reconstruction and thus deals with different rates of evolution implicitly. FPDist uses the relative contributions of FDist and PDist to account for low or high rates of evolution with high rates of evolution of measured traits resulting in high FDist values for small PDist values and low rates of evolution of measured traits resulting in small FDist for high PDist values (e.g. Fig. 1). Integrating both information on FDist and PDist within the FPDist framework, we propose will consequently be able to disentangle these different cases. Of course, ecologically important unmeasured traits may be the product of complex evolutionary histories with differing rates, and a given phylogeny may not capture this well. Further, how the phylogeny is constructed is critically important. The distribution of PDist values will be suboptimally 'binned' if a super tree containing polytomies is used. A fully resolved dichotomous tree with reliable branch length estimates is preferred.

Functional-phylogenetic distance thus provides a compromise between phylogenetic and functional information, which can be tuned by the phylogenetic-weighting parameter, a . When $a = 1$, FPDist is phylogenetic distance and when $a = 0$, FPDist is functional distance. Furthermore, varying the weighting parameter, a , will additionally affect FPDist when convergences or divergences are observed (Fig. 1c). In particular, FPDist will increase with a for an evolutionarily converged species pair due to an increasing contribution of PDist, and decrease for a divergent pair due to a decreasing contribution of PDist (Fig. 1c). The phylogenetic-weighting parameter, a , is thus key for estimating the difference between species from the traitgram and the relative importance of converged/diverged species pairs in comparison to conserved ones.

To standardise comparisons between PDist and FDist contributions within FPDist, we scale both pairwise distances between 0 and 1 in our examples. However, the distributions of PDist and FDist may be substantially different, and depending on the use of a combined measure, researchers may want to also account for differences in their distributions not just their magnitudes. For example, the distance matrices could be non-linearly scaled between 0 and 1 with a mean of 0.5, but meaningful information would be lost in this transformation. A given data set may reflect ecological and

evolutionary processes generating many cases of convergences, leading on average to lower FDist than PDist values, or conversely, where a deep bifurcation in the phylogenetic tree, results in a large number of large PDist values (Fig. 1b). Thus, transforming the FDist matrix would mean that smaller differences in FDist are equivalently important as larger distances in PDist. But other distributions of the distances are possible, needing careful consideration. This scaling issue can be addressed by careful interpretation of the phylogenetic-weighting parameter, a , introduced below (Fig. 1c).

Implications for measures of diversity at the community level

This new phylogenetic-functional measure of species differences can be used as a substitute for any other pairwise distance to assess whether community assembly results in non-random assemblages. In particular, it can be aggregated at the community level, using any distance-based presence-absence or abundance-weighted diversity measure, such as Rao's quadratic entropy (Botta-Dukat 2005) or mean pairwise distance (Webb *et al.* 2002) or a number of other metrics (e.g. Schleuter *et al.* 2010), and distances can be compared to null values generated by randomising the distance matrix. For the remainder of this article, we will use mean pairwise functional-phylogenetic distance (MFPD), based on presence-absence, as a measure of functional-phylogenetic diversity, but any choice of distance-based diversity measure is possible.

Using typical approaches with functional or phylogenetic measures alone assumes that community assembly depends on the mechanisms selecting a subset of species from a regional species pool for membership in a local community. For example, researchers infer that when communities are comprised of species that are more similar than expected by chance (i.e. short distances, under-dispersed or clustered), they may be structured by abiotic conditions that select for suitable trait values (Helmus *et al.* 2010). However, it is theoretically possible for under-dispersion to result from intense competition that places similar selection pressures on multiple species (e.g. the evolution of plant height during competition for light; Mayfield & Levine 2010). Conversely, competition for biotic resources often selects for species with low niche overlap, therefore leading to communities comprised of species that are more different than expected by chance (i.e. large distances or over-dispersed) (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; but see Mayfield & Levine 2010). Therefore, interpreting patterns of over- and under-dispersion presents a fascinating challenge that requires detailed system-specific knowledge (Mayfield & Levine 2010). Our traitgram and FPDist framework provides a tool for visualising and measuring these patterns more comprehensively than either a phylogenetic or functional approach alone.

While previous hypothesis tests use either traits or phylogenies, our new combined approach allows researchers to not only potentially detect over- and under-dispersion but also provides the ability to assess the importance of conserved vs. converged or diverged traits (Fig. 2). We identify three factors that can lead to detect over- or under-dispersion in terms of MFPD: (1) the dominant community assembly pattern, (2) the dominant pattern of trait evolution and (3) the mismatch between the traits that were measured and those that truly drive community assembly (Fig. 2). Our ability to detect patterns of over and under-dispersion not only depends on the process of assembly but also on the other two factors. When the traits that are relevant to community assembly are phylogeneti-

