

REVIEW AND SYNTHESIS

Ecophylogenetics redux

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Abstract

Species' evolutionary histories shape their present-day ecologies, but the integration of phylogenetic approaches in ecology has had a contentious history. The field of ecophylogenetics promised to reveal the process of community assembly from simple indices of phylogenetic pairwise distances – communities shaped by environmental filtering were composed of closely related species, whereas communities shaped by competition were composed of less closely related species. However, the mapping of ecology onto phylogeny proved to be not so straightforward, and the field remains mired in controversy. Nonetheless, ecophylogenetic methods provided important advances across ecology. For example the phylogenetic distances between species is a strong predictor of pest and pathogen sharing, and can thus inform models of species invasion, coexistence and the disease dilution/amplification effect of biodiversity. The phylogenetic structure of communities may also provide information on niche space occupancy, helping interpret patterns of facilitation, succession and ecosystem functioning – with relevance for conservation and restoration – and the dynamics among species within foodwebs and metacommunities. I suggest leveraging advances in our understanding of the process of evolution on phylogenetic trees would allow the field to progress further, while maintaining the essence of the original vision that proved so seductive.

Keywords

Brownian motion, clustering, community assembly, competition, filtering, null models, over-dispersion, phylogenetic distance.

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INTRODUCTION

The history of community ecology is complex, and a perceived lack of progress in the field has led more than one researcher to suggest the field's imminent demise (Lawton 1999; Ricklefs 2008). Sitting between population ecology and macroecology, community ecology has been criticised for lacking general laws that allow strong prediction, and the contingency and complexity of ecological interactions means that any single observation can be aligned with any one of dozens of causal pathways. Ecophylogenetics – a portmanteau of ecology and phylogenetics – defined a new field of research that promised to reveal the process of community assembly from the phylogenetic relationships of the species within them. In what has become a seminal paper, Webb and colleagues outlined a seductively simple framework, leveraging the rapidly accumulating data on species evolutionary relationships, to infer the mechanism structuring ecological communities from easy to calculate indices of phylogenetic pairwise distances (Webb *et al.* 2002). While the ideas presented by Webb and colleagues were further refined and extended (e.g. Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009; Mouquet *et al.* 2012), there was also increasing awareness that the mapping of process to pattern might not be so simple (e.g. Gerhold *et al.* 2015; Cadotte *et al.* 2017; Münkemüller *et al.* 2020).

Many of the assumptions underlying ecophylogenetics approaches have their roots in much earlier work, for example

in the species:genus ratios used by Elton (1946); Webb (2000) provided an explicit phylogenetic framework. The basic premise was straightforward: assuming ecological traits were phylogenetically conserved, such that closely related species tended to share more similar trait values than distantly related species, then competition for limiting resources would tend to inhibit co-existence of close relatives – phylogenetic overdispersion – among whom we would predict competition would be strong, whereas environmental filtering would tend to favour the coexistence of close relatives – phylogenetic clustering – as they would share more similar environmental preferences (Figure 1). Phylogenetic community structure was typically quantified by measuring the mean pairwise distances among species within the community, and then compared to some null expectation, most usually generated by randomising community membership across species in the regional species pool. Coinciding conveniently with the increasing availability of large and comprehensive phylogenetic trees for many groups, the field exploded (Cadotte & Davies 2016).

ECOPHYLOGENETICS CHALLENGED

The rapid adoption of ecophylogenetic methods in community ecology provided new insights into how species assemble across space (e.g. Cavender-Bares *et al.* 2004; Kembel 2009; Graham *et al.* 2009) and time (e.g. Helmus *et al.* 2010; Cavender-Bares & Reich 2012). Some common trends emerged. A remarkable frequency of communities appeared

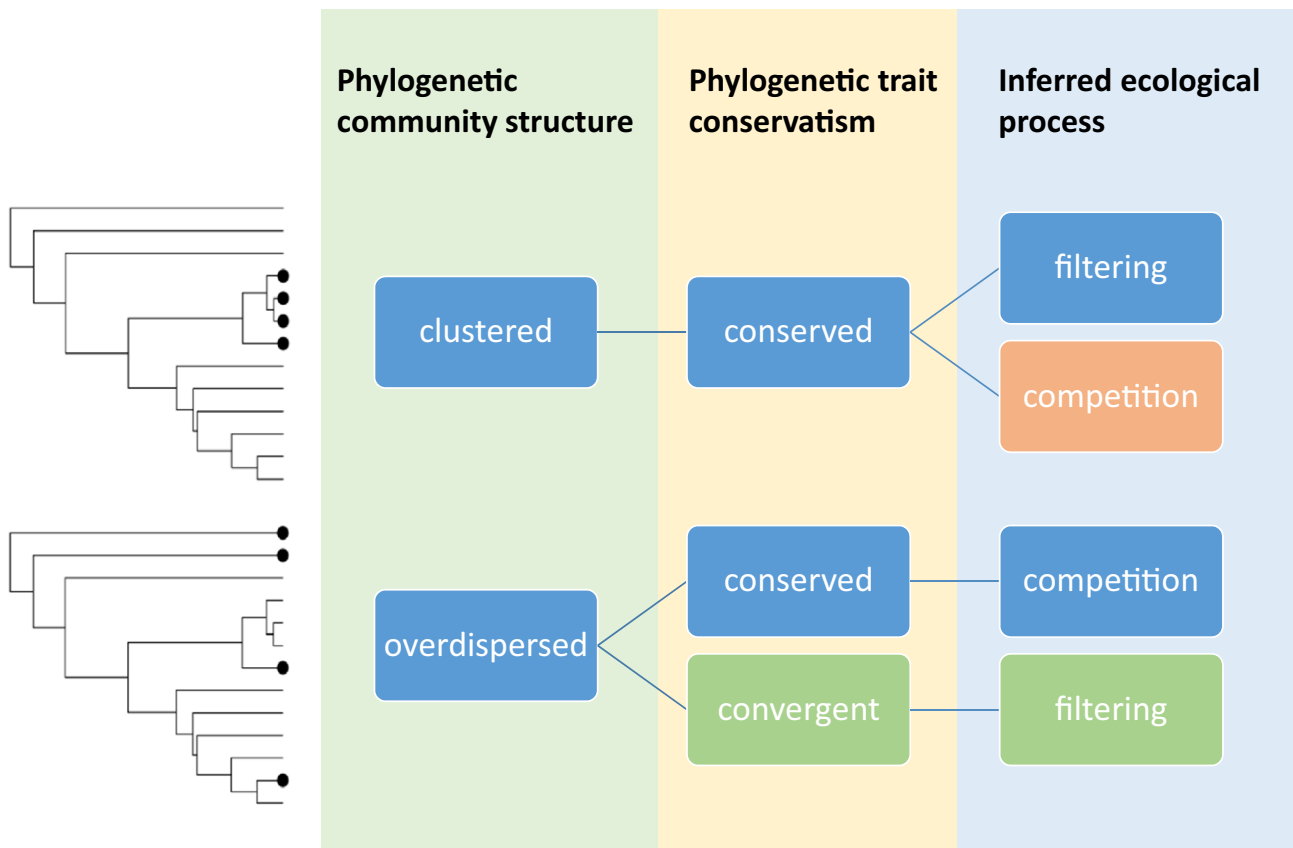


Figure 1 Ecological process does not map uniquely to ecophylogenetic pattern. Two alternative phylogenetic community structures illustrated on the phylogenies to the left – filled circles represent co-occurring species within a community – demonstrating phylogenetic clustering (top) and phylogenetic overdispersion (bottom). Assuming phylogenetic conservatism of traits, phylogenetic clustering is traditionally interpreted as evidence for (environmental) filtering, and phylogenetic overdispersion as evidence for competition (blue boxes). If traits are convergent, such that less closely related species have more similar trait values, then phylogenetic overdispersion can also indicate filtering (green boxes). Strength of phylogenetic conservatism can be quantified relative to expectations from a model of Brownian motion (see main text); however, as illustrated in Figure 2, traits evolved under assumptions of Brownian motion do not necessarily align closely with the underlying phylogeny – Brownian motion captures the expected variance in trait values, not their absolute differences. If coexistence is maintained through equalizing mechanisms that reduce fitness differences rather than niche differences, then phylogenetic clustering (on conserved traits) can additionally suggest evidence for competition (Mayfield & Levine 2010) (orange box).

