

# Understanding the concepts of community phylogenetics

Charlotte Ndiribe<sup>1,2</sup>, Nicolas Salamin<sup>1,2</sup> and Antoine Guisan<sup>1,3</sup>

<sup>1</sup>Department of Ecology and Evolution, Biophore, University of Lausanne, Lausanne, Switzerland,

<sup>2</sup>Swiss Institute of Bioinformatics, Genopode, Lausanne, Switzerland and

<sup>3</sup>Institute of Earth Sciences, Geopolis, University of Lausanne, Lausanne, Switzerland

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## ABSTRACT

**Background:** Community phylogenetics is an emerging field of research that has made important contributions to understanding community assembly. The rapid development of this field can be attributed to the merging of phylogenetics and community ecology research to provide improved clarity on the processes that govern community structure and composition.

**Question:** What are the major challenges that impede the sound interpretation of the patterns and processes of phylogenetic community assembly?

**Methods:** We use four scenarios to illustrate explicitly how the phylogenetic structure of communities can exist in stable or transient phases, based on the different combinations of phylogenetic relationships and phenotypic traits among co-occurring species. We discuss these phases by implicating a two-way process in the assembly and disintegration of the given ecological community.

**Conclusions:** This paper synthesizes the major concepts of community phylogenetics using habitat filtering and competition processes to elucidate how the understanding of phylogenetic community structure is currently hindered by the dynamics of community assembly and disassembly.

*Keywords:* community assembly, community phylogenetics, niche conservatism, trait evolution.

## INTRODUCTION

### Community phylogenetics: the foundation and the foregoing

Community phylogenetics [or phylogenetic community ecology (*sensu* Webb *et al.*, 2002)] seeks to understand the processes that govern species assemblages on the basis of the phylogenetic relationships shared among co-existing species (Webb *et al.*, 2002; Emerson and Gillespie, 2008; Vamosi *et al.*, 2009). As a field primarily devoted to characterizing the structure of ecological communities, the basic tenets of community ecology, as well as the conceptual challenges and sound interpretation of assembly processes, directly apply to community phylogenetics

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Correspondence: C. Ndiribe, Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland. e-mail: charlotte.ndiribe@unil.ch

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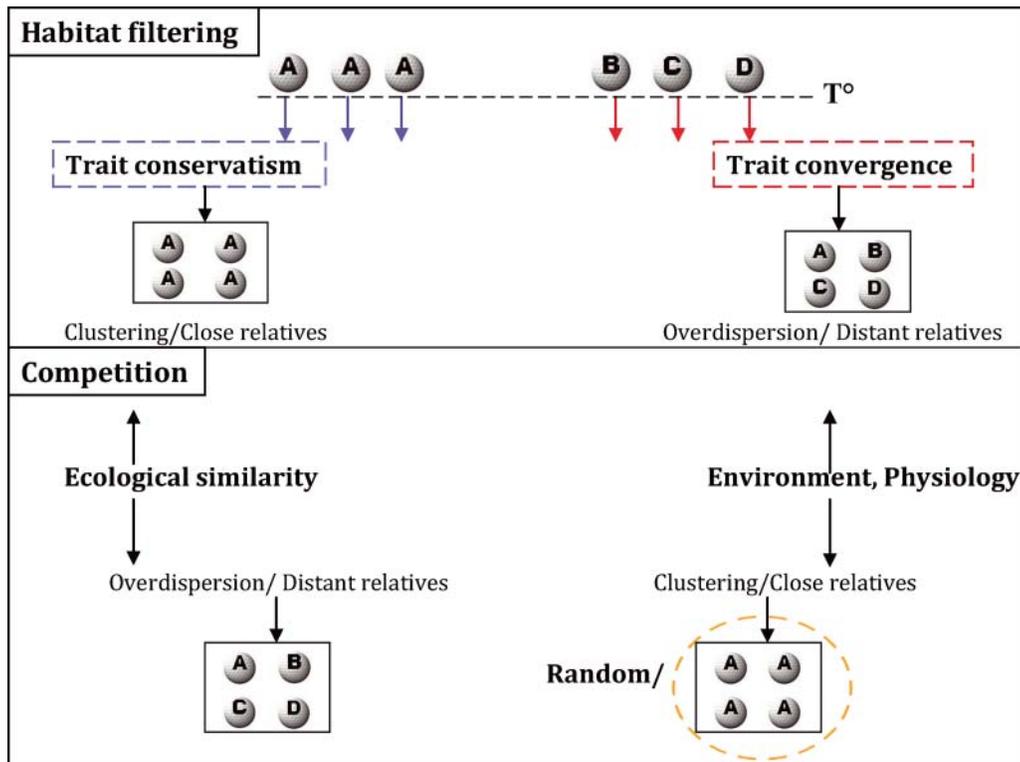
(Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009). By far the most confused use and interpretation of terminology revolves around the processes that dictate community assembly. More than eight decades of research provide concrete evidence that environmental habitat filtering and limiting similarity or competitive exclusion are widely the two dominant processes that underlie community assembly (Darwin, 1859; Gause, 1934; MacArthur and Levins, 1967; Diamond, 1975; Tilman, 1987; Pacala and Tilman, 1994; Weiher and Keddy, 1999). Habitat filtering was introduced to elucidate patterns of species co-existence based on similar species' ecophysiology and environmental tolerances (Keddy, 1992; Weiher and Keddy, 1999). On the other hand, the competitive exclusion theory states that no two highly ecologically similar species can co-exist in the same resource space and time (Gause, 1934; MacArthur and Levins, 1967; Diamond, 1975).

The contemporary interpretation of habitat filtering and competition in community phylogenetics relies on the use of phylogenetic (phenotypic) clustering and phylogenetic (phenotypic) overdispersion, respectively (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009). Phylogenetic clustering is the pattern associated with habitat filtering which sieves species with similar habitat preferences into the same environments, and these species are often more closely related than predicted from a regional species pool. In contrast, phylogenetic overdispersion is the community structure that results from interspecific competition or the local co-occurrence of distantly related species (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2004; Kraft *et al.*, 2007; Mayfield and Levine, 2010). The reflection of one assembly pattern over the other in a community therefore depends on the intensity of habitat filtering, competitive interactions, and the evolutionary conservatism or convergence among ecologically relevant traits (Davies, 2006; Silvertown *et al.*, 2006; Cavender-Bares *et al.*, 2009).