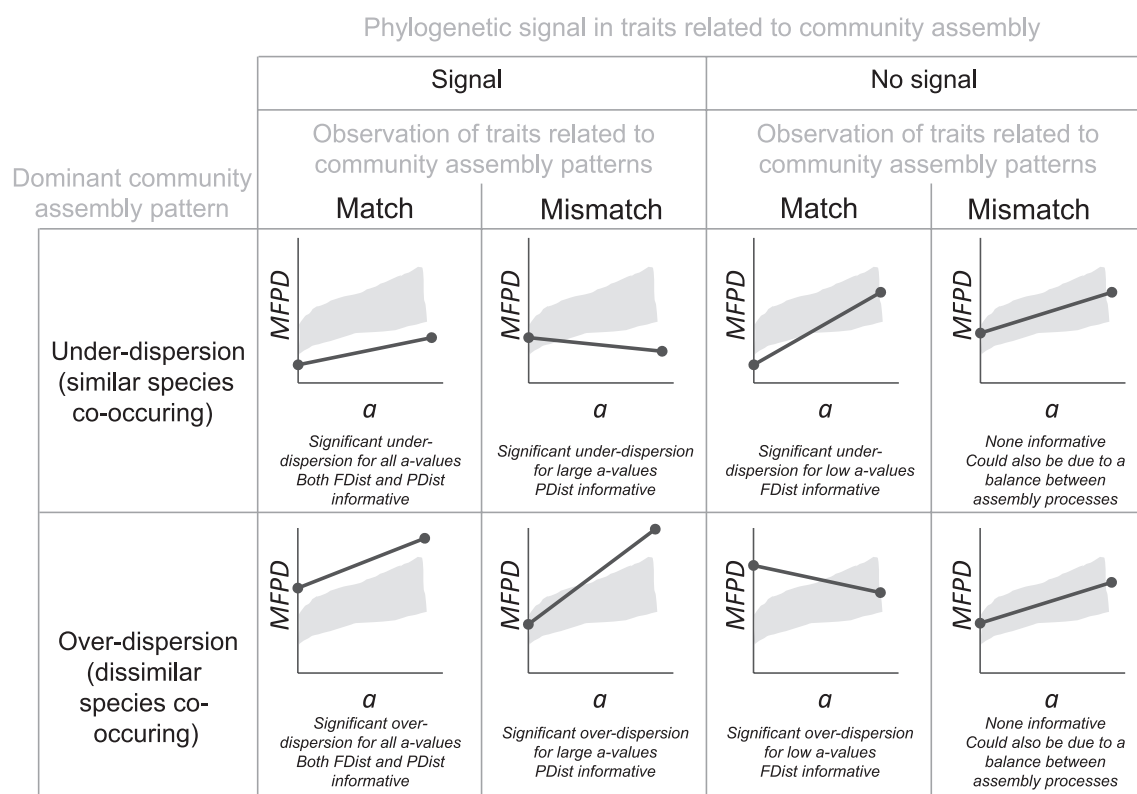


Figure 2 Predictions for mean pairwise functional phylogenetic distances (MFPD) at the community level across the range of possible values for the phylogenetic-weighting parameter, *a*. Observed patterns (black lines) are expected to change according to: (1) the dominant pattern of community assembly (under-dispersion *vs.* over-dispersion), (2) the presence or absence of a phylogenetic signal in traits related to community assembly patterns (signal *vs.* no signal) and (3) how well do the measured traits match those that truly drive community assembly processes (match *vs.* mismatch). Shaded regions give the null distribution obtained for random communities.

cally conserved, phylogenies contain important ecological information, which increases the chances of detecting community patterns when using phylogenetic information, i.e. for high values of *a* (Fig. 2). Similarly, significant patterns of over- or under-dispersion are also more likely to be detected for low values of *a* if we are able to accurately measure ecologically relevant traits (Fig. 2). Analyses varying *a* can also estimate optimal values of *a*, where pattern explanation is maximised. For example, maximum likelihood or variance explained can be used for this estimation.

The power of combining traits and phylogeny

While Fig. 2 outlines several possible effects of *a* on MFPD, there are other, more complex possibilities. MFPD provides additional information about diversity, not provided by either mean phylogenetic distances (MPD) or mean functional distances (MFD). For example, consider two communities with identical phylogenies and identical trait distributions, but different traitgrams (Fig. 3). In the first traitgram (Fig. 3a), species A and B are similar both functionally and phylogenetically. However, in the more complex traitgram (Fig. 3b), although A and B are phylogenetically very similar, they are functionally very different. Therefore, in this case, the trait and the phylogeny provide complementary information. This additional information in the traitgram can be summarised using mean functional-phylogenetic distances, MFPD (Fig. 3c). The two assemblages have identical MFPD when *a* = 0 or *a* = 1, because in these extreme cases MFPD

uses only functional or phylogenetic information respectively. Whereas, for intermediate values of *a*, the differences between the assemblages become more apparent (Fig. 3c). This example illustrates that the traitgram approach provides more information about diversity than either a phylogenetic or functional approach alone; only when the two sources of information are combined do the differences between these assemblages become apparent.