to show non-random phylogenetic structure, at small scales phylogenetic dispersion was more likely to be observed, but phylogenetic clustering was overall more common, and became stronger at larger spatial scales and as the species pool expanded. Two influential review papers (Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009) provided an overview of the field, and discussed predictions for mutualistic and multi-trophic interactions. However, some notes of caution were also sounded, specifically (1) apparent over-dispersion could switch to clustering when expanding the species pool, (2) Type II errors were inflated for species-poor communities and as community size approached the size of the species pool (Kraft *et al.* 2007), (3) multiple traits or trait combinations could map to similar ecological function, (4) competition might not always lead to limiting similarity and competitive exclusion (see also the following section) and (5) a single snapshot of community structure might not capture the dynamic process of community assembly (Gerhold *et al.* 2015).

Experimental evidence was also undermining some of the central tenets of ecophylogenetic theory as originally formalised by Webb (2000). Close relatives were not always each other's strongest competitors (Cahill Jr *et al.* 2008; Venail *et al.* 2014), and phylogenetic distance did not necessarily correlate strongly with ecological distance (Narwani *et al.* 2013). In some cases, detectable filtering on traits, such as wing-length and body mass in humming birds along an elevational gradient, were not reflected in ecophylogenetic patterns, even when traits demonstrated phylogenetic conservatism (Graham *et al.* 2012). Furthermore, within communities demonstrating significant phylogenetic structure, patterns in one clade could differ from patterns in another clade (Elliott *et al.* 2016).

ECOPHYLOGENETICS AND MODERN COEXISTENCE THEORY

The field of ecophylogenetics was further challenged by developments in co-existence theory. Chesson (2000) demonstrated

mathematically how coexistence was maintained by a trade-off between fitness differences and competitive abilities. Mayfield & Levine (2010) illustrated how assumptions of modern coexistent theory undermined the presumed link between pattern and process that had been a bedrock of contemporary ecophylogenetic thinking. If coexistence is maximised when competitive differences are small, and competitive ability is trait-mediated, then we would predict competition would lead to phylogenetic clustering (assuming traits are phylogenetically conserved) – opposite to common interpretations in the literature (Figure 1). The seminal paper by Webb and colleagues (Webb *et al.* 2002) discussed in some detail the complexities of species coexistence, including predictions from Chesson (2000): ‘[s]pecies may coexist within a habitat by non-niche-partitioning, equalizing (*sensu* Chesson 2000) processes . . .’ (p. 482) and ‘[w]here related, similar species do co-occur, attention must be given to mechanisms that permit the co-existence of similar rather than different organisms’ (p.488.). The conclusions from Mayfield and Levine should not, therefore, have come as a surprise, but in the enthusiasm of the moment many of the cautionary warnings in Webb *et al.* (2002) had been over-looked.

More nuanced work that followed explored the linkages between phylogenetic relatedness, niche differences and the average fitness differences that determine relative competitive abilities. In a study of annual plant species, Godoy and colleagues (Godoy *et al.* 2014) found that phylogenetic distance was unrelated to (stabilising) niche differences, but species fitness was phylogenetically structured, such that less closely related species had greater competitive asymmetry. As it is non-trivial to obtain direct field measures of both niche differences and competitive differences (Chesson 2008), phylogeny might thus provide a useful proxy. In a field observation study of closely related *Carex* (sedge) species, Elliott & Davies (2017) assumed phylogenetic distance as proxy for niche differences and inferred competitive (fitness) differences from the expected trade-off between ecological generalism and competitive ability. In this study, there was evidence for greater co-occurrence among species that are phylogenetically distant (i.e. assumed large niche differences) and with similar niche widths (i.e. assumed small competitive differences), which broadly fits within Chesson’s coexistence framework and suggests phylogenetic proxies may have utility. However, as the axes of fitness differences and niche differences are not entirely separable – the same trait might covary with both – attempts to place them on orthogonal axes may be misguided (Barabás *et al.* 2018), and whether or how phylogenetic history might inform modern coexistence theory is not yet fully resolved.

PHYLOGENETIC MODELS AND A RETURN TO EVOLUTIONARY ROOTS

While the number of papers continued to accumulate, the field underwent a period of introspection, and the major assumptions that connected pattern to process were re-examined (Gerhold *et al.* 2015; Cadotte *et al.* 2017; Swenson 2019). The common application of ecophylogenetic methods in ecology had resulted in a drift from the evolutionary theory on which it was founded. Transforming phylogenetic branch lengths to

match to models of trait change would provide a better coherence between phylogenetic distances and trait differences (Cadotte *et al.* 2017), yet such approaches are rarely adopted in the ecophylogenetics literature (but see Letten & Cornwell 2015). By connecting ecophylogenetics back to its evolutionary roots it also becomes self-evident why phylogenetic structure is a poor index of community process based on one or a few traits, irrespective of the underlying phylogenetic signal in those traits (see Figure 2). Critically, even more evolutionary informed models fail to address the fundamental challenge in disambiguously inferring ecological process from ecophylogenetic pattern (Münkemüller *et al.* 2020).

More sophisticated ecophylogenetic approaches, such as the phylogenetic mixed models of community structure of Ives & Helmus (2011) – PLMMs and their generalised form for presence–absence data (PGLMMs) – provided an alternative to the metrics of phylogenetic dispersion that had become entrenched in the field. These methods looked to partition the contributions of phylogeny, traits and environment to community composition (Li & Ives 2017; Li *et al.* 2017), but were more agnostic as to process. Other methodological developments with similar aims that emerged around the same time and earlier included, among others, metacommunity phylogenetics (Leibold *et al.* 2010; Peres-Neto *et al.* 2012), phylogenetic gradient analysis (Peres-Neto & Kembel 2015), and RLQ ordination (see Pavoine *et al.* 2011). By disaggregating predictors of community composition into their separate components, their relative importance could be explored, for example a strong signal of environment might be consistent with abiotic filtering, assuming the relevant environmental axis was included in the model. While PGLMMs were initially challenging to fit, new implementations have made their application much more straightforward (e.g. Li *et al.* 2020), and it is perhaps too early to tell whether they will be fully embraced by the community. However, many of these earlier methods failed to gain much traction, despite often having demonstrably more power to detect phylogenetic and trait structuring in community composition. It appeared that high statistical power was not sufficient for widespread adoption. The appeal of the original metrics was perhaps because they promised to reveal the processes structuring communities from phylogeny alone.

