

# Ecophylogenetics: advances and perspectives

Nicolas Mouquet<sup>1,\*†</sup>, Vincent Devictor<sup>1,†</sup>, Christine N. Meynard<sup>2,†</sup>, Francois Munoz<sup>3,†</sup>, Louis-Félix Bersier<sup>4</sup>, Jérôme Chave<sup>5</sup>, Pierre Couteron<sup>3</sup>, Ambroise Dalecky<sup>6</sup>, Colin Fontaine<sup>7</sup>, Dominique Gravel<sup>8</sup>, Olivier J. Hardy<sup>9</sup>, Franck Jabot<sup>10</sup>, Sébastien Lavergne<sup>11</sup>, Mathew Leibold<sup>12</sup>, David Mouillot<sup>13,14</sup>, Tamara Münkemüller<sup>11</sup>, Sandrine Pavoine<sup>7,15</sup>, Andreas Prinzing<sup>16</sup>, Ana S.L. Rodrigues<sup>17</sup>, Rudolf P. Rohr<sup>4,18</sup>, Elisa Thébaud<sup>19</sup> and Wilfried Thuiller<sup>11</sup>

<sup>1</sup> *Institut des Sciences de l'Evolution, UMR 5554, CNRS, Université Montpellier 2, CC 065, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France*

<sup>2</sup> *INRA, UMR CBGP (INRA/IRD/Cirad/Montpellier SupAgro), Campus international de Baillarguet, CS 30016, 34988 Montferrier-sur-Lez, France*

<sup>3</sup> *IRD and UM2, Botanique et Bioinformatique de l'Architecture des Plantes, TA A51/PS2 34398 Montpellier Cedex 5, France*

<sup>4</sup> *Unit of Ecology and Evolution, Department of Biology, University of Fribourg, Ch. du Musée 10, CH-1700 Fribourg, Switzerland*

<sup>5</sup> *Laboratoire Evolution et Diversité Biologique, UMR 5174, CNRS/Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse, France*

<sup>6</sup> *IRD, UMR CBGP (INRA/IRD/Cirad/Montpellier SupAgro), Campus International de Baillarguet, CS 30016, 34988 Montferrier-sur-Lez, France*

<sup>7</sup> *Museum National d'Histoire Naturelle, Département Ecologie et Gestion de la Biodiversité, UMR CNRS UPMC 7204, 61 rue Buffon, 75005 Paris, France*

<sup>8</sup> *Université du Québec à Rimouski, Département de biologie, Chimie et Géographie, 300 Allée des Ursulines, Québec, G5L 3A1, Canada*

<sup>9</sup> *Evolution Biologique et Ecologie, CPI60/12, av. F.D. Roosevelt 50, 1050 Brussels, Belgium*

<sup>10</sup> *Laboratoire d'Ingénierie pour les Systèmes Complexes, Cemagref, 24 avenue des Landais 63172 Aubière, France*

<sup>11</sup> *Laboratoire d'Ecologie Alpine, BP 53, 2233 Rue de la Piscine, 38041 Grenoble Cedex 9, France*

<sup>12</sup> *Section of Integrative Biology, University of Texas at Austin, 1 University Station C0930, Austin, TX 78712, USA*

<sup>13</sup> *Laboratoire ECOSYM UMR 5119, Université Montpellier 2, 34095 Montpellier Cedex 5, France*

<sup>14</sup> *ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld 4811, Australia*

<sup>15</sup> *Mathematical Ecology Research Group, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*

<sup>16</sup> *Equipe "Ecologie de la Diversification", Unité de Recherche Ecobio, Campus de Beaulieu, Bât. 14A, 35042 Rennes, France*

<sup>17</sup> *Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR5175, 1919 route de Mende, 34293 Montpellier Cedex 5, France*

<sup>18</sup> *Integrative Ecology Group, Estación Biológica de Doñana, CSIC, C/Américo Vespucio s/n, E-41092 Sevilla, Spain*

<sup>19</sup> *CNRS, UMR 7618 "Biogéochimie et écologie des milieux continentaux", 46 rue d'Ulm, 75005 Paris, France*

## ABSTRACT

Ecophylogenetics can be viewed as an emerging fusion of ecology, biogeography and macroevolution. This new and fast-growing field is promoting the incorporation of evolution and historical contingencies into the ecological research agenda through the widespread use of phylogenetic data. Including phylogeny into ecological thinking represents an opportunity for biologists from different fields to collaborate and has provided promising avenues of research in both theoretical and empirical ecology, towards a better understanding of the assembly of communities, the functioning of ecosystems and their responses to environmental changes. The time is ripe to assess critically the extent to which the integration of phylogeny into these different fields of ecology has delivered on its promise. Here we review how phylogenetic information has been used to identify better the key components of species interactions with their biotic and abiotic environments, to determine the relationships between diversity and ecosystem functioning and ultimately to establish good management practices to protect overall biodiversity in the face of global change. We evaluate the relevance of information provided by phylogenies to ecologists, highlighting current potential weaknesses and needs for future developments. We suggest

\* Address for correspondence (E-mail: nmouquet@univ-montp2.fr).