### Conceptual and methodological challenges

Interpreting these patterns of community assembly remains controversial (Chase, 2003), because of the difficulty in differentiating between the relative importance of habitat filtering and competition in communities (Davies, 2006; Mayfield and Levine, 2010). As pointed out by Mayfield and Levine (2010) in a recent review, opposing patterns of community assembly can mask the detection of assembly processes. Specifically, competition may lead to either phylogenetic overdispersion or phylogenetic clustering, as opposed to only phylogenetic overdispersion (Webb *et al.*, 2002). Furthermore, a mixture of trait conservatism and convergence may influence the same phylogenetic pattern (Fig. 1) (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2004, 2009). For instance, in a comprehensive listing of several biological systems across the world, Emerson and Gillespie (2008) showed that patterns of phylogenetic overdispersion or clustering depended on whether relevant traits were evolutionarily convergent or conserved. Importantly, no assembly pattern could be readily attributed to a unique trait state. This further emphasizes how the interpretation of community assembly is affected by spatial and temporal scale dynamics (Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2006; Kraft *et al.*, 2007). In this context, the organization of diversity, for example, through different spatial components (i.e. the alpha, beta, and gamma niches) can be difficult to untangle (Kneitel and Chase, 2004; Ackerly *et al.*, 2006), especially as traits that predominantly exhibit evolutionary conservatism may not be involved in co-existence within communities (Silvertown *et al.*, 2006).

In the past, controversial debates (e.g. Clement/Gleason, Diamond/Connor and Simberloff) over the structure in ecological communities were mainly devoted to understanding the climax concept of ecological succession and historical contingency (Belyea and Lancaster, 1999; Chase, 2003). These views were divided into whether communities were structured



**Fig. 1.** The dual role of habitat filtering and competition in phylogenetic community structure. Depending on the degree of evolutionary conservatism or convergence of phenotypes, co-occurring species may exhibit patterns of phylogenetic (phenotypic) clustering or phylogenetic (phenotypic) overdispersion. Under habitat filtering and trait conservatism, clustered communities of close relatives are expected in local communities sieved from a given regional species pool, whereas habitat filtering and trait convergence are assumed to create phylogenetically overdispersed communities. Under competition and trait conservatism, a high level of ecological similarity among co-occurring species is expected to give rise to phylogenetic overdispersion, whereas competition and trait convergence may create random communities, or perhaps rarely, phylogenetic clustering in communities when the environment and physiological responses interact with species' phenotypes. The dual role of both assembly processes (i.e. habitat filtering and competition) in driving phylogenetic community assembly remains controversial and difficult to disentangle under natural settings. Here, the balls A, B, C, and D are hypothetical species passing through an environmental filter (e.g. temperature,  $T^\circ$ ), while the boxes depict local communities. A is repeated in the boxes to depict close relatedness.

by deterministic niche processes (i.e. habitat filtering and competition) or stochastic processes (Chase, 2003). Coherent with the stochastic view, two neutral models of community assembly – namely, the theory of island biogeography (MacArthur and Wilson, 1967) and the unified neutral theory of biodiversity and biogeography (Hubbell, 2001) – predict that random patterns in co-occurrence arise from the stochastic dynamics of dispersal and the competitive equivalence among species (see Emerson and Gillespie, 2008). Among several instances, the idea that communities are constantly evolving through stochastic speciation, extinction, and

ecological drift (Cavender-Bares *et al.*, 2009) remains a major difficulty in reconciling the stochastic view with the deterministic view of community structure.

A more recent debate within community phylogenetics, however, addressed whether the concept of phylogenetic niche conservatism (PNC) is a pattern or process (see Losos, 2008a, 2008b; Wiens, 2008; Wiens *et al.*, 2010). Phylogenetic niche conservatism may be seen as an important aspect of community phylogenetics, with a corollary that closely related species exhibit high ecological similarity, and hence should co-occur less often than expected by chance (Webb *et al.*, 2002; Wiens and Graham, 2005; Losos, 2008b). However, the key question at the core of this debate is how competition can arise from stable conserved niches. Despite the simplicity of this question, there appears to be a lack of consensus among authors, in particular regarding how communities differ at the equilibrium or transient state, and whether these differences are, invariably, detectable through the diffusion of regional species richness into local assemblages (Ricklefs and Schluter, 1993; Kraft *et al.*, 2007). Although PNC is relevant to the integration of several assumptions of ecological context and scale in assembly (Wiens, 2008), interpreting PNC is generally complicated, such as when competition is driven by traits that are conserved through time, and/or habitat filtering occurs through convergent evolution (Kraft *et al.*, 2007; Vamosi *et al.*, 2009; Pausas and Verdú, 2010).

Unfortunately, the vast majority of metrics in community phylogenetics, such as the net relatedness index (NRI) and nearest taxon index (NTI) [for a comprehensive list, see Vamosi *et al.* (2009)], are relatively crude for evaluating the multi-dimensional structure of communities. These metrics are mostly conceptually related or strained by cumbersome architecture in performing similar tasks (Helmus *et al.*, 2007a; Pavoine and Bonsall, 2011). They are not well suited to tackle questions on the hierarchical organization of community diversity, such as interpreting the role of hierarchical differences in species' competitive abilities in driving exclusion from communities (Mayfield and Levine, 2010). These challenges create a huge burden for community phylogenetics to surmount, but likely persist because of (i) the inadequate scientific justification of assembly concepts [i.e. the so-called 'jargons' of community ecology (Peters, 1976; Schoener, 1986; Frazier, 1994; Fauth *et al.*, 1996; Simberloff, 2004)], (ii) ecologists have only recently begun to evaluate assembly rules with phylogenies (e.g. since Webb, 2000), or perhaps (iii) polarity in the inheritance of plesiomorphic characters drives the phylogenetic hypothesis to ultimately result in ambiguous patterns of assembly (Miller and Wenzel, 1995; Losos, 2011).