NEW APPLICATIONS: EXPANDING THE ECOPHYLOGENETIC DOMAIN

While the initial focus of ecophylogenetic methods was on differentiating between environmental filtering and competition, they have permeated the field of community ecology. It is possible that, in sum, the impact of ecophylogenetic approaches beyond their original narrow focus has been greater; it has certainly been rather less controversial. By moving away from inferring community assembly processes from ecophylogenetic pattern, we avoid many of the criticisms that have been levelled at the field, and when we instead use ecophylogenetic metrics as independent predictors in models testing evolutionary hypotheses, we leverage their greater potential (see also Gerhold *et al.* 2015). I illustrate here some notable examples of how ecophylogenetic approaches, applied more broadly,

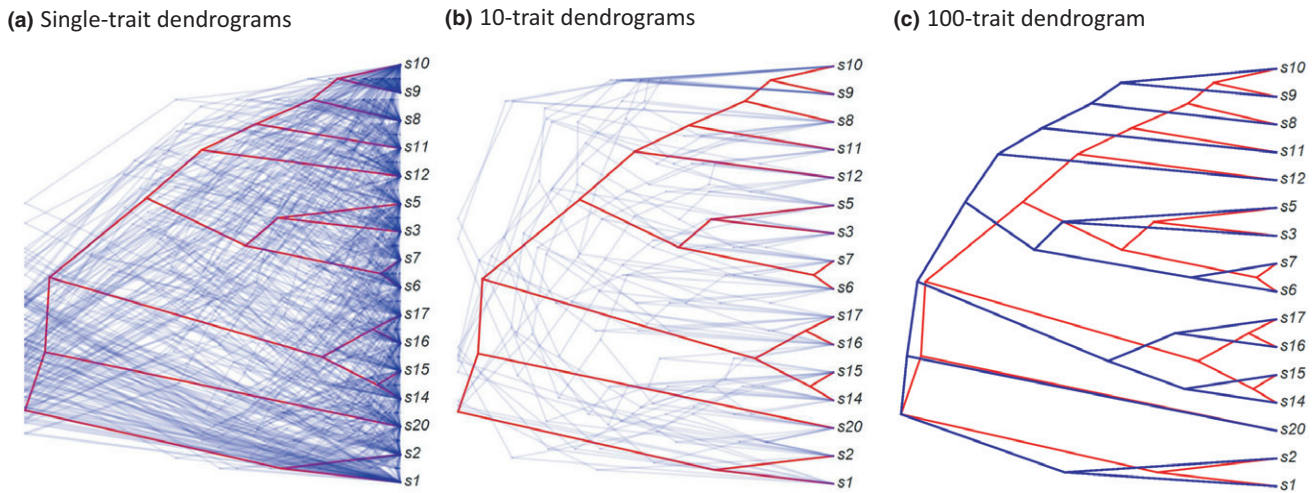


Figure 2 Single traits do not recapitulate the phylogenetic topology on which they were simulated. Phylogenetic signal is typically measured with respect to a Brownian motion model of evolution (e.g. Pagel's lambda [Pagel 1999] or Blomberg's K [Blomberg *et al.* 2003]) – strong phylogenetic conservatism is indexed by a close match to Brownian expectations. However, Brownian motion is a model for the movement of particles in a liquid – akin to a random walk – an inherently noisy process. Traits simulated under a model of Brownian motion on a simple birth-death tree for 16 taxa, and then used to construct a trait dendrogram from the Euclidean distance matrix, show clearly that phylogenetic distances are a poor proxy for ecological distances when defined by a single trait (Letten & Cornwell 2015; Cadotte *et al.* 2017). Dendrograms from independently evolved traits (a) are highly variable, and do not closely match the cophenetic distances on the true tree – shown in red (see note below): mean correlation between trait differences and phylogenetic cophenetic distances: $r = 0.27$. It is only when we consider multiple traits does phylogenetic distance become a useful surrogate for trait differences. Dendrograms inferred from a matrix of 10 simulated traits (b, showing 10 overlaid dendrograms each inferred from a separate matrix of 10 traits sampled from the same set of simulated traits used in the figure to the left), show greater consistency, but still depart from the topology of the true tree, especially in the deeper branching patterns: mean correlation between trait differences and phylogenetic cophenetic distances, $r = 0.71$. Dendrogram inferred from the complete matrix of 100 traits (c) converges on the phylogenetic cophenetic distances: correlation between trait differences and phylogenetic cophenetic distances, $r = 0.99$. Note: trait dendrograms do not provide an optimal representation of trait space, and so we would not necessarily expect dendrograms to converge on the true tree topology. To facilitate comparison between the trait dendrograms and the phylogenetic distances separating taxa, I show in red the phylogenetic dendrogram reconstructed from the phylogenetic cophenetic distance matrix. Plots were generated using a modified version of the densityTree function from the R package phytools (<https://github.com/liamrevell/phytools>).

have provided significant advances across the field of community ecology. These examples highlight exciting new research fronts, and also directions for the future.

Janzen–Connell Hypothesis

Many pests and parasites infect multiple host species. However, the phylogenetic distribution of their hosts is non-random, and there is growing evidence that parasites of both animals and plants demonstrate phylogenetic conservatism in their host range such that they tend to infest closely related hosts (e.g. Gilbert & Webb 2007; Davies & Pedersen 2008). If plant pests mediate species coexistence – as proposed independently by Dan Janzen (1970) and Joseph Connell (1971) – then pests might also structure the phylogenetic composition of plant communities. The Janzen–Connell hypothesis describes a density-dependent process by which host-specific plant pests and pathogens reduce recruitment near conspecific adults, suppressing the abundance of the most dominant species in a community, and thereby maintain community diversity (see Wright 2002). As originally presented, the Janzen–Connell mechanism simply differentiated between conspecific and heterospecific hosts. A simple phylogenetic extension of the Janzen–Connell model (see Cavender-Bares *et al.* 2009) would suggest that pests might suppress recruitment not only of conspecifics, but also of closely related heterospecifics,

facilitating the maintenance of more phylogenetically diverse communities (Webb *et al.* 2006). Liu *et al.* (2012) refer to this as the phylogenetic Janzen–Connell effect, and provide experimental evidence that tree seedling survival rate was higher for seedlings grown in soil collected from more distantly related host trees, suggesting phylogenetic specificity of soil fungal pathogens. Parker *et al.* (2015) provide further support for the phylogenetic Janzen–Connell effect in a grassland coastal community, showing that total pest pressure is best explained by the phylogenetically weighted abundance of co-occurring species. The phylogenetic Janzen–Connell thus provides a mechanism for maintaining not only the species diversity, but also the phylogenetic diversity of communities, as phylogenetically rare species will benefit from lower pest pressure.

Darwin's Naturalisation Hypothesis & the Enemy Release Hypothesis

Invasive species present a significant threat to biodiversity (Bellard *et al.* 2016; Brondizio *et al.* 2019), and the transport of species around the globe has accelerated with increasing trade and movement of people. However, only a few species establish and become naturalised following introduction, and only a subset of these go on to become invasive (Richardson & Pyšek 2012). Darwin suggested that species introduced into novel communities with few close relatives may be more likely

to establish because resource use overlap, and thus competition, would be lower – Darwin's Naturalisation Hypothesis (Daehler 2001). An alternative explanation for the establishment success of more distantly related invaders is the Enemy Release Hypothesis (Keane & Crawley 2002). In the latter, phylogenetic conservatism in the host breadth of native pests and pathogens, as described above, provides a disease- and pest-free ecological opportunity for introduced species phylogenetically distant from native flora or fauna. While we typically lack direct data on disease pressure and the ecological niche of native and non-native species, the phylogenetic pairwise distances between native and invading species provide a simple test of the assumed pattern. In a study of non-native grasses in California, Strauss *et al.* (2006) showed that invasive species were less closely related to native species than introduced but non-invasive grasses, supporting predictions of both the Enemy Release Hypothesis and Darwin's Naturalisation Hypothesis.

More recent phylogenetic studies, applying similar approaches, have shown that patterns can be scale sensitive (Levin *et al.* 2020; Park *et al.* 2020), helping resolve Darwin's 'naturalisation conundrum'. The conundrum reflects the competing predictions made by Darwin on the expected relatedness between non-native and native taxa (Diez *et al.* 2008). While Darwin's Naturalisation Hypothesis makes predictions that non-native species should be less closely related to the native species pool, his 'preadaptation' hypothesis suggests that non-native species more closely related to the native pool would be advantaged as they are more likely to share adaptations to similar environments. In a study of non-native species in the US, Park *et al.* (2020) reveal that preadaptation is supported at larger spatial scales, whereas the Naturalisation Hypothesis is supported in warmer and more humid environments, and at smaller scales. In a complementary study on non-native trees in South Africa, Bezeng *et al.* (2015) also show support for both processes, preadaptation better explains whether a non-native tree is able to establish, the Naturalisation Hypothesis better explains whether or not it becomes invasive, thus the process of naturalisation can be separated from the process of invasion. A next challenge is to resolve whether escape from competition or enemy release provides the more general explanation for the success of more distantly related invaders at local scales. Addressing this challenge will require catching the pest-free window that allows invading species to expand in native communities (Agrawal *et al.* 2005).