At intermediate values of *a*, MFPD will be larger when trait-based and phylogenetic information are complementary, in comparison with when they are redundant. For example, the relatively large MFPD in Fig. 3b resulted from the fact that species that were similar phylogenetically were functionally distinct (species A and B), and species that were functionally similar were phylogenetically distinct (species A and C). Such complementarity can be quantified as a negative covariance between functional and phylogenetic distances. In general, the difference in MFPD between communities that differ in their FDist-PDist covariances by an amount ΔCOV is given by the following:

$$\Delta\text{MFPD} = -a(1-a) \left[\frac{(\text{MPD})(\text{MFD})}{(a\text{MPD}^2 + (1-a)\text{MFD}^2)^{3/2}} \right] \Delta\text{COV} \quad (2)$$

assuming that all other moments of the distributions of FDist and PDist remain identical in both communities (Appendix 1). This equation proves that MFPD provides information about diversity that is not contained in either MFD or MPD.

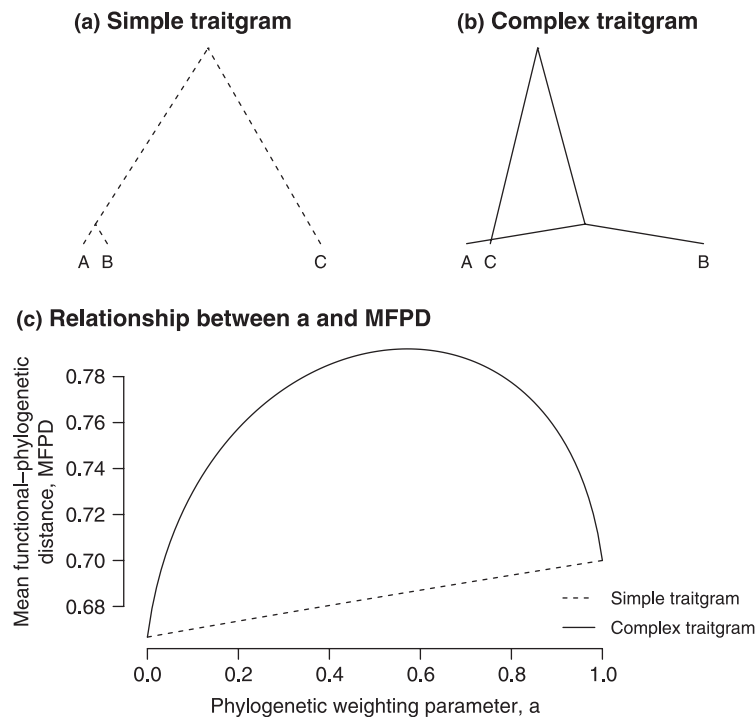


Figure 3 Two traitgrams (panels A and B) with identical mean functional distances (MFD) (panel C, $a = 0$) and mean phylogenetic distances (MPD) (panel C, $a = 1$) can have quite different mean pair-wise functional phylogenetic distances (MFPD) at intermediate values of the phylogenetic-weighting parameter, a (panel C). The reason why MFPD provides more information to discriminate these two traitgrams is that it takes into account the fact that phylogenetic and functional information are complementary in the complex traitgram (panel B) and redundant in the simple traitgram (panel A). Therefore, traitgram complexity represents an additional component of biodiversity not accounted for by either traits or phylogenies alone.

Another premise for using our combined measure is that FPDist should exhibit greater power to detect patterns of over- and under-dispersal, than either phylogenetic or trait measures alone. Using a suite of simulations, we show that FPDist better represents true functional distances when only subsets of ecologically relevant traits have been measured (Appendix 2 in Supporting Information). Further, as traits depart from Brownian evolution, FPDist again more powerfully represents true functional distances than either a subset of the traits or phylogeny alone (Appendix 2 in Supporting Information, Fig. S2-1, S2-2). Where this metric could underperform is if the unmeasured traits have evolved under non-Brownian modes, e.g. with clades showing different rates of evolution. However, even in these cases FPDist is not expected to perform any worse than FDist on average.

EMPIRICAL EXAMPLES

Here, we highlight how FPDist can shed new light on the relative contributions of phylogenetic and functional diversity on community assembly, and estimating how environmental gradients shape communities. Phylogenetic and trait-based analyses of community assembly test whether communities comprised species that are either more similar or different than expected by chance and make some assumptions on which processes could lead to such patterns (Weiher & Keddy 1995; Silvertown *et al.* 2001; Webb *et al.* 2002). It is important to note here that the mechanisms generating patterns of over- and under-dispersion in observational data are often based on a number of untested assumptions making it difficult to provide

causal links to mechanisms (Mayfield & Levine 2010). In our examples below, we focus on dispersion patterns, and are not inferring explicit assembly mechanisms.

To evaluate how FPDist can impact our ability to detect over- or under-dispersion at the community level, we used community and trait data from 50 semi-natural subalpine grasslands in the French Alps (Quétier *et al.* 2007; Lavorel *et al.* 2011; see Appendix S2 in Supporting Information). Functional distances between species were calculated as the Euclidean distance over four traits that are known to be linked with plant economics (plant height, leaf dry matter, nitrogen and phosphorus content, Cornelissen *et al.* 2003) and phylogenetic distances were calculated from a phylogeny for the species occurring in the study communities, considered as the regional pool (Thuiller *et al.* 2011, see Appendix S3).