### **Novel perspectives on interpreting phylogenetic community structure**

The use of phylogenetic approaches to detect assembly processes at the community level has also been recently applied to the phylogenetic clade level (Mayfield *et al.*, 2009; Parra *et al.*, 2010; Ndiribe *et al.*, 2013). On this premise, different assembly patterns may emerge among clades because of the different rates of trait evolution that exist among clades (Smith and Donoghue, 2008). Furthermore, co-occurring close relatives cannot be simultaneously considered as distant relatives based on patterns of phylogenetic overdispersion, rather competitive interactions provide a more plausible explanation for the dominant assembly process in the given clade community (Table 1). The clade-level approach is novel, yet relevant as an alternative approach for interpreting complex patterns of community structure. It allows the juxtaposition of assembly patterns along nodes of a phylogenetic tree such that the diffusion of regional phylogenetic (or functional) diversity through drivers of habitat filtering and limiting similarity are better visualized and understood (Parra *et al.*, 2010; Ndiribe *et al.*, 2013).

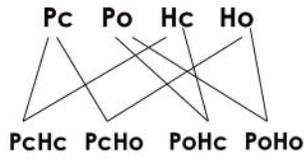
**Table 1.** Interpretation of phylogenetic community structure at the clade and community level

	Clade level	Community level
<b>Conserved traits</b>	Phylogenetic clustering and functional clustering	Phylogenetic clustering/overdispersion and functional clustering
<b>Convergent traits</b>	Phylogenetic clustering and functional overdispersion	Phylogenetic clustering/overdispersion and functional overdispersion

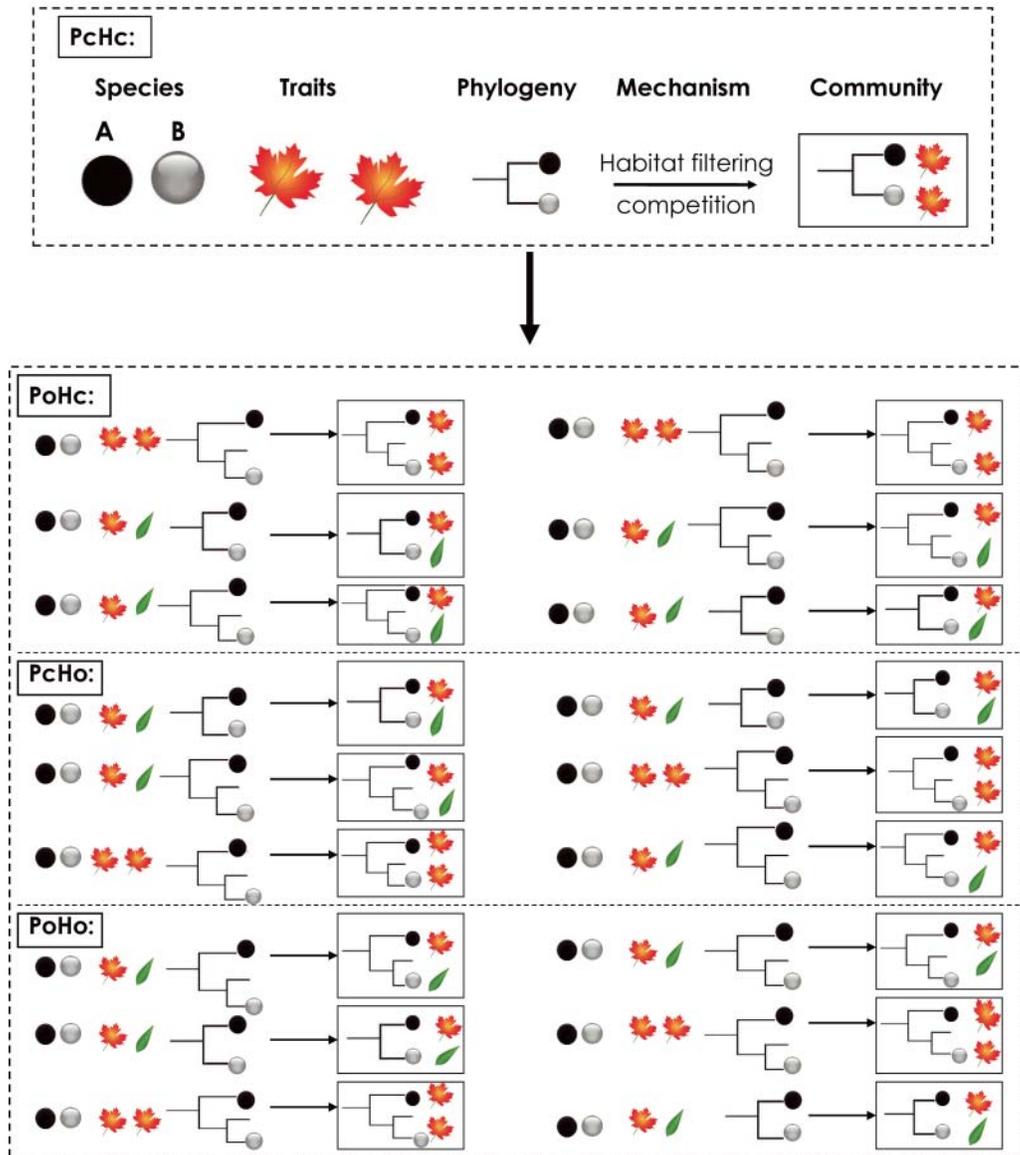
Thus, the factors that control local community diversity (including the incidence of habitat filtering or interspecific competition) may be sampled from the regional species pool, produced through historical factors of speciation and extinction (Davies, 2006; Ricklefs and Schluter, 1993; Kraft *et al.*, 2007; Emerson and Gillespie, 2008). On the other hand, the local species pool may directly influence the sequential assembly of species' communities (Tofts and Silvertown, 2000; Pottier and Evette, 2011). Differentiating one influence from the other may not be so straightforward. However, a plausible example of each is likely the large composition of closely related species from a regional species pool that experienced *in situ* diversification within a few clades in the Cape flora of South Africa (Slingsby and Verboom, 2006), and the little overall variation in the local community composition of alpine grassland systems (Zimmermann and Kienast, 1999; Pottier and Evette, 2011).

In this paper, we make efforts to clarify important aspects of the fundamental notions of community phylogenetics. We proffer explanations for the underlying processes and patterns of phylogenetic community structure (i.e. clustering vs. overdispersion) that arise from given combinations of phylogenetic relatedness and phenotypic traits. We assert that phylogenetic community assembly is driven by a 'before' and 'after' phase of interactions, which occur at the 'assembly' and 'disintegration' of the community. The term disintegration is used in the sense of dissolving an entity into integral components so as to disperse its unity (Ricklefs, 2008), which may be recomposed at a later stage.