The dilution/amplification effect

The biodiversity crisis has driven another scientific controversy to prominence – the effect of species diversity on disease prevalence. It has been proposed that more diverse host communities may reduce disease prevalence and forward transmission of pathogens – the dilution effect (Ostfeld & Keesing 2000). The increasing prevalence of Lyme disease, which is caused by the bacterium *Borrelia burgdorferi* and vectored by the black-legged tick (*Ixodes scapularis*), in less species-rich wildlife communities is frequently used as an illustration (Ostfeld & Keesing 2000). The generality of the dilution effect has,

however, been challenged as it is predicated on a number of assumptions, not least of which is the assumption that the most abundant hosts in species-poor communities must also be highly competent disease reservoirs (Schmidt & Ostfeld 2001; Randolph & Dobson 2012), and in some cases host diversity has been suggested to increase disease prevalence, for example through increased opportunities of disease spillover (Power & Mitchell 2004) – the amplification effect. The generally strong phylogenetic structure in the host breadth of pest and pathogens suggest host phylogenetic relatedness might allow us to make better predictions of whether changes in host (phylogenetic) diversity will result in increases or decreases in disease prevalence.

Using measures of mean pairwise distance among wild ungulate and herbivore communities in Africa, Wang *et al.* (2019) showed that the disease burden on livestock was higher when wildlife communities were more phylogenetically clustered, consistent with a disease amplification effect among more phylogenetically related wildlife reservoir hosts. In plants, Parker *et al.* (2015) also used pairwise phylogenetic distances between community members to show that the contribution of hosts to amplification vs dilution effects was predicted by their phylogenetic distance to other community members – a corollary of the phylogenetic Janzen–Connell effect, discussed earlier. Phylogenetically distant hosts were more likely to experience reduced disease pressure and contribute little to overall disease abundance, whereas phylogenetically close host species were more likely to act as disease amplifiers.

Facilitation and the Stress-Gradient Hypothesis

While facilitation is unquestionably an important component of community assembly, it is distinct from the traditional dichotomy of competition and environmental filtering that has dominated the ecophylogenetic literature. Verdu *et al.* (2012) suggested a general trend for facilitation to be more frequent between distant relatives, presumably because they are likely to be more ecologically separated (see also Valiente-Banuet & Verdú 2013). We can also envisage scenarios where the facilitation of close relatives is favoured, for instance plants with flowers of similar colour with which to attract pollinators, as proposed by Münkemüller *et al.* (2020). Regardless of the direction, if phylogenetic relatedness mediates facilitation, then it must also be included in models looking to test the different explanations for facilitation. For example the Stress Gradient Hypothesis predicts that interspecific interactions switch from negative (competitive) to positive (facilitative) along an environmental gradient of increasing abiotic stress (Bertness & Callaway 1994). In a study of alpine plant communities, Pistón *et al.* (2015) used pairwise phylogenetic distances to explore facilitation between foundation species – in this instance, cushion-forming nurse plants – and co-occurring community members. In this example, interactions shift from negative to positive along the stress gradient – supporting the Stress Gradient Hypothesis – but only for facilitated species closely related to nurse plants. The interaction between cushions and more distantly related community members did not change. Butterfield *et al.* (2013) also used pairwise

phylogenetic distances to illustrate how increasing facilitation by cushion-forming nurse plants maintains community phylogenetic diversity in harsher environments.

In the above examples, increasing phylogenetic distance between interacting species appears to have reduced the strength of competition sufficiently for facilitation to emerge. Importantly, both the phylogenetic and environmental context are relevant: facilitation is observed only among more distantly related species pairs, and only in harsher environments.

Succession and restoration ecology

Nurse plant facilitation provides one approach for restoring depauperate ecological communities. Verdú *et al.* (2012) suggest that co-planting of phylogenetically distant species (those separated by > 100 MY) in nurse-based restoration could thus help kick-start the process of succession in disturbed communities. Enrichment planting to enhance diversity of recovering ecosystems, such as in secondary forests, may also benefit from phylogenetically structured additions, with seedlings more phylogenetically distant from the dominant canopy community having greater establishment success (Schweizer *et al.* 2013) (see the Janzen–Connell hypothesis, above). Such management practices might have long-lasting benefits. For example in grasslands, more phylogenetically diverse seed mixes, as quantified using mean pairwise phylogenetic distances, result in more phylogenetically diverse mature communities (Barak *et al.* 2017). Ecophylogenetic metrics have also been used to explore impacts of seed source and mixture – phylogenetic monitoring – as illustrated by Khalil *et al.* (2017) in a grassland restoration example (see also Cavender-Bares & Cavender 2011).

The phylogenetics of succession, however, is complex. For instance in the early stages of succession, early colonising species presumably experience reduced competition, and traditional ecophylogenetic theory might then predict a stronger effect of filtering and greater phylogenetic clustering relative to later successional stages (Letcher *et al.* 2012). As a consequence, phylogenetically informed restoration actions might vary with successional stage. In heavily degraded habitats, such as old mine sites, restoration during early successional stages might benefit from the addition of seedlings from closely related plants that share common traits that support soil formation and stabilisation, whereas in the later stages of succession communities might be enriched via the addition of more phylogenetically distant species (Shoener *et al.* 2015). But not all systems show increasing phylogenetic dispersion through later stages of succession (Letten *et al.* 2014). In addition, there may be variation in the phylogenetic structuring of different age cohorts as communities progress through the different stages of succession. For example in tropical forest, Letcher (2010) observed overdispersion in small stems during the early stages of succession, and overdispersion in larger stems during later stages of success. It is likely, therefore, that different size classes are subject to different ecological pressures; yet identifying these processes remains a challenge, and they are not revealed by phylogenetic patterns alone.

Priority effects and historical contingency

The search for phylogenetic structure in ecological assemblages implicitly assumes that the taxonomic composition of community membership is somewhat deterministic (even if the processes structuring communities remain obscure). However, the order of arrival of species into a community may have large impacts on subsequent species establishment success – priority effects (Fukami 2015). Such historical contingencies might result in alternative community stable states, alternative transient dynamics, or compositional cycles (Fukami 2015), and presumably impact phylogenetic community structure. Priority effects may arise through niche pre-emption (inhibitory) and niche modification (either inhibitory or facilitative) (Fukami 2015). In the former, only species sharing a common resource base (niche) are affected, because species niches show phylogenetic conservatism (Wiens *et al.* 2010), we would thus predict niche pre-emption to be more common among closely related species.

Observing priority effects and impacts of historical contingency requires temporal data that are difficult to obtain or experimentally manipulate for most organisms. Because of their short generation times, microbial communities provide useful model systems. Peay *et al.* (2012) observed priority effects in nectar yeast communities, and used pairwise phylogenetic distances to show that effects were stronger between close relatives, supporting the niche-pre-emption hypothesis. Later arrivals were less likely to establish and attain high densities when initial colonisers were close relatives, but early arriving species experienced little negative impacts from later arrivals, irrespective of relatedness (see Tan *et al.* [2012] for similar findings). Migrant communities offer another useful study system, effectively allowing observations of priority effects following each seasonal migration. For instance Klingbeil & Willig (2016) contrasted the phylogenetic structure of resident and migrant bird communities and revealed that assemblages with a greater proportion of migrants exhibited a more random community structure, whereas assemblages dominated by residents tended to be phylogenetically overdispersed, consistent with a more deterministic process of community assembly. The authors hypothesise that priority effects in the migrant assemblages lead to alternative, and thus less predictable, phylogenetic community structures as the identity of early arrivers determine the colonising success of later arriving species.