† These authors contributed equally to this work.

that despite the strong progress that has been made, a consistent unified framework is still missing to link local ecological dynamics to macroevolution. This is a necessary step in order to interpret observed phylogenetic patterns in a wider ecological context. Beyond the fundamental question of how evolutionary history contributes to shape communities, ecophylogenetics will help ecology to become a better integrative and predictive science.

*Key words:* conservation biology, community ecology, ecological networks, ecophylogenetics, ecosystem functioning, evolution, phylogenetics.

## CONTENTS

I. Introduction .....	770
II. From phylogenetic structure to community assembly rules .....	771
(1) Measuring and testing community phylogenetic structure .....	771
(2) Phylogeny as a proxy .....	772
(3) Relating community patterns to processes .....	773
(4) Perspectives: the need for a general framework .....	773
III. Network organisation and properties .....	774
(1) Evolving network complexity .....	774
(2) Analyzing the links between phylogeny and interaction networks .....	774
(3) Using phylogenetic signal to understand and predict interaction network properties .....	776
(4) Perspectives on network phylogenetics .....	776
IV. Relationship between phylogenetic diversity and ecosystem functioning .....	776
(1) Phylogenetic diversity as a proxy for ecosystem functioning? .....	776
(2) Perspectives: towards an ecosystem phylogenetics? .....	777
V. Value of phylogenetics in conservation biology .....	778
(1) Taxonomy and systematics .....	778
(2) Species prioritisation .....	778
(3) Going beyond biodiversity representation .....	779
(4) Perspectives: increasing the predictive power of ecology for conservation .....	780
VI. Conclusions .....	780
VII. Acknowledgements .....	781
VIII. Glossary .....	781
IX. References .....	782

## I. INTRODUCTION

Species distributions are shaped by the interplay between evolutionary and ecological processes (Ricklefs, 1987). To date however, these processes have been studied primarily in isolation, and have yet to be tightly integrated. Evolution is largely concerned with the emergence of biological diversity (e.g. diversification of species traits during adaptive radiations (Schluter, 2000) whereas ecology usually takes this diversity for granted and is concerned by its interaction with the environment (e.g. how a given species trait distribution affects community properties (McGill *et al.*, 2006)). Furthermore, macro-evolutionary processes are mainly described against the backdrop of large-scale climatic or geological events, whereas ecological processes are generally interpreted at small temporal and spatial scales assuming that evolutionary processes can be ignored. Attempts to reconcile these disciplines began in the 1960s in the field of evolutionary ecology (Hutchinson, 1965), focusing especially on the role of competition in explaining local species persistence (Diamond, 1975) and character displacement in populations (Hutchinson, 1959). Increasing evidence has shown that

evolutionary background and large-scale processes, such as dispersal and colonization, are fundamental in shaping local communities (Leibold *et al.*, 2004; Graham & Fine, 2008). As an integrative research program, evolutionary ecology has become a fertile scientific ground, especially as understanding the impact of climate change and current threats on biodiversity call requires a joint understanding of evolutionary dynamics and community ecology (Fussmann, Loreau & Abrams, 2007; Johnson & Stinchcombe, 2007; Lavergne *et al.*, 2010; Vellend, 2010).

There have been two main approaches for integrating evolutionary thinking into ecology. The first level decouples ecological and evolutionary processes, assuming that community structure depends on relatively recent ecological phenomena acting according to species traits while species traits are the output of long-term evolutionary processes; hence ecological and evolutionary processes are assumed to be essentially independent. The key questions addressed refer to ecological processes structuring communities, not evolutionary processes; interest in evolution is limited to the resulting pattern of phylogenetic signal (Webb *et al.*, 2002). A second level of integration considers the long-term

interactions between ecological and evolutionary processes where evolution of species traits is seen as an outcome of selection pressures due to ecological processes (e.g. Schluter, 2000; Rundle & Nosil, 2005). This approach emphasizes the interplay between ecological processes and the evolutionary consequences of these processes.