Indeed, several ecologists agree that communities can exist in equilibrium or transient stages (e.g. Belyea and Lancaster, 1999; Hubbell, 2001; Ricklefs and Bermingham, 2001; Chase, 2003; Emerson and Gillespie, 2008), but this idea is generally considered only within 'assembly', and has not been discussed enough to enable its investigation in a natural setting. A highly permissible state for several species occurring at the level of the regional pool, especially in systems with small species pools, is a high amount of evolutionary and ecological similarity (Chase, 2003). Thus, a stable community composed of species with high phylogenetic and phenotypic similarity or clustering (PcHc) can be altered to exist in one of three states, namely phylogenetic overdispersion and phenotypic clustering (PoHc), phylogenetic clustering and phenotypic overdispersion (PcHo) or phylogenetic overdispersion and phenotypic overdispersion (PoHo) (Fig. 2). We illustrate these ideas of community structure using four plausible scenarios at the community level (Table 2), which portrays the ecological community as both a stable and evolving unit. We acknowledge that the assumptions behind these scenarios are dependent on several factors, such as the phylogenetic relatedness defined by the genetic markers used to reconstruct the phylogeny, and whether the phenotypic traits considered are under selection or directly involved in resource prehension (e.g. leaf for light, root for water uptake). However, all combinations of phylogenetic relatedness and phenotypic traits (i.e. PcHc, PoHc, PcHo, and PoHo) illustrated by



PcPo: phylogenetic clustering and overdispersion  
 HcHo: phenotypic trait clustering and overdispersion



these scenarios have already been shown to occur in natural communities (but see Emerson and Gillespie, 2008).

### *Scenario 1 (PcHc)*

This is a classical case of phylogenetic and phenotypic clustering under the assumption of conserved species' traits (Webb *et al.*, 2002; Pausas and Verdú, 2010). The community presented here is mostly created by strong filtering interactions (especially if the phenotypes considered are under selection) from the regional species pool, while competition plays an inevitable role in its subsequent re-organization or disintegration (Silvertown *et al.*, 2006). A stable community that exhibits high levels of conservatism can be surmounted by internal and external factors that drive it to change. One such internal factor is clearly explained by the competition-relatedness hypothesis (Cahill *et al.*, 2008), which postulates that closely related species will compete more intensely for resources when traits responsible for ecological similarity are conserved within the phylogeny. In addition, the ecological compression hypothesis holds that the initiation of dispersion in space increases in effect as a function of the carrying capacity of species in a community, and is maintained through the process of interspecific competition (MacArthur and Wilson, 1967). On the other hand, external factors may arise from exotic species invasion (Byers, 2000), anthropogenic land-use pressures and disturbances (Cavender-Bares *et al.*, 2009), or sudden shifts in key environmental trajectories (e.g. due to climate change) that favour negative interspecific interactions (Tilman, 1987; Kneitel and Chase, 2004). Furthermore, the competitive exclusion principle holds that such a high level of similarity between two species A and B should soon lead to fierce competition, and cause the species to minimally co-exist (Gause, 1934; MacArthur and Levins, 1967). Thus, while habitat filtering is likely the initial cause of community assembly, competitive exclusion may drive the stable equilibrium community to disintegrate (Helmus *et al.*, 2007b; Cavender-Bares *et al.*, 2009).

In line with the predictions of the competition-niche similarity hypothesis (MacArthur and Levins, 1967), and the competition-trait similarity hypothesis, competitive interactions are more likely to result among co-occurring species that have a limited range of resource acquisition and regeneration strategy (Kunstler *et al.*, 2012). Depending on the temporal dimension in which species interactions occur, phylogenetic and phenotypic limiting similarity should drive species emigration into new communities (Mouillot *et al.*, 2005; Violle *et al.*, 2011). Finally, niche complementarity may be a further conduit for the transition of scenario 1 to scenario 2. For example, in Floridian oaks, niche complementarity was shown to cause

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**Fig. 2.** Plausible scenarios of phylogenetic community structure based on the phenotypes and phylogenetic relationships (distant relatedness, referred to in Table 2, shows species B on a different branch) between two co-occurring species, A and B. Each scenario is assumed to begin directly from the regional species pool, or transit from the local pool above it. The dominant processes of community assembly are habitat filtering and competition, which are represented by a 'before' and 'after' phase in different combinations in communities. The theoretical probability of detecting either clustering or overdispersion, as unique and in combination with another pattern, is always 75% chance (3 out of 4 communities). The six diagrams within each scenario (except PcHc) depict patterns of phylogenetic community structure emerging from the dominant stereotype (e.g. PoHc). After the first horizontal level, the subsequent communities depict plausible states of phylogenetic community structure shaped by numerous assembly and disassembly processes, most of which are not yet identified or established in the literature. Thus, we refrain from providing specific assembly/disassembly processes along each trajectory of change within the PoHc, PcHo, and PoHo.

**Table 2.** Four scenarios that describe assembly processes and patterns in local communities emerging from a regional species pool of highly similar species. Each scenario is based on specific combinations of phenotypic traits, phylogenetic relationships (i.e. close or distant relatedness), and interactions among co-occurring species

Scenario	Species	Phenotypic traits	Phylogenetic relatedness	Interactions (before)	Phenotypic pattern	Phylogenetic pattern	Interactions (after)	Inference
1	PcHc A, B	Similar	Close	Filtering (strong)	Clustering	Clustering	Competition (strong)	Conservatism
2	PoHc A, B	Similar	Distant	Competition (mild)	Clustering	Overdispersion	Competition (mild)	Convergence
3	PeHo A, B	Dissimilar	Close	Competition (mild)	Overdispersion	Clustering	Filtering (mild)	Convergence
4	PoHo A, B	Dissimilar	Distant	Filtering (mild)	Overdispersion	Overdispersion	Filtering (strong)	Conservatism

reduced density-dependent mortality among oak species (Cavender-Bares *et al.*, 2004). At the baseline, factors that minimize interspecific competition and promote higher ecological divergence, such as resource partitioning, will be most exploited by these species (Werner, 1977; Gross *et al.*, 2007), as they migrate into new communities.