Ecosystem stability and productivity, and conservation

The conservation of phylogenetic diversity (PD), most usually defined as the sum of the branch lengths connecting a taxon set, has been argued as important as greater PD has been suggested to capture greater feature diversity (Faith 1992). While the exact mapping of feature diversity on to PD is perhaps less straightforward than commonly assumed (Tucker *et al.* 2018; Mazel *et al.* 2018), at the community scale, there is some evidence that more phylogenetically diverse assemblages are more productive (Cadotte 2013) and promote ecosystem stability (Cadotte *et al.* 2012). It has also been suggested that preserving PD, and thus feature diversity, may maintain

future options in an uncertain world, and thus PD is also a measure of option value (Faith 2018). Phylogenetic diversity is a summative metric, and it captures variation in both species diversity and species phylogenetic dispersion. However, both dimensions may contribute separately to ecosystem function and the association between biodiversity and ecosystem productivity.

The positive links between biodiversity and ecosystem function have been attributed to two broad mechanisms: the selection effect, in which more diverse communities are more likely to include a species with a large contribution to ecosystem function, and species complementarity, in which ecosystem functioning is enhanced through species (niche) differences (Loreau 2000). Phylogenetic diversity is likely to maximise the selection effect – a more phylogenetically diverse species assemblage is more likely to sample a species with a large effect because PD maximises both species richness and feature diversity. However, phylogenetic dispersion is better able to capture species niche complementarity because a more even spacing of species on the phylogeny is predicted to translate into a more even spacing of species in niche space (Cadotte 2013; Davies *et al.* 2016). In a study of forest productivity, Paquette & Messier (2011) used a measure of phylogenetic species variability (PSV) (Helmus *et al.* 2007) – equivalent to the mean pairwise distance between species – to better show the unique contribution of phylogenetic dispersion (PSV was a significant predictor of ecosystem productivity, but its effect size was less than that of species richness). The pairwise phylogenetic distances between species were also associated with increased productivity in bacterial communities, but the underlying mechanisms differed between species-poor and species-rich communities: the selection effect dominated species poor communities, whereas the complementarity effect was dominant in species-rich communities (Venail & Vives 2013).

Recent analyses have suggested that, at local scales, there has been no systematic change in the species richness of communities over time, but that the composition of species has altered (Dornelas *et al.* 2014; Blowes *et al.* 2019). While the implications of these changes are not yet clear, history suggests they could foreshadow future extinctions (Pandolfi *et al.* 2020). If we wish to preserve not just species diversity, but also the integrity and functioning of ecosystems, we need to integrate both species richness and species' functional contributions into conservation planning (Hillebrand *et al.* 2018). When species functional roles are unknown or difficult to measure, PD may provide a useful conservation target (Vane-Wright *et al.* 1991; Faith 1992). However, the invasion of evolutionarily distinct species could increase PD while providing little or negative ecosystem benefits (Elliott & Davies 2019). The phylogenetic structure of a community – its phylogenetic dispersion – provides an alternative metric for characterising community responses to environmental change, and a guide for conservation management (e.g. Arroyo-Rodríguez *et al.* 2012).

Foodwebs

Phylogeny has been shown to be a useful predictor of trophic relations in foodwebs. Because closely related species are likely to fill similar trophic niches, they are also likely to have

similar positions in the web (Cattin *et al.* 2004). Knowledge of the location of a species in foodwebs can provide information on the severity of cascading extinctions should that species be pruned from the web. For example foodwebs are highly sensitive to the removal of well-connected species, while removing species with few connections has less effect (Dunne *et al.* 2002). Webs with high trophic redundancy are also more robust to species removal (Sanders *et al.* 2018), but as links are sequentially pruned, sensitivity to subsequent extinctions is amplified (Allesina *et al.* 2009). If phylogeny can provide a guide to species trophic position, it might then also help make predictions on the sensitivity of foodwebs to species extirpations. For instance webs with many closely related species (phylogenetic under-dispersion) might be more robust because of greater functional redundancy.

Foodwebs typically span across the branches of the tree-of-life whereas current well-resolved phylogenetic trees are limited to particular clades (although see Kumar *et al.* 2017); tests of phylogenetic structure in foodwebs have therefore typically derived pairwise evolutionary distances by counting nodes separating species on the Linnaean taxonomy (e.g. Cattin *et al.* 2004; Bersier & Kehrli 2008; Chiu & Westveld 2011; Eklöf *et al.* 2012; Naisbit *et al.* 2012). Such measures are necessarily coarse, although it has been suggested that this coarse resolution might better reflect the phylogenetic depth of structure within webs (Eklöf *et al.* 2012). Thus, while taxonomy, as a surrogate for phylogeny, has been shown to be a useful predictor of various network properties, such as intervality (e.g. Eklöf & Stouffer 2016), and there is increasingly strong evidence for phylogenetic conservatism in trophic links (e.g. Gripenberg *et al.* 2019), we currently still lack complete and fully resolved phylogenetic trees of entire webs.

Recent approaches allow us to 'fill-out' missing links among species within webs (e.g. Gray *et al.* [2015] and Morales-Castilla *et al.* [2015], who present frameworks also informed by phylogeny), and have allowed the construction of very large webs, such as the foodweb of tetrapods in Europe (O'Connor *et al.* 2020). The tetrapod web is species-rich, although it does not, of course, include links with primary producers or with insect herbivores, nonetheless, such approaches combined with progress towards assembling a comprehensive tree of life (Hinchliff *et al.* 2015) hold much promise for the future.

Metacommunities

Traditional ecophylogenetic analyses consider communities as discrete assemblages, independent samples drawn from a larger species pool. However, except in rare circumstances, a local community may be better described as a spatial aggregation of species that is linked to other local communities through dispersal, which together comprise a metacommunity (Leibold *et al.* 2004). The metacommunity framework acknowledges the non-independence of local communities and inherently transcends spatial scales. Leibold *et al.* (2004) proposed four general metacommunity archetypes: neutral model, patch dynamics, mass effects and species sorting. While these archetypes may not be mutually exclusive, species sorting and mass effects are the most often evaluated (Logue *et al.* 2011). Thompson *et al.* (2020) provide a more generalisable framing

of competitive metacommunity dynamics based on three core processes: (1) density-independent responses to the abiotic environment, (2) density-dependent biotic interactions and (3) dispersal. Ecophylogenetic methods extend naturally to both paradigms. Species sorting and density-independent response to abiotic conditions fit within the environmental filtering metaphor embedded in traditional ecophylogenetic theory. Mass effects similarly assume an environmental filter, but species may persist in sink habitats if inward dispersal is sufficient. Density-dependent interactions may also be captured using ecophylogenetic approaches; however, the challenges to the utility of such methods posed by modern coexistence theory (see above), apply equally to their application within metacommunity ecology (Leibold & Chase 2017).

While phylogenetic approaches have been explored for quantifying metacommunity structure, they have tended to differ from more traditional ecophylogenetic methods (but see Pontarp *et al.* [2012] for an example applied to simulated metacommunities). For instance Pillar and Duarte (2010) present a novel framework, integrating phylogeny, traits and abundance, to evaluate the dissimilarity between communities. Using fuzzy weighting of community composition by phylogenetic similarities, they were able to test for phylogenetic signal at the metacommunity level. Leibold *et al.* (2010) developed a phylogenetic expansion of Legendre *et al.*'s (1997) fourth corner method to tease apart the effects of historical biogeography and environmental filtering, and Chalmandrier *et al.* (2015) used a phylogenetic extension of Hill numbers (Chao *et al.* 2010) to weight the contribution of rare vs. common species in structuring metacommunities (see also Hsieh & Chao 2017). It is perhaps worth noting that these approaches do not use the phylogenetic structure of species within (meta)communities to make inferences on the strength of species sorting.