These contrasting approaches are often hard to reconcile because of a lack of conceptual and analytical tools integrating ecological and evolutionary processes but also due to the different temporal and spatial scales involved. A major advance was the development of ‘community phylogenetics’ which proposed the use of phylogenetic data to assess the likelihood of alternative scenarios of community assembly (Webb *et al.*, 2002; Emerson & Gillespie, 2008; Cavender-Bares *et al.*, 2009). It was hypothesized that community structure should differ depending on both the ecological mechanisms (e.g. competitive exclusion, environmental filtering) and on the distribution of species characteristics within the phylogeny (evolutionary history). Phylogenetic community ecology has since blossomed (e.g. Fig. 1) as extensive phylogenies of important taxonomic groups became available to the broad ecological research community (e.g. Davies *et al.*, 2004; Thuiller *et al.*, 2011). Phylogenies are now commonly used to reveal community assembly rules (see Section VIII, glossary, for definition) and properties and have also permeated other important fields of ecology (Cavender-Bares *et al.*, 2009) forming the basis of a new discipline called ‘Ecophylogenetics’ (Cadotte, 2009).

Appealing as this new research program might be, it suffers from its ever-increasing richness while each ecological sub-discipline integrates the phylogenetic information from very different perspectives (Webb *et al.*, 2002; Chave, Chust

& Thébaud, 2007; Emerson & Gillespie, 2008; Avise, 2009; Cadotte *et al.*, 2009; Cavender-Bares *et al.*, 2009; Leibold, Economo & Peres-Neto, 2010; Matthews *et al.*, 2011). There are also still a number of critical assumptions that have been only partly discussed in the recent literature (Cavender-Bares *et al.*, 2009; Mayfield & Levine, 2010; Pavoine & Bonsall, 2011). It is now important to assess how the use of phylogenetic information can help ecology to be a more integrative science.

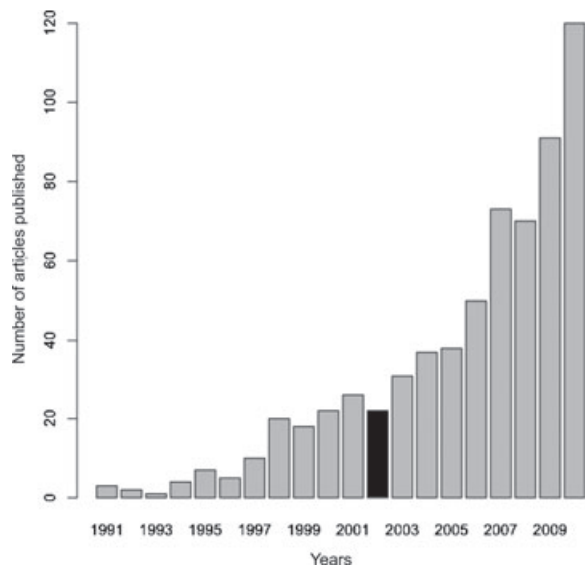
Herein we provide a critical evaluation of the various ways that phylogeny has been used to gain insight in community and ecosystems ecology. We focus on community assembly rules, the structure of network organization and properties, the relationship between diversity and ecosystem functioning, and on conservation biology. For each of these areas, we evaluate how adding an evolutionary hypothesis through the use of a phylogeny has yielded useful insights into ecology, and highlight potential weaknesses and areas for future improvements and developments.

## II. FROM PHYLOGENETIC STRUCTURE TO COMMUNITY ASSEMBLY RULES

Revealing the mechanisms that drive community assembly in ecological communities has a long and contentious history in ecology (Diamond & Case, 1986; Chase & Leibold, 2003; Chave, 2004). A central and controversial issue is to assess which differences between species characteristics (niches), if any, can explain community assembly. Webb and collaborators (Webb, 2000; Webb *et al.*, 2002) proposed that this can be investigated by measuring community phylogenetic structure (see Section VIII, glossary, for definition) and using phylogeny as a proxy for species ecological similarity/dissimilarity (see Section VIII, glossary, for definition). We discuss below the validity of this ‘phylogeny-as-a-proxy’ hypothesis to capture species trait variation and to reveal community assembly rules.