#### *Scenario 2 (PoHc)*

This scenario depicts phylogenetic overdispersion and phenotypic clustering as driven by mild competitive interactions (Webb *et al.*, 2002), and is a classical case of convergent community assembly (Smith and Wilson, 2002; Fukami *et al.*, 2005). The precepts of community phylogenetics support that species are able to move into new communities while retaining their ancestral phenotypic properties (Wiens and Graham, 2005; Losos, 2008b), particularly if these characters confer a certain level of fitness in the new environment (Wiens *et al.*, 2010). Consequently, distantly related species may be found in communities with similar environmental conditions due to evolutionary convergence (Ackerly *et al.*, 2006; Davies, 2006). Although most authors would argue that either competition or habitat filtering drives the assembly of this type of community (Cavender-Bares *et al.*, 2006; Emerson and Gillespie, 2008; Mayfield and Levine, 2010), a clear process, such as competition, has not yet been implicated in its disintegration. For instance, at the initial formation stage of this community, competition may drive phenotypic clustering in the community when the hierarchical distances between species' traits are favoured by biotic interactions (Mayfield and Levine, 2010), whereas at the later stage of this community, functional limiting similarity may initiate or sustain the competitive interactions because species' phenotypes are too similar (Weiher and Keddy, 1999; Mouillot *et al.*, 2005).

Cavender-Bares *et al.* (2004) exemplified this type of phylogenetic structure with Floridian oak communities. They found that phylogenetic overdispersion was driven more by phenotypically clustered than phenotypically overdispersed traits directly involved with habitat specialization and species co-existence. Similarly, with dusky salamanders in North America, Kozak *et al.* (2005) reported that the long-term stability of phylogenetically overdispersed communities was driven by both niche differences and the conserved evolution of ecomorphological traits (e.g. body size). Depending on the temporal scale in which species interactions are considered, competition is expected to give way to more stable interactions as species acquire higher ecological specialization (Futuyma and Moreno, 1988). For instance, phenotypic clustering was found to be favoured during the course of forest succession, as the forest composition shifted towards species with traits that conferred higher competitive ability (Kunstler *et al.*, 2012).

#### *Scenario 3 (PcHo)*

This is an example of phylogenetic clustering and phenotypic overdispersion, whereby the community is assembled through competition and later disintegrated by habitat filtering. Phylogenetic community structure may exhibit phylogenetic clustering and phenotypic overdispersion when co-occurring close relatives differ in one or more important trait axes (Kawano, 2002). The initial mild competition among co-existing species may be strengthened by character displacement (Brown and Wilson, 1956; Losos, 1990). At the early stage of this community, competition is likely driven by the high level of phylogenetic similarity among species – phylogenetic limiting similarity (Darwin, 1859; Violle *et al.*, 2011). High phylogenetic similarity among co-occurring species has been suggested to occur in areas with overlapping environmental conditions (Webb *et al.*, 2002; Emerson and Gillespie, 2008; Duarte, 2011), or where species have access to new ecological opportunities via limited dispersal efforts, and also in communities

of sympatric species (Losos, 1990; Losos *et al.*, 1998). A mild increase in habitat filtering may lead to the subsequent community disintegration, if species' traits are evolutionarily convergent and important for habitat specialization (Webb *et al.*, 2002).

Classic examples of this community structure include the study of Losos *et al.* (1998), which demonstrates evolutionary change in traits connected with adaptive radiation in Caribbean *Anolis* lizards, and the study of Kawano (2002) on phylogenetic clades of giant rhinoceros beetles in South-East Asia. It has also been exemplified in high fire-prone tree communities of the Mediterranean Basin (Verdú and Pausas, 2007), and in experimental bacterial communities (Horner-Devine and Bohannan, 2006; Violle *et al.*, 2011). The three scenarios so far highlight the importance of interspecific competition in ecological community structure (Tilman, 1987; Weiher and Keddy, 1995; Violle *et al.*, 2011). Importantly, they strongly suggest that competition cannot occur in the absence of high levels of phylogenetic or phenotypic similarity.

#### *Scenario 4 (PoHo)*

This scenario portrays phylogenetic and phenotypic overdispersion driven by habitat filtering processes (Emerson and Gillespie, 2008). Here, dissimilar traits and distantly related species are filtered into similar communities (Silvertown *et al.*, 2006; Violle *et al.*, 2011), through microhabitat filters such as facilitation [e.g. from the sheltering effect of another species (Valiente-Banuet and Verdú, 2007)] or herbivory (Webb *et al.*, 2006; see Cavender-Bares *et al.*, 2009). In this case, the conserved evolution of the regeneration niche (i.e. the ecological conditions required for recruitment and viability) does not involve the classical phylogenetic and phenotypic clustering (Valiente-Banuet and Verdú, 2007). With increasing evolutionary distance, species are more likely to differ along a higher number of trait axes, thereby reducing the strength of competitive interactions (Davies, 2006), and giving more weight to the influence of habitat filtering. Habitat filtering may drive distantly related species that possess dissimilar phenotypic architecture to co-exist under broadly similar environments (Pausas and Verdú, 2010). This may be expressed alongside biotic filtering (Keddy, 1992; Weiher and Keddy, 1999; Luzuriaga *et al.*, 2012), such as when perennial plants dictate the distribution of annual plants (Luzuriaga *et al.*, 2012).

The initial consideration of the abiotic environment as a filter for functionally similar species makes this scenario puzzling. However, if it is considered that factors other than traits may sieve more phylogenetically dissimilar species into the same environment (Emerson and Gillespie, 2008; Cavender-Bares *et al.*, 2009), then other filtering processes become more plausible under this type of community structure. For instance, historical biogeography and dissimilar chronologic evolution can create communities composed of more distantly related species than predicted by chance (Ricklefs and Schluter, 1993; Wiens, 2012). Similarly, diversity anomalies (i.e. the differences in diversity in similar environments within different regions) may reflect the greater influence of large-scale historical and regional processes on local diversity above that of the micro-environment (Ricklefs, 2008). This process may also be typical of communities in which little or no dispersal limitations preclude species establishment over large areas (e.g. Vittoz and Engler, 2007; Pottier and Evette, 2011). The most classic example of PoHo by far is the wood warbler communities of North America. In their study, Lovette and Hochachka (2006) demonstrated that phylogenetic niche conservatism favoured co-occurrence among distantly related species that exhibited phenotypic overdispersion in foraging strategy.