Synthesis

The diverse applications of ecophylogenetics across community ecology emphasise how species' evolutionary histories can help our understanding of their present-day ecologies. However, the insights we gain are only as robust as the assumptions underlying our models – as laid bare by Mayfield & Levine (2010) – and the rigour of our analyses. Gerhold *et al.* (2015) and Münkemüller *et al.* (2020) provide several excellent suggestions on how ecophylogenetic studies can be better designed and, ultimately, the need for experimental tests. For example a particular weakness of many studies has been to first index the phylogenetic structure of a community, and then make conclusions about species interactions within it. Because multiple processes can give rise to similar ecophylogenetic pattern, such *post hoc* hypothesising or HARKing – hypothesising after the results are known (Kerr 1998) – can result in fragile statistical inference. Another and perhaps more insidious failing is that we tend not to recognise the number of choices we make when conducting our analyses.

ECOPHYLOGENETICS: GOOD PRACTICE

Many fields in science are undergoing a replication crisis, whereby published results from one study do not replicate in

follow-up studies (Ioannidis 2005). One reason for this crisis is that studies based on small sample sizes and noisy data are biased towards over-estimating effect sizes when we threshold by P-values (Loken & Gelman 2017). An additional, but not independent, issue that has fed into the replication crisis is researcher degrees of freedom – the numerous choices we make when analysing a dataset (Simmons *et al.* 2011) – sometimes referred to as the 'garden of forking paths' (Loken & Gelman 2017). While it is now generally appreciated that data dredging or 'fishing' for statistical significance is bad practice, we frequently interrogate data with multiple models, applying various transformations, inclusion criteria, interaction terms, etc. and report significant findings without recording the trail of rejected tests. Oftentimes, the more we interrogate data, the more rigorous we feel in our analyses; however, we risk the same pitfalls as fishing, and may even assume a misplaced confidence in our results. In ecophylogenetics, we make many choices when conducting analyses (see also Münkemüller *et al.* 2020).

The ecophylogenetic garden of forking paths

When analysing phylogenetic structuring in vascular plants, we first need to define the taxonomic breadth of the study. For instance gymnosperms may or may not be included (Cadotte *et al.* 2017), and because their common ancestor with angiosperms dates back to approximately 300 MYR, this decision can greatly impact the mean pairwise distances between species (e.g. see Massante *et al.* 2019). The choice of species pool and spatial scale can also dramatically impact standard effect sizes (Cavender-Bares *et al.* 2006; Kembel & Hubbell 2006; Swenson *et al.* 2006). The choice of null model (Vamosi *et al.* 2009), whether to transform the branch lengths on the phylogenetic tree (Letten & Cornwell 2015) and whether or not to weight by species abundance (Kembel 2009) add further forks. Finally, we can choose from one (or several) of the numerous phylogenetic structure metrics (Tucker *et al.* [2017] list 70 possible phylo-diversity metrics) to describe the species assemblage.

The ecophylogenetic garden of forking paths quickly becomes a maze within which we can become disoriented. Preregistration – formally detailing data collection and analysis protocols prior to conducting a study – has been suggested as one solution to reduce researcher degrees of freedom (Nosek *et al.* 2018). However, it is not yet widely practiced in ecology, where unforeseen events, such as storms, disease, fire and droughts, can dramatically impact planned data collection protocols, yet also provide valuable research opportunities, impossible to foresee and plan for (e.g. Spiller *et al.* 1998; Donihue *et al.* 2018). Nonetheless, it would be relatively straightforward to declare the ecophylogenetic pipeline before performing any analysis, and state fundamental hypotheses – are species assemblages predicted to be more or less closely related than our null – *a priori*. In ecophylogenetic studies, it is not uncommon to first look for patterns and then search for a process that might explain observations. This approach has merit as part of exploratory data analysis (see below), but it is rarely recognised as such. As a hypothesis-testing framework, it is not only confounded by the problem that multiple

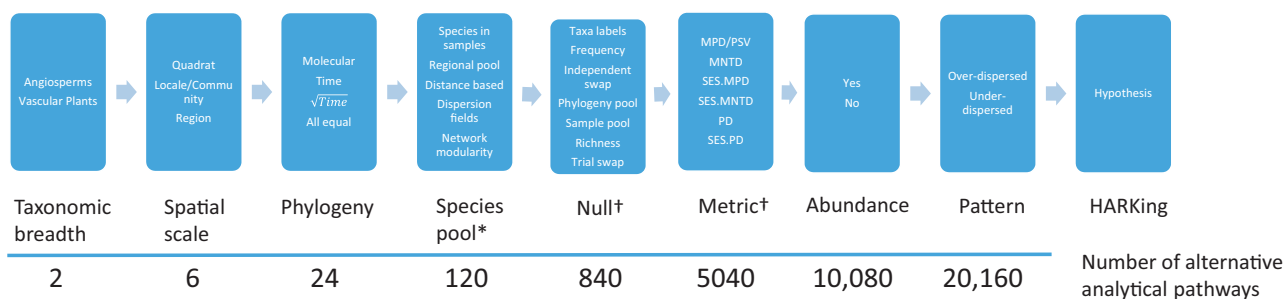
processes can give rise to similar patterns, but by the fact that multiple patterns can emerge from the same data when different analytical pathways are followed. For more robust hypothesis testing, I suggest in Figure 3 a simple heuristic as a guide to navigate the ecophylogenetic garden of forking paths. Once declared, deviations from this pipeline should be explained (if not precluded), and all results should be reported, not just those that pass the significance filter (Gelman 2018).

Exploratory data analyses

While employing ecophylogenetic methods in a clearly defined hypothesis-testing framework provides a more powerful approach to disentangling underlying mechanisms, ecophylogenetic approaches might nonetheless still be useful for exploratory analyses. Macroecology and biogeography have a long and productive history based largely on observation data and exploratory analyses. Similarly, ecophylogenetics has revealed general trends in the phylogenetic structure of community assemblages, for example less clustered

communities at finer taxonomic and spatial scales (see Vamosi *et al.* 2009). Such patterns are consistent with a hypothesis of either greater competitive displacement at fine scales and/or stronger environmental filtering at larger scales; however, it is not a test of either hypothesis. Patterns over space should be interpreted similarly. For instance greater phylogenetic clustering of assemblages at high elevations, would be consistent with stronger environmental filtering in harsher abiotic environments (Graham *et al.* 2009). However, abiotic filtering might also generate phylogenetic over-dispersion if filtering is on traits that show evolutionary convergence. For instance high elevation sites today might provide refugia for cold-adapted species, perhaps filtering on glacial relicts with convergent traits suited to climates at the last glacial maximum (Shoener *et al.* 2018). Exploratory ecophylogenetic analyses thus allow us to generate hypotheses on processes structuring communities (e.g. the scales at which competition vs filtering may be the dominant mechanism shaping communities). Independent tests are then required to evaluate these hypotheses (Gerhold *et al.* 2015; Münkemüller *et al.* 2020).

(a) Cumulative number of decisions we make when we analyse phylogenetic community structure



(b) Ecophylogenetic pipeline

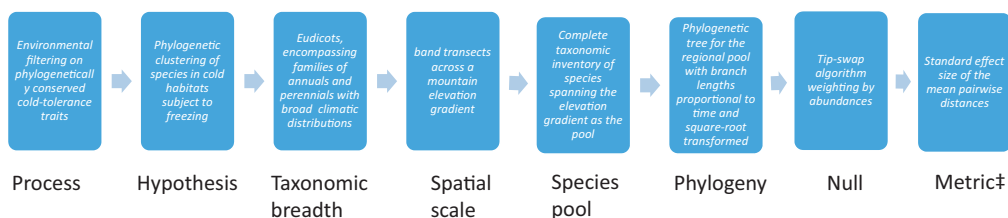


Figure 3 Navigating the ecophylogenetic garden of forking paths – the ecophylogenetic pipeline. We make numerous choices (a) when analysing ecophylogenetic data – researcher degrees of freedom – which can result in fragile statistical inference. In the example here, I illustrate eight analytical steps, each with numerous options, generating a possible 20,160 alternative analytical pathways. Although this number of pathways might seem high, I include only commonly used options, and the circumscription of the spatial scale and species pool provides almost limitless possibilities. By clearly defining the ecophylogenetic pipeline (b) prior to data collection and analysis, we can reduce model over-fitting, and thus provide a stronger hypothesis testing framework. Here, I propose a simple heuristic that involves, moving left to right, i) identifying the process of interest, ii) forming a hypothesis on how the process structures species assemblages, iii) identifying the appropriate taxonomic depth at which structuring is most likely to be present, iv) identifying the relevant spatial scale and v) species pool to capture the process, vi) declaring the tree topology and branch lengths, vii) specifying the appropriate null model and viii) phylo-diversity index, and finally ix) performing the analysis. Text in boxes gives an example of a hypothetical ecophylogenetic study. Note that in the proposed ecophylogenetic pipeline the hypothesis is generated before data collection, but in the ecophylogenetic garden of forking paths, the hypothesis often comes after the results are known – HARKing (Kerr 1998). *See Lessard *et al.* (2016) for definitions of alternative species pools. †Options for null models and metrics as provided in the widely used R package Picante (Kembel *et al.* 2010). ‡Münkemüller *et al.* (2020) provide additional guidelines for developing hypotheses, and make the excellent suggestion of using data simulations to verify that the chosen analytical approach has sufficient power to detect the process of interest.