### (1) Measuring and testing community phylogenetic structure

The starting point for the application of this approach is to measure community phylogenetic structure and to compare it to an appropriate null model (see Section VIII, glossary, for definition). Various statistics have been developed to integrate phylogenetic information in community analyses (see for instance Helmus *et al.*, 2007; Hardy, 2008; Cadotte *et al.*, 2010; Pavoine & Bonsall, 2011). Their relative merits rest on the questions they can address and on how well the variation in phylogenetic composition can be analyzed and compared to a null expectation. As in other areas of community ecology, randomization algorithms are used to represent the expected distribution of community phylogenetic structure under a random (null) process of community assembly (Gotelli & Graves, 1996), and to yield confidence intervals for the observed patterns. The power of



**Fig. 1.** Results of a search in the *ISI Web of Science* using the key words ‘Phylogenetics OR phylogeny’ AND ‘community ecology’. The black column indicates the year of publication of the influential paper by Webb *et al.* (2002) on phylogenetic community ecology.

the test should also be carefully assessed, using, for instance, simulated data (Hardy, 2008). Problems can arise when there is structure in the data that is unrelated to the null hypothesis tested. The null hypothesis will then be more easily rejected even though it is true, resulting in an inflation of Type I errors. Appropriate constraints are thus needed to differentiate the influence of phylogenetic relatedness, species abundances and spatial structure on the local community assembly (see table 2 of Hardy, 2008).

Alternative randomization procedures that have been proposed in phylogenetic community ecology involve constraining species abundance and randomizing the species' positions in the phylogenetic tree (Cavender-Bares, Keen & Miles, 2006), or constraining the tree but randomizing species abundances within sites (Gotelli & Entsminger, 2003). The first approach tests whether the species phylogenetic relatedness within communities differs from the null expectation of phylogenetically randomly distributed ecological traits. A limit of this randomization scheme is that it affects not only the pattern of relatedness between species but also the distribution of their abundances across the phylogeny. Therefore, randomizations of the phylogenetic positions constrained by the species abundances have been proposed (Hardy, 2008). The second approach fixes the composition of the regional pool, to keep the frequency of occurrence pattern due to environmental filtering in the regional pool constant, and tests which species from this pool are present in local communities in relation to local environmental filters. Because the phylogeny is fixed, the null model then helps to address whether, given the evolutionary history of the taxa in the region, the phylogenetic relatedness has influenced species assembly in local communities. But any geographic pattern in the distribution of species would also be changed by the randomization scheme, and thus further spatial constraints should be applied to the randomization scheme (Hardy, 2008).

In a broader perspective, ecological processes act over a range of spatial and temporal scales and require analyzing and testing the variation in community phylogenetic structure across scales (Emerson & Gillespie, 2008). One option (implemented for instance in Spacodi software - Eastman, Paine & Hardy, 2011) is to consider the variation across clades and at different depths of the phylogenetic tree using nested null models (Cavender-Bares *et al.*, 2006; Losos *et al.*, 2006; Ollier, Couteron & Chessel, 2006; Hardy & Senterre, 2007; Pavoine, Love & Bonsall, 2009; Pavoine, Baguette & Bonsall, 2010). Similar techniques may be used to partition spatial phylogenetic diversity, using geographical distances or classes of habitats (Hardy & Senterre, 2007; Pavoine *et al.*, 2009; Morlon *et al.*, 2011), and to compare the relative strength of spatial and phylogenetic signals (Freckleton & Jetz, 2009).

## (2) Phylogeny as a proxy

The hypothesis of Webb and collaborators (Webb, 2000; Webb *et al.*, 2002) of phylogeny as a proxy for species similarity is central to phylogenetic community ecology

(Cavender-Bares *et al.*, 2009). Yet, its use presupposes two implicit assumptions that are rarely tested. First, that the niche of a species can be represented by an abstract trait summarizing the multidimensional combination of ecological traits that affect the fitness of the species at any locality. Second, that phylogenetic distance between species is related to species similarity in this abstract niche trait, with closely related species resembling each other more than distantly related species, i.e. the niche trait shows a phylogenetic signal (see Section VIII, glossary, for definitions of phylogenetic signal and conservatism). This twofold assumption is in principle testable if both a phylogenetic tree and a niche-related measure are available, as is the case for Darwin's finches in the Galapagos islands (Grant & Grant, 1996) or for anolis lizards in the Caribbean islands (Losos, 1990). Unfortunately a clear link between species traits and ecological niches is rarely available and particular traits are often assumed to delineate species niches with no further empirical support. This limitation leads to a potential circularity in the phylogeny-as-a-proxy approach. Combining experimental and observational studies for a subset of well-studied taxa is now required to identify the fundamental traits that are more likely to influence the species role in the ecosystem or the species use of the environment. Functional ecology is in quest of such integration and advocates that a limited set of fundamental traits can be directly related to the main niche-based processes (Lavorel & Garnier, 2002; McGill *et al.*, 2006).