To answer the question of whether communities consist of significantly clustered or over-dispersed species, we compared observed and random expected mean pairwise FPDist over the range of phylogenetic-weighting parameter values, a , from 0 to 1. As indicated in Fig. 2, the ability to detect such patterns of over- and under-dispersion depends on the structuring mechanism (environmental filtering vs. competition), whether traits are phylogenetically conserved, and whether the appropriate traits have been measured.

From our analysis of the subalpine grasslands data, we found a variety of patterns; nine of the 50 communities were significantly over- or under-dispersed for at least some values of the phylogenetic-weighting parameter, a . Here, we concentrate on three representative communities, and further describe the variability of patterns in Supporting Information (see Appendix S3 Fig. S3-2).

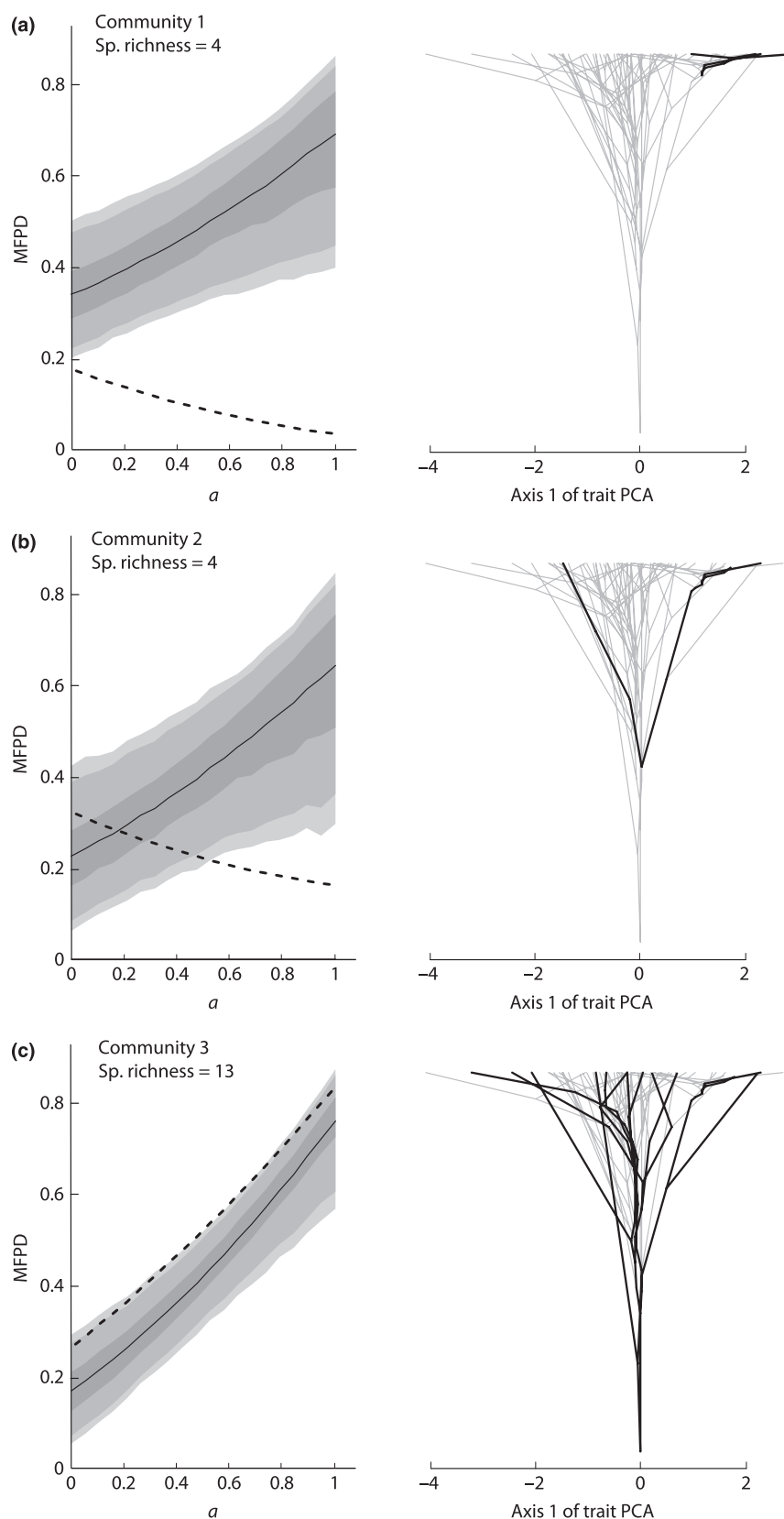


Figure 4 Mean pair-wise functional phylogenetic distances across the full range of the phylogenetic-weighting parameter, a (left panels), for three subalpine grasslands (a–c). Shaded regions give the null distribution given the community-specific richness (light grey, 0.025–0.975 = 95%, medium grey, 0.05–0.95 = 90%, dark grey, 0.25–0.75 = 50%), with the average of this distribution indicated with a solid line. The dotted lines show the observed mean pairwise distances. Also, shown are the traitgrams for each community (right panels) with black lines indicating the species present in the community and grey shows the remaining species in the species pool. The first community (a) shows under-dispersion for all values of a , while (b) reveals under-dispersion as $a \rightarrow 1$ and (c) shows over-dispersion at intermediate values of a .