Exploratory data analysis might also allow us to identify lineages with a large effect on community structure. Jackknife or bootstrapping techniques provide one approach to isolate the individual contributions of lineages to phylogenetic structure (Figure 4; see also Davies *et al.* 2016; Molina-Venegas *et al.* 2019). Such lineages might be associated with key traits or functions that mediate interactions among co-occurring species. For example lineages associated with a cushion life form have been hypothesised to buffer alpine plant communities from harsh abiotic conditions, and thus moderate a more general productivity–phylogenetic diversity relationship (Butterfield *et al.* 2013). In grassland systems, lineages associated with nitrogen fixation (i.e. Legumes) have large ecological effects, and might influence community structure directly through increased nutrient availability, and indirectly via shifting competitive interactions. In both cases, we might expect communities with such key-stone lineages to have different phylogenetic structure. However, we do not always have such a clear hypothesis on the important traits. By identifying lineages of large effect we can help guide the search for key ecological traits in systems less well-known (Davies *et al.* 2016).

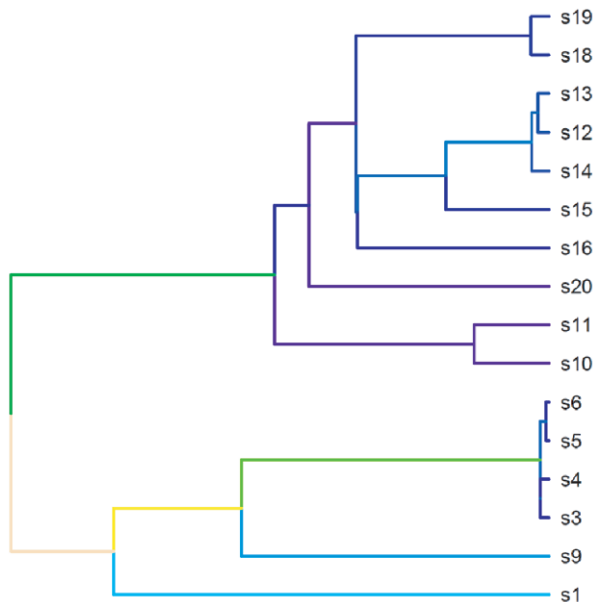
An alternative, but complementary approach to identifying evolutionary features that contribute most to community phylogenetic structure has been to consider the phylogenetic depth at which ecophylogenetic signature arises. For example, comparisons of phylogenetic distances between the nearest

neighbours (i.e. the mean nearest neighbour distance [MNTD] or nearest taxon index [NTI]) are suggested to better capture signal towards the tips of the phylogeny than tree-wide indices that consider pairwise distances between all taxa (i.e. mean pairwise distance [MPD] or net relatedness index [NRI]) (Webb 2000). If we consider the different niche axes that might determine species co-occurrence vs habitat preferences – the α and β niches, respectively, of Ackerly *et al.* (2006) – we could test predictions that the former should be more apparent in tip-level metrics whereas the latter should be more apparent from tree-wide metrics (Hardy & Senterre 2007).

Non-independence

In both hypothesis testing and exploratory analyses, care must be taken in the statistical interpretation of pattern. In standard statistical models, we assume that errors are independent and identically distributed; violating this assumption can bias parameter estimates and inflate Type I errors. In biogeography, spatial autocorrelation among observations is a well-recognised problem, and a number of statistical procedures have been developed to correct for it (Dormann *et al.* 2007). In community-level analyses, that is models with communities as sampling units, non-independence might arise from both spatial structure in the environment – adjacent locations are likely to share similar environmental features – and via species co-distributions (Hardy 2008), and different statistical

Lineage contribution to the mean of the pairwise distances among all species



Lineage contribution to the mean of the pairwise distances between nearest neighbours

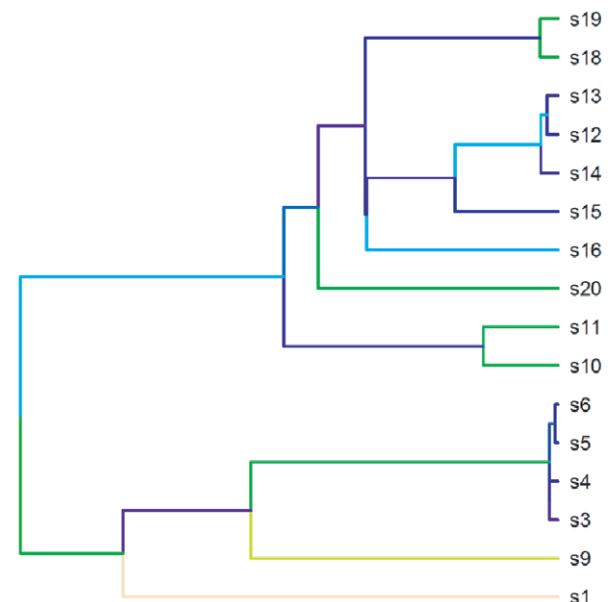


Figure 4 Some lineages contribute disproportionately to the phylogenetic structure of a community. Simulated birth-death tree with branches shaded by their relative contribution to the mean of the pairwise distances separating species, commonly used indices of phylogenetic dispersion – lighter shading indicates greater contribution (see Davies *et al.* [2016] for details). Identifying lineages with large influence might help guide the search for key traits important in structuring communities. For measures of the mean pairwise distances among all taxa (left), lineages towards the root of the tree and those subtending imbalanced clades will tend to have greater influence. For measures of the mean nearest taxon distance (right), both evolutionary isolated branches and lineages with close relatives can have large influence. See the NODESIG command in the Phylocom software (Webb *et al.* 2008) for a conceptually similar approach to identifying over- and under-represented clades.

approaches may apply to these different types of processes and mechanisms (Peres-Neto & Legendre 2010). In ecophylogenetics, non-independence in spatially structured communities can run deep as not only might communities have species in common, they will almost certainly share phylogenetic branch lengths, that is, even if there is no overlap in species composition, the two sets of species will likely share common ancestors. Cadotte *et al.* (2017) highlight this problem in the context of experimental competition trials; however, it pervades most cross-community comparisons. Freckleton & Jetz (2009) present a method that allows us to jointly model effects of space and phylogeny in cross-species comparative analyses. Such approaches could be adapted to cross-community analyses, for instance substituting the species variance-covariance matrix given by the shared path lengths on the phylogeny, for one that captures the phylogenetic overlap between communities or, in a metacommunity context, through extensions of Legendre's (1997) fourth-corner (Leibold *et al.* 2010) and related methods (Peres-Neto *et al.* 2012).