Finally, within the context of species invasibility, community colonization can occur without the competitive exclusion of native species (Werner, 1977; Emerson and Gillespie, 2008). In a rather novel sense, the net reduction of limiting interactions in this type of community

suggests that most stable ecological entities (e.g. at the local scale) are likely composed of more phylogenetically and phenotypically dissimilar sets of species. The overall positive interactions may chart the course of the community back to the initial state (i.e. scenario 1), when communities are rapidly filled by closely related species that possess similar phenotypes from the local pool.

**Box 1. The role of competition and habitat filtering in phylogenetic community structure**

Competition among closely related species has been widely supported. For example, Darwin (1859) stated that: ‘*As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera.*’ Close relatives may compete more than distant relatives in certain environments (Webb *et al.*, 2002; Davies, 2006). The negative interaction is likely to inhibit co-occurrence and drive the disintegration of stable communities. Depending on short- or long-term intervals, species may acquire evolutionary innovations or new ecological specialization that would initiate ecological transitions back to a stable state (Futuyma and Moreno, 1988; Emerson and Gillespie, 2008).

Habitat filtering is largely linked to patterns of phylogenetic and phenotypic clustering (Webb *et al.*, 2002; Vamosi *et al.*, 2009), and very rarely to patterns of community overdispersion (Cavender-Bares *et al.*, 2004; Ndiribe *et al.*, 2013). On the contrary, the dual role of competition (see Fig. 1) in driving phylogenetic overdispersion and clustering is more-or-less clear in theory (Cavender-Bares *et al.*, 2009; Mayfield and Levine, 2010). Patterns of overdispersion are not only attributed to competition but facilitation (Valiente-Banuet and Verdú, 2007), for instance, when a nurse species provides benefits for another species in close proximity (facilitated species), which is often more distantly related than expected (Valiente-Banuet and Verdú, 2007; Elias *et al.*, 2009). However, the role of facilitation in phylogenetic community structure is still a difficult puzzle to unravel, particularly as it is first masked by the appearance of competition (Elias *et al.*, 2009), and has been recently demonstrated in close relatives (Burns and Strauss, 2011). Since facilitation is mostly associated with stressful environments, depending on the system, it may be easily detected from the spatial arrangement of distantly related species in communities, or it may be subtle and mis-interpreted as competition (Valiente-Banuet and Verdú, 2007; Cavender-Bares *et al.*, 2009). Some work is still needed to clearly define and illustrate non-random patterns of phylogenetic community structure.

## SYNTHESIS

### Community assembly and disintegration through time

Given the different possible combinations of phylogenetic community structure (Fig. 2), we assert that species co-existence is better interpreted as a two-way dynamic process, specifically, as consisting of an ‘assembly’ and ‘disintegration’ phase. For instance, habitat filtering may drive species ‘assembly’ into a community, while competition will act to ‘disintegrate’ the stability among co-occurring species at a later phase. While ‘assembly’ is overtly popularized in community ecology, the concept of ‘disintegration’ is yet to achieve a similar momentum. The idea that communities may be driven by a two-way process (Belyea and Lancaster, 1999; Mayfield and Levine, 2010) has not received the attention needed to understand the dynamics of this process, or develop the statistical tools to efficiently tackle this challenge. Limits to current interpretation further restricts researchers to searching for one assembly process at a time (e.g. Tilman, 1977; Roughgarden, 1983; Mayfield *et al.*, 2009; Lebrija-Trejos *et al.*, 2010),

as opposed to considering ecological communities as governed by a top and bottom process, which, in turn, realistically explains why unstable assemblages may emerge from the same space where stable assemblages had previously been observed. Although the environment influences species interactions, community ecology as a whole is yet to provide synthesized explanations on how negligible changes in the abiotic environment (temperature, precipitation, soil salinity, etc.) alter or interchange patterns of community structure (e.g. from clustering to overdispersion).

What we find grievously missing is a thorough understanding of the temporal sequence in patterns of species co-existence. There is a need to retrace our steps to understanding, for instance, the role of seasonality in shaping the dynamics and patterns of a given system (tropical, temperate, etc.). If a clear understanding of the temporal sequence between the colonization and exclusion of a species from a natural community is unravelled, then we can begin to address questions such as: (1) Are species' range limits simply overlapping points in time, or actual boundaries defined by niche conservatism? And (2) what are disassembly rules in community structure? Insular environments (islands, mountain tops, aquatic habitats, etc.) provide the ideal discrete theatre for measuring the temporal sequence of community assembly and disintegration (Emerson and Gillespie, 2008). Generating sufficient empirical evidence from islands and continents alike would benefit the community phylogenetics literature, as well as set the stage for clearly interpreting large-scale biogeographic patterns (Wiens, 2012), for effective environmental restoration and management. Finally, we are optimistic that developing this idea (with a similar fervour given to phylogenetic community ecology) could provide greater clarity in the interpretation and prediction of assembly processes. The drivers of disintegration can be more readily disentangled from the drivers of assembly. Indeed, understanding communities in terms of both assembly and disintegration is likely a promising way to accurately predict the outcome of future communities in the face of accelerating global change (Cavender-Bares *et al.*, 2009; Nogués-Bravo and Rahbek, 2011).

Throughout this paper, we have discussed several important concepts of community phylogenetics. We have exemplified how these concepts can guide the proper interpretation of community structure. This is quite a challenge given that community assembly may be complexly interwoven by several opposing forces that render accurate interpretation almost impossible (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009). For example, the effects emanating from two different assembly processes rarely lead to the detection of a pattern, but the cancellation of both processes into neutrality (Hubbell, 2001). In addition, an assembly process may be masked by a different pattern from which it is commonly associated (Cavender-Bares *et al.*, 2004; Horner-Devine and Bohannan, 2006; Mayfield and Levine, 2010). Nevertheless, there are several potentials in the conceptual and methodological advancement of community phylogenetics that will similarly benefit related research areas such as ecosystem functioning and biodiversity conservation (Wiens *et al.*, 2010; Pavoine and Bonsall, 2011).