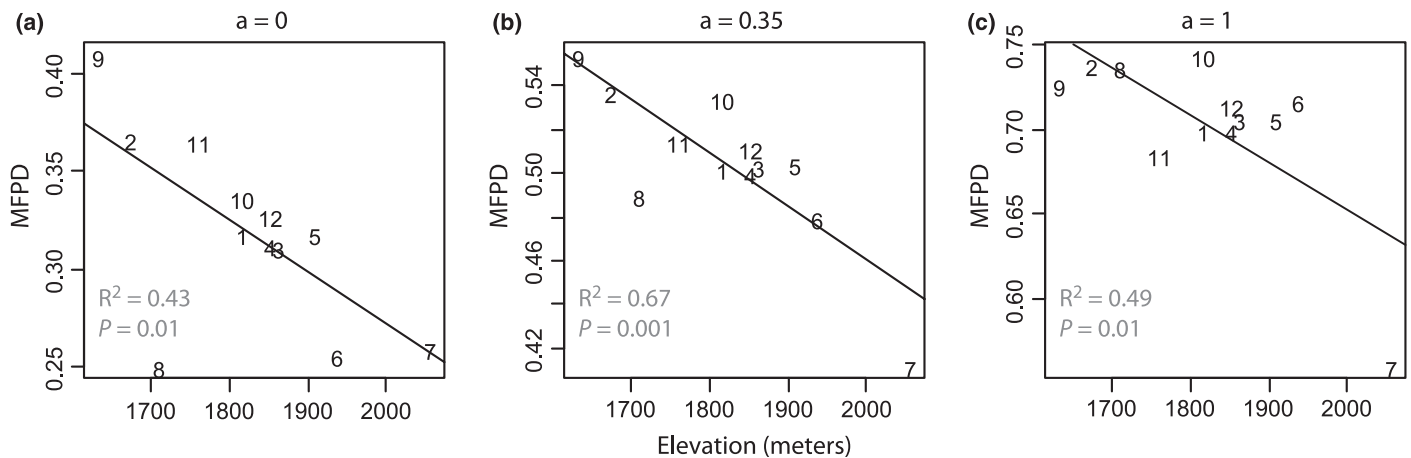


Figure 5 Mean pair-wise functional-phylogenetic distances (MFPD) as a function of an elevation gradient, for different values (panels) of the phylogenetic-weighting parameter, a , for a set of communities that have undergone similar management conditions. The value $a = 0.35$ in the centre panel maximised the correlation (R^2) between mean pair-wise functional-phylogenetic distance and elevation, as displayed in the inset showing the relationship between R^2 and a . Communities are numbered on the plots.

The first representative community was significantly under-dispersed for all values of a (Fig. 4a). This community is comprised of closely related, functionally similar species, as illustrated in the traitgram, though the magnitude of the under-dispersion increases with increasing a -values. By comparing the pattern in Fig. 4a with predictions in Fig. 2, it could be assumed that the measured traits are linked to the assembly processes and that there is a phylogenetic signal in other traits that are important for the assembly process, which results in under-dispersion.

The second highlighted community, which is species poor, was significantly under-dispersed for large values of a (above 0.5), but not significantly different from the null distribution for smaller values of a (Fig. 4b). The species in this community span large functional distances, but represent a clade of closely related species, generating the observed under-dispersion. Comparing with predictions (Fig. 2), we suggest that unmeasured traits that correspond to the phylogeny reflect assembly processes that lead to under-dispersion.

The final highlighted community reveals a more complex traitgram, with convergences and divergences in trait values along the branches, and combinations of clades of closely related species and phylogenetically distinct species. Assembly analysis here reveals that the community is significantly over-dispersed for intermediate values of a (Fig. 4c). **This pattern of over-dispersion at intermediate a -values indicates that this community is significantly different from the null distribution in its higher order moments of functional and phylogenetic distances** (Fig. 3, Appendix 1). Put more simply, this community illustrates a case where both measured traits and phylogeny contribute to the observed pattern of over-dispersion.