The second critical issue is whether similarity in the abstract niche trait is related to phylogenetic relatedness (conservatism). Phylogenetic signal has often been used to investigate trait conservatism (Blomberg, Garland & Ives, 2003; Losos, 2008) leading to its use as an inverse measure of niche conservatism in the community phylogenetic literature (Cavender-Bares *et al.*, 2009). This inference has been controversial (Wiens & Graham, 2005; Losos, 2008) and more recent analyses have shown that it is not always warranted (Wiens *et al.*, 2010). Webb *et al.* (2002) have related niche conservatism to evolutionary convergence (e.g. see Section VIII, glossary, for definition) but the problem is that a single measure of phylogenetic signal cannot correctly acknowledge situations of evolutionary convergence. The sole use of phylogenetic signal seems to emerge from the misconception that it directly measures evolutionary rates, a view that has been challenged in the recent literature (reviewed by Wiens *et al.*, 2010). Revell Harmon & Collar (2008) showed that phylogenetic signal is the result of a complex interplay between rates of evolutionary change and the strength of evolutionary constraints so that some conditions (e.g. strong stabilizing selection combined with strong evolutionary constraints) can produce a weak phylogenetic signal even in cases of low evolutionary rates. These results show that evolutionary rate and phylogenetic signal are not necessarily negatively related and that scenarios of trait evolution where species tend to retain ancestral ecological characteristics (usually qualified as phylogenetic niche conservatism) can lead to patterns of weak phylogenetic signal.



Adding to this phylogenetic signal *versus* niche conservatism debate, ecology has long lacked an operational definition of the niche itself (Hubbell, 2001; Chase & Leibold, 2003). If niches cannot be thoroughly measured while testing the phylogeny-as-a-proxy assumption, is there any inherent advantage in using phylogenetic information (Kraft, Valencia & Ackerly, 2008)? Yet, simply ignoring phylogenetic information and resorting only to trait measurements is a perilous strategy, as it is not possible to ascertain if the most relevant traits were identified. A large body of literature has dealt with trying to identify traits that may be of primary relevance in characterizing species niches [e.g. leaf-height-seed scheme (LHS); (Westoby, 1998)], and some studies have attempted to validate such traits as relevant to characterize species niches descriptors (e.g. for a test of the LHS scheme, see Lavergne, Garnier & Debussche, 2003). To date however such studies have not yet been sufficiently developed or used over sufficiently broad arrays of organisms to determine how successful this approach may be.

To sidestep the debate on phylogenetic conservatism, a more general perspective for ecophylogenetics could be that the existence of a community phylogenetic structure is informative *per se* and that the comparison with other ecological information reveals the underlying processes (Hardy, 2008; Mayfield & Levine, 2010; Pavoine & Bonsall, 2011). Within this logic, many evolutionary and ecological forces lead to phylogenetic signal of traits, so that phylogenetic relatedness can be considered an integrative measure of trait similarity between species. The question then becomes whether there is sufficient phylogenetic signal in traits to generate non-random phylogenetic structure of communities, and whether it can be related to community assembly rules (Pavoine & Bonsall, 2011). As such, the pattern that may really matter for studies of phylogenetic community ecology is the existence of phylogenetic signal in the persistence of species *per se*, regardless of its origins and causes. The concept of niche conservatism, on the other hand, implies a process perspective and it should be restricted to studies seeking to understand the evolutionary drivers of niche and lineage diversification.

### (3) Relating community patterns to processes

Under the assumption that phylogenetic signal can be informative about species niche similarity, it is possible to make testable predictions on community phylogenetic structure. Environmental filtering and species interactions, especially competition, have been thought to produce specific signatures of phylogenetic clustering or overdispersion, both within and among communities (Webb *et al.*, 2002; Hardy & Senterre, 2007; Cavender-Bares *et al.*, 2009). Environmental filtering should produce local assemblages with similar abiotic niches, and therefore phylogenetically clustered communities. By contrast, competition should produce assemblages with little niche overlap due to limiting similarity (MacArthur & Levins, 1967), and hence phylogenetically overdispersed communities.