## CONCLUDING REMARKS

Phylogenetic tools will remain important for understanding community assembly as long as closely related species exhibit ecological patterns different from distantly related species (Cavender-Bares *et al.*, 2009). In addition to investigating assembly processes at the scale of local communities, community phylogenetics studies should give more attention to disentangling assembly patterns at the phylogenetic clade level (Mayfield *et al.*, 2009; Parra *et al.*, 2010; Ndiribe *et al.*, 2013), to better understand how different rates of trait evolution influence assembly. Sound

theoretical and empirical knowledge is required to fully understand the complex nature of the origin and maintenance of diversity that are hierarchically transmitted from the regional species pool into local communities (Silvertown *et al.*, 2006; Ricklefs, 2008). Although the concept of disintegration is already linked to scale in community ecology, to define broken boundaries, and pattern/process that has no well-defined spatial extent (Ricklefs, 2008), a two-dimensional process of assembly and disintegration is yet to be fully incorporated into the measurement of community structure. We acknowledge that evaluating ecological communities in terms of an assembly and disintegration phase will be computationally and empirically challenging. Yet, developing efficient tools to model community evolution through time will yield more accurate interpretations and predictions of assembly processes, and prove undoubtedly useful in the face of global climate change.

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### REFERENCES

- Ackerly, D.D., Schilck, D.W. and Webb, C.O. 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology*, **87**: S50–S61.
- Belyea, L.R. and Lancaster, J. 1999. Assembly rules within a contingent ecology. *Oikos*, **86**: 402–416.
- Brown, W.L. and Wilson, E.O. 1956. Character displacement. *Syst. Zool.*, **5**: 49–64.
- Burns, J.H. and Strauss, S.Y. 2011. More closely related species are more ecologically similar in an experimental test. *Proc. Natl. Acad. Sci. USA*, **108**: 5302–5307.
- Byers, J.E. 2000. Competition between two estuarine snails: implications for invasions of exotic species. *Ecology*, **81**: 1225–1239.
- Cahill, J.F., Kembel, S.W., Lamb, E.G. and Keddy, P.A. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspect. Plant Ecol. Evol. Syst.*, **10**: 41–50.
- Cavender-Bares, J., Ackerly, D.D., Baum, D.A. and Bazzaz, F.A. 2004. Phylogenetic overdispersion in Floridian oak communities. *Am. Nat.*, **163**: 823–843.
- Cavender-Bares, J., Keen, A. and Miles, B. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology*, **81**: S109–S122.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. and Kembel, S.W. 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.*, **12**: 693–715.
- Chase, J.M. 2003. Community assembly: when should history matter? *Oecologia*, **136**: 489–498.
- Darwin, C. 1859. *On the Origin of Species*. London: John Murray.
- Davies, T.J. 2006. Evolutionary ecology: when relatives cannot live together. *Curr. Biol.*, **16**: 645–647.
- Diamond, J.M. 1975. Assembly of species communities. In *Ecology and Evolution of Communities* (M.L. Cody and J.M. Diamond, eds.), pp. 342–444. Cambridge, MA: Belknap Press.
- Duarte, L.D.S. 2011. Phylogenetic habitat filtering influences forest nucleation in grasslands. *Oikos*, **120**: 208–215.
- Elias, M., Gompert, Z., Willmott, K. and Jiggins, C. 2009. Phylogenetic community ecology needs to take positive interactions into account. *Commun. Integr. Biol.*, **2**: 113–116.
- Emerson, B.C. and Gillespie, R.G. 2008. Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol. Evol.*, **23**: 619–630.

- Fauth, J.E., Bernardo, J., Camara, M., Resetarits, W.J., Van Buskirk, J., Jr. and McCollum, S.A. 1996. Simplifying the jargon of community ecology: a conceptual approach. *Am. Nat.*, **147**: 282–286.
- Frazier, J.G. 1994. The pressure of terminology stresses – urgency of robust definitions in ecology. *Bull. Br. Ecol. Soc.*, **25**: 207–209.
- Fukami, T., Martijn Bezemer, T., Mortimer, S.R. and Putten, W.H. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecol. Lett.*, **8**: 1283–1290.
- Futuyma, D.J. and Moreno, G. 1988. The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.*, **19**: 207–233.
- Gause, G.F. 1934. *The Struggle for Existence*. Baltimore, MD: Williams & Wilkins.
- Gross, N., Suding, K.N., Lavorel, S. and Roumet, C. 2007. Complementarity as a mechanism of coexistence between functional groups of grasses. *J. Ecol.*, **95**: 1296–1305.
- Helmus, M.R., Bland, T.J., Williams, C.K. and Ives, A.R. 2007a. Phylogenetic measures of biodiversity. *Am. Nat.*, **169**: E68–E83.
- Helmus, M.R., Savage, K., Diebel, M.W., Maxted, J.T. and Ives, A.R. 2007b. Separating the determinants of phylogenetic community structure. *Ecol. Lett.*, **10**: 917–925.
- Horner-Devine, M.C. and Bohannan, B.J.M. 2006. Phylogenetic clustering and overdispersion in bacterial communities. *Ecology*, **87**: S100–S108.
- Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.
- Kawano, K. 2002. Character displacement in giant Rhinoceros beetles. *Am. Nat.*, **159**: 255–271.
- Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.*, **3**: 157–164.
- Kneitel, J.M. and Chase, J.M. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.*, **7**: 69–80.
- Kraft, N.J.B., Cornwell, W.K., Webb, C.O. and Ackerly, D.D. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am. Nat.*, **170**: 271–283.
- Kozak, K.H., Larson, A., Bonett, R.M. and Harmon, L.J. 2005. Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: Desmognathus). *Evolution*, **59**: 2000–2016.
- Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E. *et al.* 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecol. Lett.*, **15**: 831–840.
- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F. and Poorter, L. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, **91**: 386–398.
- Logan, R.A. 2001. Science mass communication: its conceptual history. *Sci. Commun.*, **23**: 135–163.
- Losos, J.B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. *Evolution*, **44**: 558–569.
- Losos, J.B. 2008a. Rejoinder to Wiens (2008): phylogenetic niche conservatism, its occurrence and importance. *Ecol. Lett.*, **11**: 1005–1007.
- Losos, J.B. 2008b. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.*, **11**: 995–1007.
- Losos, J.B. 2011. Seeing the forest for the trees: the limitations of phylogenies in comparative biology. *Am. Nat.*, **177**: 709–727.
- Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. and Rodríguez-Schettion, L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**: 2115–2118.
- Lovette, I.J. and Hochachka, W.M. 2006. Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology*, **87**: S14–S28.