These examples serve as a warning for interpreting phylogenetic or functional under-dispersion alone as evidence that similar species occur in the same habitat. In the second example (Fig. 4b), a researcher may conclude that the community is not under-dispersed if they only measured functional distances, yet clearly phylogenetically similar species inhabit this community. Such conclusions depend critically on whether the measured traits are involved in the assembly processes, how they have evolved along the phylogeny and what ecological processes are at play (Fig. 2). Thus, analysing a

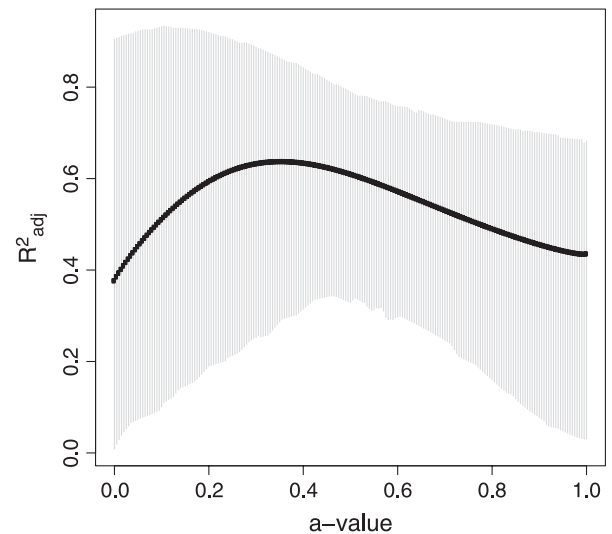


Figure 6 Adjusted R-squared (R^2_{adj}) values of the regression between MFPD and elevation across the range of a -values. Black dots represent the observed values, while the grey segments display the 0.1–0.9 confidence interval obtained from a bootstrap procedure with 200 draws. The maximum R^2_{adj} is obtained at $a = 0.355$.

range of a -values can potentially provide more complex and informative insights than when simply looking at functional or phylogenetic information separately as it brings more insight on the overall distribution of FDist and PDist matrices.

Related to the observation that some communities comprised more similar species than expected, is how these average pairwise distances change across an environmental gradient. It has long been recognised that environmental gradients are important drivers of patterns of community diversity (Whittaker 1956). While early research asked how environmental factors affected compositional similarity among communities (e.g. Curtis 1959; Hill 1973), more recent trait- and phylogeny-based work has gone further, testing if environmental gradients, which provide strong filters, affect

phylogenetic or functional distances in assemblages at different points along a gradient (Cavender-Bares & Wilczek 2003; de Bello *et al.* 2013). The prediction is that harsher environmental conditions, such as low water availability or low temperatures, should strongly select for species that possess traits imbuing them with the ability to tolerate abiotic stresses, resulting in under-dispersed trait values (e.g. Cavender-Bares & Wilczek 2003; Spasojevic & Suding 2012; de Bello *et al.* in press).

We addressed this question of the importance of an environmental gradient by testing the relationship between mean functional-phylogenetic distance (MFPD) and elevation with the previously described alpine grasslands case study. We investigated this relationship across the range of the phylogenetic-weighting parameter, a (Fig. 5). We restricted the data to a subset of communities from a single land-use type (terraced and mown grasslands) to control for the effect of external disturbance. Terraced and mown grasslands are dominated by *Bromus erectus*, *Sesleria caerulea*, *Festuca laevigata*, all species that extend over the larger elevational gradient (Quétiér *et al.* 2007). As expected, we found that MFPD is negatively correlated with elevation for all values of a , which we infer to mean that **high elevation environmental conditions strongly selecting for communities of ecologically similar species**. The variance explained by elevation was maximised at $a = 0.35$ (maximal $R^2 = 0.67$, Figs 5 and 6), an intermediate value of a . This suggests that combining phylogenetic and functional information may better reveal the effects of environmental filtering on community assembly along gradients, because both measured and unmeasured traits are influencing species persistence or coexistence across the gradient and that the two distance matrices (FDist and PDSit) differ in some way or they have weak or negligible covariance. In our example, the highest R^2 value obtained (0.67) represents a substantial increase in variance explained over mean pairwise functional-phylogenetic distances calculated from functional or phylogenetic distances only (an average R^2 increase of 0.21 Fig. 5).

CONCLUSIONS

The search for general patterns and rules governing community assembly has led researchers to examine functional and phylogenetic distances. The recent explosion of phylogenetic and functional diversity metrics has opened new lines of inquiry, but this advance has been limited by the inability to synthesise both sources of information. We illustrated the potential power of combining functional and phylogenetic distances for analysing patterns of community assembly with several analyses from simulated and natural communities. Our **simulations show that FPDist usually provides better estimates of species' overall ecological differences than either functional or phylogenetic distances alone**. More importantly, FPDist has greater power to detect community assembly patterns and can potentially tell us how measured and unmeasured traits contribute to these observed patterns.