This basic framework has some limitations, and should be refined to investigate further the effect of several individual traits and various evolutionary processes on phylogenetic community structure (Mayfield & Levine, 2010). For instance, drought sensitivity of tropical trees was found to increase phylogenetic niche clustering (Engelbrecht *et al.*, 2007), while sensitivity to disturbances of herbaceous plants was found to increase phylogenetic niche overdispersion (Grime, 2006). Phylogenetic niche overdispersion can also result from the ability of some lineages to radiate explosively into a wide range of habitat conditions [e.g. the Hawaiian lobeliads (Givnish *et al.*, 2009) and *Tetragnatha* spiders (Gillespie, 2004)]. Testing the effect of competition on trait variation is similarly challenging. Competition can either trigger character displacement (Schluter, 2000; Dayan & Simberloff, 2005) and lead to phylogenetic overdispersion, or result in trait convergence and phylogenetic clustering if the trait is related to competitive ability and thus selected for (Mayfield & Levine, 2010).

Large-scale biogeographic variations will also influence the phylogenetic structure of communities at different scales and should be taken into consideration. Given that local communities are assembled from a regional species pool (Ricklefs, 1987), non-random phylogenetic structures observed at local scales may also originate from regional-scale processes (Bartish *et al.*, 2010). Therefore, phylogenetic structure and biogeographical history can be contrasted with separate historical and ecological influences on regional biotas (e.g. McPeck & Brown, 2000). For instance, Leibold *et al.* (2010) used phylogenetic information to relate the distribution of daphniid cladocerans and calanoid copepods in a lake metacommunity to environmental filters. They found that daphniids were mainly influenced by environmental filters and not by biogeographic history, whereas the reverse was true for the copepods. Since the species in these two clades coexist in the same set of lake communities, these results suggest that evolutionary-biogeographic processes can strongly and unexpectedly interact with ecological processes.

### (4) Perspectives: the need for a general framework

Although using phylogenetic information in community ecology has produced a strong interest within the scientific community (Fig. 1), various limitations of the phylogeny-as-a-proxy approach remain to be solved. As highlighted above, these limitations are related to: (i) methodological issues in the interpretation of null models against which phylogenetic community structure can be compared; (ii) the challenges of directly relating phylogeny, species traits and ecological niches; and (iii) the interplay between evolutionary and ecological processes at different temporal and spatial scales that may generate similar hypotheses regarding phylogenetic structures. In order to continue progressing in phylogenetic community ecology, future research should concentrate on each of these areas of debate.

Promising developments will come from integrative approaches where phylogenetic structure and other ecological information (e.g. spatial distributions, species traits, spatial

scales) are used in conjunction. For example, using phylogenetic, functional and co-occurrence information along an environmental gradient may highlight which traits are important for environmental sorting and at which phylogenetic scale (Pavoine *et al.*, 2011). Therefore, rather than concentrating on whether or not the traits considered are related to species' niches, a more productive avenue may come from identifying traits with strong phylogenetic signal and assessing whether these are related to the environmental drivers proposed. The traits and gradients identified in this way could then be taken as hypotheses to be tested in further experimental studies to understand mechanistically such relationships.

Another promising approach may come from contrasting opposing views on the relative roles of the distribution of abundances, species traits or spatial scales. This could highlight which assumptions are more likely to change conclusions regarding community assembly, at what scales they should be studied, and help to prioritize further data gathering for future research. The design of appropriate metrics and null models is here central, and simulation studies may prove particularly useful to test their statistical power (e.g. Kembel, 2009). In simulations, the different community assembly rules and species niches can be manipulated at the same time as the sampling and analytical scenarios (Münkemüller *et al.*, in press; Zurell *et al.*, 2010). Simulations should also be used to discuss the imprint of evolutionary processes on the phylogenetic signal (Revell *et al.*, 2008). The constraints to the null models can then be discussed in the light of the constraints hypothesized in the simulations. Going through simulations and applications back and forth will improve inference and discussion of the underlying theory.

Above all, the current limitations stress the need for a general framework including coexistence mechanisms and macroevolutionary dynamics. The initial phylogeny-as-a-proxy hypothesis has been useful to trigger a debate and bring together community ecologists with macro-evolutionary biologists, but it was largely based on a set of oversimplified assumptions (Mayfield & Levine, 2010). Process-based biogeographical models including explicit interaction rules and speciation modes are now needed to study the extent to which phylogenetic information will deliver its promise to shed light on the mechanisms that drive species distributions.