NEW DIRECTIONS: PHYLOGENY AS A NULL MODEL

When one or a few traits are thought important for determining species coexistence, as in the literature exploring evolutionary character displacement (Dayan & Simberloff 2005), phylogenetic relationships among species can inform our null expectation (Davies *et al.* 2007; Davies *et al.* 2012) (Figure 5). For example Brownian motion provides a neutral evolutionary model to which we can compare empirical trait

distributions. Character displacement is predicted to result in more even trait spacing to reduce niche overlap. We can thus test whether observed patterns of spacing are more or less even relative to phylogenetic expectations under Brownian motion (or other evolutionary models), usefully circumventing the need to define the species pool, required in more traditional randomisation approaches (see Gotelli & Graves 1996), to which ecophylogenetics patterns are highly sensitive (as the discussion earlier).

The example presented in Davies *et al.* (2012), uses information on the variance in size ratios of body sizes to evaluate evidence of character displacement within the desert mammal community of Yotvata, Israel. In this example, the observed size ratios are contrasted with two evolution nulls generated by simulating traits on the known species phylogeny assuming either a Brownian motion model of evolution or an Ornstein–Uhlenbeck processes, representing a model of bounded evolution. This test-statistic provides a good test of overdispersion (evenness in trait spacing); however, it is a poor test of underdispersion (clustering in traits). Low variance in size ratios indicates even trait spacing, and we can generate our null expectation simply from the phylogeny of the species within the community. However, without reference to the larger species pool, we can only detect evidence of trait clustering if we have information on the potential bounds of trait space or knowledge of the true rate of evolution (i.e. σ^2 in the Brownian simulations) to parameterise the underlying model of trait divergence. In part, this reflects the different scales at which processes generating trait clustering vs. trait dispersion

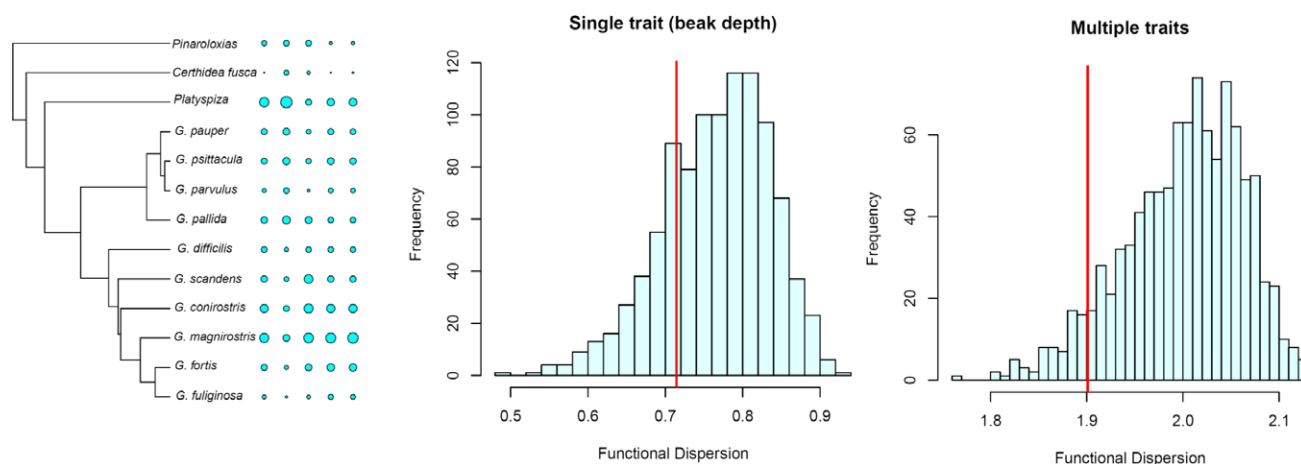


Figure 5 Phylogeny can be used to generate an evolutionary null of expected trait distributions with which to compare empirical observations and test ecological and evolutionary hypotheses. Left panel, phylogenetic tree of Darwin's finches (*Geospiza*) and standardised trait values (filled circles) shown at the tips for wing length, tarsus length, culmen length, beak depth and gonyx width (left to right), data available from the R package Geiger (<https://github.com/mwpennell/geiger-v2>). Darwin's finches are famously thought to have adaptively radiated on the Galápagos Islands and diverged in their beak morphology, which is associated with dietary partitioning. We might, therefore, predict that species would show greater differences in their beak morphology than expected from their phylogenetic relationships. However, when we overlay the observed trait dispersion for beak depth (middle panel, vertical red line) on a frequency histogram showing expected dispersion of traits simulated on the *Geospiza* phylogeny under a model of Brownian motion (1000 replicates), we can see that the observed dispersion for beak depth falls comfortably within the distribution of simulated values. Thus, there is no evidence that beak depth is more variable than predicted from phylogenetic relationships and a null model of neutral evolution. Furthermore, the observed trait dispersion for the five traits combined (right panel, vertical red line) falls even further towards the left of the null expectation (frequency histogram showing expected trait dispersion estimated from multiple independently evolving traits, $n = 5$, 1000 replicates). Here, we might conclude that beak morphology encompasses a smaller volume of trait space than expected under a neutral model of evolution. Possible explanations for trait under-dispersion include a constrained model of trait evolution, such as characterised by an Ornstein–Uhlenbeck process, correlated evolution among trait axes, or environmental filtering on the niche hypervolume. Trait dispersion quantified using the function dbFD from the R package FD.

operate – if all species observed within a community have experienced the same trait filter, we have no expectations as to the spacing of traits within that community (i.e. trait values within the clustered species set could be overdispersed, underdispersed or random).

Considering the volume of trait space occupied, vs. the pairwise distances between traits, can allow us to address a wider breadth of hypotheses that easily scales to multiple traits. I present an example of Darwin's finches, using a distance-based metric of functional diversity (Laliberté & Legendre 2010) on scaled trait values (Figure 5). Here, I am able to show that beak depth is no more variable than expected from our phylogenetic expectations, and when multiple axes of beak morphology are considered, the volume of occupied trait space narrows further, arguably opposite to what we might have predicted from a model of adaptive radiation (Losos *et al.* 2003; Losos 2008). While I present these data as illustration only, the models are straightforward to apply and provide a simple index of phylogenetic niche conservatism in multi-dimensional trait space.

Evolutionary models and ecophylogenetic methods can also be combined in novel ways such that each informs the other. For example clades displaying unusual phylogenetic structuring might be linked to macroevolutionary shifts in the trajectory of traits that mediate coexistence. Pearse *et al.* (2019) illustrates that this appears to be the case in small rodent communities; in this example, clades that tend to demonstrate unusual phylogenetic structuring within communities are also characterised by distinct modes of body size evolution. The next step is to match models of species interactions and community structure to models of trait evolution (Harmon *et al.* 2019).

The integration of phylogenetic comparative methods, such as independent contrasts (Felsenstein 1985) and the phylogenetic regression (Grafen 1989), in ecology was initially met with some resistance, yet such approaches are now mainstream. A similar shift is required in community ecology. Gerhold *et al.* (2015) describe thinking of 'phylogenetic-pattern-as-result' and 'phylogenetic-pattern-as-cause', and in his recent book, Swenson (2019) simply refers to using phylogeny as 'backbone'. We should embrace the fact that the interactions between species within communities are shaped by their shared evolutionary histories – phylogeny – and we should integrate this information into our models of community ecology. For example when examining evidence for character displacement or trait filtering, we might be easily misled if we do not consider the phylogenetic relationship of co-occurring species, and at larger spatial scales, the biogeographic and climatic history of diversification may also be relevant (Hardy & Senterre 2007).

SUMMARY

Ecophylogenetic methods provide a valuable set of tools, but they must be used thoughtfully. In isolation such metrics tell us little about the mechanism structuring community assembly other than it is typically non-random with respect to some null sampling of the species pool – even communities assembled through neutral dynamics can show strong phylogenetic structuring. Phylogenetic ecology has much to offer once freed

from the narrow focus of using pairwise distance to differentiate between filtering and competition, which was almost certainly never the intention of the authors of Webb *et al.* (2002) who were so instrumental in defining the field.

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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13682>.

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