Our synthetic biodiversity measure, MFPD, is unique in that it captures different measures of biodiversity (functional and phylogenetic) and can be used to analyse patterns of community assembly. However, we recognise that our approach does not address questions about how specific traits or niche dimensions drive species coexistence and community assembly. Indeed, much insight has been generated by analysing traits separately instead of combining them into single measures (e.g. Cavender-Bares *et al.* 2006;

Spasojevic & Suding 2012; de Bello *et al.* in press), and researchers should still examine how individual traits influence community assembly. However, when the links between measured traits and species niches is unknown, the default practice is to find multivariate descriptions of species overall differences. Furthermore, previous work has emphasised the importance of simultaneously describing multiple facets of biodiversity for a more complete picture of ecological patterns (e.g. Mason *et al.* 2005). Also, traits can be selected for inclusion in an analysis either for *a priori* reasons (mechanistic links to function, resource economics, etc.) or as part of a comprehensive sweep of traits meant to capture overall phenotypic differences. Merging phylogenetic and trait information makes sense when the latter approach is taken, because trait distances may lack clear connections to the niche and ecological processes. However, our approach will often be useful even when a few well-understood traits are measured, because additional ecologically relevant information may be present in the phylogeny.

Finally, our use of functional traits and phylogenetic distances assumes that these are fixed at the species level. However, recent work in community ecology has emphasised the need to include trait differences among individuals within a species (Johnson *et al.* 2006; Albert *et al.* 2011; Violle *et al.* 2012). The impetus for this shift comes from the fact that species trait values can be quite variable, and this variability of trait values expressed by individuals within a species both provides the raw material for evolution and is a primary driver of biotic interactions. Consequently, considering intraspecific variation is required for a true reconciliation between ecological and evolutionary approaches. Our FPDist method provides an important tool to include intraspecific information. The traitgrams we show stop at the species level, but could easily be extended to include genetic or trait information at the population or individual level.

Community assembly ultimately depends on how organisms cope with the physical environment and abiotic interactions. Species may enter and persist in a local community because of their ecological fit to local conditions, and community ecologists strive to understand and predict this fit. By adopting an approach that utilises both phylogenetic and trait information, we gain greater power and better insight into the mechanisms sorting species into communities. While both phylogenetic and trait-based measures have weaknesses, the functional-phylogenetic measures introduced here, provides an approach to lessen those weaknesses and to distinguish among a greater number of community assembly patterns.

ACKNOWLEDGEMENTS

We thank Pedro Peres-Neto and Jonathan Davies for organising a workshop on community phylogenetics at the Université du Québec à Montréal, and for valuable input into the ideas presented here. We are further grateful to Allison Derry, Stephane Dray, Hedvig Nenzen, Denis Reale, Mark Urban and Mark Vellend for helpful discussions about considering traits and phylogeny. We thank Sandra Lavorel for the subalpine grasslands data as well as Cristina Roquet Ruiz for the subalpine grassland phylogenetic tree and Wilfried Thuiller for discussions about FPDist. MWC was generously supported by a Discovery Grant (386151) from the National Sciences and Engineering Research Council of Canada (NSERC). CHA was supported by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework

Program (DYVERSE project, no. 272284). SCW was supported by NSERC grant no. 7738-07 to Pierre Legendre.

AUTHORSHIP

All authors contributed equally to developing the proposed methodology, writing the manuscript and writing R code. MC conceived of the original idea. SW ran and analysed the simulations. CA analysed the field data.