### III. NETWORK ORGANISATION AND PROPERTIES

Phylogenetic information can also shed light on complex ecological settings such as trophic, mutualist and host-parasite networks (Montoya, Pimm & Sole, 2006; Ings *et al.*, 2009). The study of interaction networks (e.g. see Section VIII, glossary, for definition) has historically focused on understanding their dynamical (e.g. persistence) and structural characteristics (e.g. connectance, modularity, nestedness), ignoring the evolutionary background (Bascompte, 2009). There is however substantial evidence on the evolutionary dynamics of such interactions (e.g. plant-herbivore, host-parasite,

mutualists) and integrating network studies within a phylogenetic framework would be a stride forward.

#### (1) Evolving network complexity

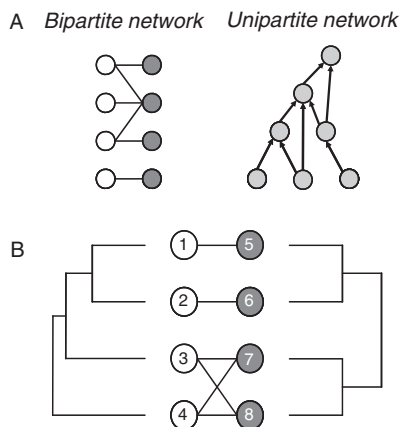
Networks are complex entities, difficult to study mechanistically. As a result, until recently, relatively little work had been done to model how interaction networks emerge through evolutionary processes. Contributing to this difficulty is the tradition of simplifying these networks by lumping phylogenetically unrelated species with those having qualitatively identical interactions into 'tropho-species' (Cohen *et al.*, 1993).

Among the several phenomenological approaches developed, the niche concept has played a central role. For instance stochastic networks generated under the 'niche model' (Williams & Martinez, 2000)—which predicts trophic interactions based on the assumption that a consumer feeds within a given range of prey body sizes—have structures close to real networks. The 'nested hierarchy model' (Cattin *et al.*, 2004) was the first to introduce evolutionary constraints. It hypothesizes that the rules in the network build-up constrain species to be organized into 'clades' that share similar prey, thus having similar niches. Although based on different processes, both the niche and the nested hierarchy models predict a variety of food-web characteristics such as the proportion of basal species and of omnivores, and food-chain length (Williams & Martinez, 2000; Cattin *et al.*, 2004).

Mechanistic evolutionarily models were also built on the principles of speciation, extinction and migration (Caldarelli, Higgs & McKane, 1998; Drossel, Higgs & McKane, 2001; McKane, 2004; Loeuille & Loreau, 2005; Rossberg *et al.*, 2005). By contrast with purely ecological models (May, 1973; Gross *et al.*, 2009), these evolutionary models tend to produce diverse and persistent communities (Caldarelli *et al.*, 1998; Loeuille & Loreau, 2005; Loeuille, 2010). These approaches are however still in their infancy (Loeuille & Loreau, 2009) and using phylogenetic information will help build more integrated macro-evolutionary models of network complexity.

#### (2) Analyzing the links between phylogeny and interaction networks

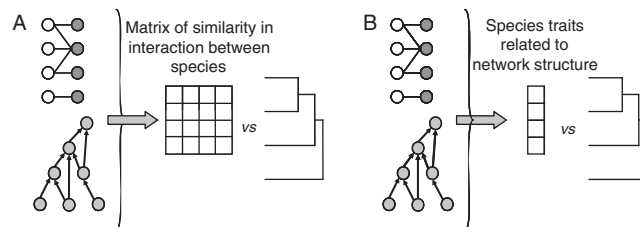
Using phylogenetic information can potentially bring novel insights on network organisation (Rezende, Jordano & Bascompte, 2007a). Again this is done by examining how phylogenetic proximity relates to niche similarity between species, with niche similarity being defined here as shared interacting partners in the network. Phylogenetic signal in a network context has been looked for in two ways. First, by looking at the identity of interacting partners. In this case, the presence of a phylogenetic signal indicates that related species tend to interact with the same species. For example, two closely related plants are pollinated by the same pollinator assemblage. Second, by looking at the structural characteristics of species in the network. The presence of a phylogenetic signal indicates that two related species tend to



**Fig. 2.** Links between phylogeny and network architecture. (A) Two types of ecological networks are commonly used to study the links between interaction patterns and phylogeny. Bipartite networks (left), such as pollination or host-parasitoid networks, describe the interactions between two guilds of species. Food webs (right) are unipartite networks with directed links, depicting who-eats-whom through several trophic levels. (B) Schematic example of the link between phylogeny and network architecture in bipartite networks. Here, the structure of the network is partially linked with phylogeny: closely related species 7 and 8 interact with identical species and closely related species 1 and 2 interact, respectively, with species 5 and 6 which are also closely related. Such a correspondence between the two phylogenies can be investigated using the ‘parfit’ test (Legendre *et al.*, 2002).

exhibit the same structural characteristics. For example, two related plant species tend to have similar specialization or tend to belong to the same network compartment.