- Luzuriaga, A.L., Sánchez, A.M., Maestre, F.T. and Escudero, A. 2012. Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PLoS One*, **7**: e41270.
- MacArthur, R.H. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, **101**: 377–385.
- MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Mayfield, M.M. and Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.*, **13**: 1085–1093.
- Mayfield, M.M., Boni, M.F. and Ackerly, D.D. 2009. Traits, habitats, and clades: identifying traits of potential importance to environmental filtering. *Am. Nat.*, **174**: E1–E22.
- McGill, B.J., Enquist, B.J., Weiher, E. and Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, **21**: 178–185.
- Miller, J.S. and Wenzel, J.W. 1995. Ecological characters and phylogeny. *Annu. Rev. Entomol.*, **40**: 389–415.
- Moullot, D., Simková, A., Morand, S. and Poulin, R. 2005. Parasite species coexistence and limiting similarity: a multiscale look at phylogenetic, functional and reproductive distances. *Oecologia*, **146**: 269–278.
- Ndiribe, C., Pellissier, L., Antonelli, S., Dubuis, A., Pottier, J., Vittoz, P. *et al.* 2013. Phylogenetic plant community structure along elevation is lineage specific. *Ecol. Evol.*, **3**: 4925–4939.
- Nogués-Bravo, D. and Rahbek, C. 2011. Communities under climate change. *Science*, **334**: 1070–1071.
- Pacala, S.W. and Tilman, D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Nat.*, **143**: 222–257.
- Parra, J.L., McGuire, J.A. and Graham, C.H. 2010. Incorporating clade identity in analyses of phylogenetic community structure: an example with hummingbirds. *Am. Nat.*, **176**: 573–587.
- Pausas, J.G. and Verdú, M. 2010. The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *BioScience*, **60**: 614–625.
- Pavoine, S. and Bonsall, M.B. 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biol. Rev.*, **86**: 792–812.
- Peters, R.H. 1976. Tautology in evolution and ecology. *Am. Nat.*, **110**: 1–12.
- Pottier, J., Dubuis, A., Pellissier, L., Götzenberger, L., Zobel, K. and Guisan, A. in press. How do species pool filtering and spatial partitioning drive plant assemblages over contrasted environmental conditions? *Ecol. Monogr.*
- Ricklefs, R.E. 2008. Disintegration of the ecological community. *Am. Nat.*, **172**: 741–750.
- Ricklefs, R.E. and Bermingham, E. 2001. Nonequilibrium diversity dynamics of the Lesser Antillean avifauna. *Science*, **294**: 1522–1524.
- Ricklefs, R.E. and Schluter, D. 1993. Species diversity: regional and historical influences. In *Species Diversity in Ecological Communities* (R.E. Ricklefs and D. Schluter, eds.), pp. 350–363. Chicago, IL: University of Chicago Press.
- Roughgarden, J. 1983. Competition and theory in community ecology. *Am. Nat.*, **122**: 583–601.
- Schoener, T.W. 1986. Overview: kinds of ecological communities – ecology becomes pluralistic. In *Community Ecology* (J. Diamond and T. Case, eds.), pp. 467–479. New York: Harper & Row.
- Silvertown, J., McConway, K., Gowing, D., Dodd, M., Fay, M.F., Joseph, J.A. *et al.* 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proc. R. Soc. Lond. B*, **273**: 39–44.
- Simberloff, D. 2004. Community ecology: is it time to move on? *Am. Nat.*, **163**: 787–799.
- Slingsby, J.A. and Verboom, G.A. 2006. Phylogenetic relatedness limits co-occurrence at fine spatial scales: evidence from the Schoenoid sedges (Cyperaceae: Schoeneae) of the Cape floristic region, South Africa. *Am. Nat.*, **168**: 14–27.
- Smith, B. and Wilson, J.B. 2002. Community convergence: ecological and evolutionary. *Folia Geobot.*, **37**: 171–183.

- Smith, S.A. and Donoghue, M.J. 2008. Rates of molecular evolution are linked to life history in flowering plants. *Science*, **322**: 86–89.
- Swenson, N., Enquist, B., Pither, J. and Thompson, J. 2006. The problem and promise of scale dependency in community phylogenetics. *Ecology*, **87**: 2418–2424.
- Tilman, D. 1977. Resource competition between plankton algae: an experimental and theoretical approach. *Ecology*, **58**: 338–348.
- Tilman, D. 1987. The importance of the mechanisms of interspecific competition. *Am. Nat.*, **129**: 769–774.
- Tofts, R. and Silvertown, J. 2000. A phylogenetic approach to community assembly from a local species pool. *Proc. R. Soc. Lond. B*, **267**: 363–369.
- Valiente-Banuet, A. and Verdú, M. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecol. Lett.*, **10**: 1029–1036.
- Vamosi, S.M., Heard, S.B., Vamosi, J.C. and Webb, C.O. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol. Ecol.*, **18**: 572–592.
- Verdú, M. and Pausas, J.G. 2007. Fire drives phylogenetic clustering in Mediterranean basin woody plant communities. *J. Ecol.*, **95**: 1316–1323.
- Violle, C., Nemergut, D.R., Pu, Z. and Jiang, L. 2011. Phylogenetic limiting similarity and competitive exclusion. *Ecol. Lett.*, **14**: 782–787.
- Vittoz, P. and Engler, R. 2007. Seed dispersal distances: a typology based on dispersal modes and plant traits. *Bot. Helv.*, **117**: 109–124.
- 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. and Donoghue, M.J. 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, **33**: 475–505.
- Webb, C.O., Gilbert, G.S. and Donoghue, M.J. 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology*, **87**: S123–S131.
- Weiher, E. and Keddy, P.A. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, **74**: 159–164.
- Weiher, E. and Keddy, P.A. 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge: Cambridge University Press.
- Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. *Am. Nat.*, **111**: 553–578.
- Wiens, J.J. 2008. Commentary on Losos (2008): niche conservatism déjà vu. *Ecol. Lett.*, **11**: 1004–1005.
- Wiens, J.J. 2012. Why biogeography matters: historical biogeography vs. phylogeography and community phylogenetics for inferring ecological and evolutionary processes. *Front. Biogeogr.*, **4**: 128–135.
- Wiens, J.J. and Graham, C.H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Syst.*, **36**: 519–539.
- Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V. *et al.* 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.*, **13**: 1301–1324.
- Zimmermann, N.E. and Kienast, F. 1999. Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *J. Veg. Sci.*, **10**: 469–482.