REFERENCES

- Ackerly, D. (2009). Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proc. Natl Acad. Sci.*, 106, 19699–19706.
- Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violle, C. (2011). When and how should intraspecific trait variability be considered in plant ecology? *Perspect Plant Ecol Evol Syst*, 13, 217–225.
- Andrewartha, H.G. & Birch, C. (1954). *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Baldwin, B.G. & Sanderson, M.J. (1998). Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proc. Natl Acad. Sci.*, 95, 9402–9406.
- de Bello, F., Lavorel, S., Lavergne, S., Albert, C.H., Boulangeat, I., Mazel, F. *et al.* (2013). Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography*, 36, 393–402.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745.
- Botta-Dukat, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.*, 16, 533–540.
- Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, 4, e5695.
- Cavender-Bares, J. & Wilczek, A. (2003). Integrating micro- and macroevolutionary processes in community ecology. *Ecology*, 84, 592–597.
- Cavender-Bares, J., Keen, A. & Miles, B. (2006). Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology*, 87, S109–S122.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009). The merging of community ecology and phylogenetic biology. *Ecol. Lett.*, 12, 693–715.
- Cooper, N. & Purvis, A. (2010). Body size evolution in mammals: Complexity in tempo and mode. *Am Nat*, 175, 727–738.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E. *et al.* (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.*, 51, 335–380.
- Curtis, J.T. (1959). *The Vegetation of Wisconsin*. The University of Wisconsin Press, Madison, WI.
- Diaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655.
- Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. *et al.* (2004). The plant traits that drive ecosystems: evidence from the three continents. *J. Veg. Sci.*, 15, 295–304.
- Evans, M.E.K., Smith, S.A., Flynn, R.S. & Donoghue, M.J. (2009). Climate, niche evolution, and diversification of the “Bird-cage” evening primroses (Oenothera, sections Anogra and Kleinia). *Am. Nat.*, 173, 225–240.
- Flynn, D.F.B., Mirotnick, N., Jain, M., Palmer, M.I. & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity-ecosystem function relationships. *Ecology*, 92, 1573–1581.
- Futuyma, D.J. (2010). Evolutionary constraint and ecological consequences. *Evolution*, 64, 1865–1884.
- Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelot, P., Ducout, B. *et al.* (2001). Consistency of species ranking based on functional leaf traits. *New Phytol.*, 152, 69–83.
- Grime, J.P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, Chichester.
- Harmon, L.J., Losos, J.B., Davies, T.J., Gillespie, R.G., Gittleman, J.L., Jennings, W.B. *et al.* (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, 64, 2385–2396.
- Harvey, P.H. & Pagel, M. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Helmus, M.R., Bland, T.J., Williams, C.K. & Ives, A.R. (2007). Phylogenetic measures of biodiversity. *Am Nat*, 169, E68–E83.
- Helmus, M.R., Keller, W., Paterson, M.J., Yan, N.D., Cannon, C.H. & Rusak, J.A. (2010). Communities contain closely related species during ecosystem disturbance. *Ecol. Lett.*, 13, 162–174.
- Hill, M.O. (1973). Intensity of spatial pattern in plant communities. *J. Ecol.*, 61, 225–232.
- Johnson, M.T.J., Lajeunesse, M.J. & Agrawal, A.A. (2006). Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.*, 9, 24–34.
- Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.*, 16, 545–556.
- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.P., Garden, D., Girel, J. *et al.* (2011). Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *J. Ecol.*, 99, 135–147.
- Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.*, 11, 995–1007.
- Losos, J.B., Warheit, K.I. & Schoener, T.W. (1997). Adaptive differentiation following experimental island colonization in Anolis lizards. *Nature*, 387, 70–73.
- Macarthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 111, 112–118.
- Mayfield, M.M. & Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.*, 13, 1085–1093.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.
- Mouquet, N., Devictor, V., Meynard, C., Munoz, F., Bersier, L.F., Chave, J. *et al.* (2012). Ecophylogenetics: advances and perspectives. *Biol. Rev.*, 87, 769–785.
- Petchey, O.L. & Gaston, K.J. (2002). Functional diversity (FD), species richness and community composition. *Ecol. Lett.*, 5, 402–411.
- Petchey, O.L., Hector, A. & Gaston, K.J. (2004). How do different measures of functional diversity perform? *Ecology*, 85, 847–857.
- Poos, M.S., Walker, S.C. & Jackson, D.A. (2009). Functional-diversity indices can be driven by methodological choices and species richness. *Ecology*, 90, 341–347.
- Quétier, F., Lavorel, S., Thuiller, W. & Davies, I. (2007). Plant-trait-based modeling assessment of ecosystem service sensitivity to land-use change. *Ecol. Appl.*, 17, 2377–2386.
- Raunkiaer, C. (1934). *The Life Forms of Plants and Statistical Plant Geography*. Oxford University Press, Oxford.
- Schleuter, D., Daufrense, M., Massol, F. & Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, 80, 469–484.
- Seehausen, O. (2006). African cichlid fish: a model system in adaptive radiation research. *Proc. Roy. Soc. B: Biol. Sci.*, 273, 1987–1998.
- Silvertown, J., Dodd, M. & Gowing, D. (2001). Phylogeny and the niche structure of meadow plant communities. *J. Ecol.*, 89, 428–435.
- Spasojevic, M.J. & Suding, K.N. (2012). Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *J. Ecol.*, 100, 652–661.
- Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B. & Araújo, M.B. (2011). Consequences of climate change on the Tree of Life in Europe. *Nature*, 470, 531–534.
- Urban, M. & Skelly, D. (2006). Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology*, 87, 1616–1626.
- Valente, L.M., Reeves, G., Schnitzler, J., Mason, I.P., Fay, M.F., Rebelo, T.G. *et al.* (2009). Diversification of the African genus Protea (Proteaceae) in the Cape biodiversity hotspot and beyond: equal rates in different biomes. *Evolution*, 64, 745–760.

- Violle, C., Enquist, B.J., McGill, B.J., Liang, L., Albert, C.H., Hulshof, C. *et al.* (2012). The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.*, 27, 244–252.
- Walker, B., Kinzig, A. & Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, 2, 95–113.
- Webb, C.O. (2000). Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.*, 156, 145–155.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.
- Weiher, E. & Keddy, P.A. (1995). Assembly rules, null models, and trait dispersion – new questions front old patterns. *Oikos*, 74, 159–164.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.*, 3, 3.
- Whittaker, R.H. (1956). Vegetation of the great smoky mountains. *Ecol. Monogr.*, 26, 1–69.

- Wiens, J.J. (2008). Commentary on Losos (2008): niche conservatism deja vu. *Ecol. Lett.*, 11, 1004–1005.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004). The world-wide leaf economics spectrum. *Nature*, 428, 821–827.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Editor, Arne Mooers

Manuscript received 11 March 2013

First decision made 10 April 2013

Manuscript accepted 26 June 2013