A number of statistical techniques quantifying the relationship between phylogenetic and network structures are now available (Fig. 2). An early but rigorous method was developed to test for co-evolution in host-parasite bipartite networks, based on the so-called fourth-corner problem (Legendre, Galzin & HarmelinVivien, 1997; Legendre, Desdevises & Bazin, 2002). This method looks at whether the phylogenies of the hosts and the parasites present similar branching topologies, which would indicate a parallel diversification history among hosts and consumers. More recent approaches do not necessarily test for co-evolution, but simply for a phylogenetic signal through different methods (Fig. 3). For example, Ives & Godfray (2006) developed a test specifically designed to find a phylogenetic signal in bipartite networks based on a generalized least-square model. These studies generally focus on local interaction networks and they show that, indeed, phylogenetically similar species tend to interact with the same set of species and/or tend to occupy similar structural positions in the network (i.e. species having similar specialization or belonging to the same compartment). This has been shown in food webs (Cattin *et al.*, 2004; Bersier & Kehrl, 2008), in host-parasitoid networks (Ives & Godfray, 2006), in frugivory and pollination networks (Rezende *et al.*, 2007b) and plant-plant facilitation networks (Verdu & Valiente-Banuet, 2011).



**Fig. 3.** Interaction networks and phylogenetic signal. There are two main methods to assess phylogenetic signal in networks. (A) By relating phylogenetic similarity with the similarity the identity of interacting partners. Simple Mantel tests can be used to relate phylogenetic similarity with the similarity in interactions for species in the network. Similarity in interaction between two species is generally measured by the Jaccard index, calculated as the number of interaction partners shared by the pair of species divided by the pair’s total number of interaction partners. This approach has been applied to both food webs (Cattin *et al.*, 2004; Bersier & Kehrl, 2008) and mutualistic networks (but see Rezende *et al.*, 2007b; Hommola *et al.*, 2009). Note however that one drawback of Mantel tests is their power (Legendre, 2000). (B) By testing for a phylogenetic signal in species traits related to network structure such as species degree (species number of interaction partners). This indirect approach has been used by Rezende *et al.* (2007b) for species degree in mutualistic networks, and by Rezende *et al.* (2009) for species trophic level in the Caribbean marine food web. This can be achieved by classical tests like the Blomberg K-statistic (Blomberg *et al.*, 2003), or with phylogenetic regressions (PGLS), i.e. a generalized least-square regression incorporating the phylogeny in the correlation structure [e.g. with Brownian motion (Felsenstein, 1985), Ornstein-Uhlenbeck process (Grafen, 1989), Pagel’s lambda (Freckleton, Harvey & Pagel, 2002), or Blomberg’s ACDC model (Blomberg *et al.*, 2003)]. Note that contrary to the Mantel tests presented in (A), this approach uses only incomplete information of the structure of the interaction network.

The strength of this phylogenetic signal often seems, however, to depend on the role of the species in the networks, or on the group to which they belong. For instance, Bersier & Kehrl (2008) separated the taxonomic similarity of predators and prey in a local food web and found a stronger signal in the identity of the interacting partners when considering species in their role as prey. This indicates that related prey species tend to be consumed by the same predators but that related predators do not consume the same prey species as much as expected from their phylogenetic relatedness. Similarly, Ives & Godfray (2006) found that the signal in the identity of interacting partners of species was stronger for hosts than for parasitoids, while Rezende *et al.* (2007b) showed that in animal-plant mutualistic networks, the identity of interacting partners was strongly phylogenetically constrained for the frugivores and pollinators but not so much for the plants. Finally, in another study, Rezende *et al.* (2009) showed that, in a Caribbean marine food web, closely related species of bony fishes tend to belong to the same compartment (groups of species that interact mostly among themselves in networks) whereas closely related shark species were dispersed in different compartments. These studies all focus on relationships

between the phylogeny of a given guild and the interactions that this guild establishes with other species. However, the phylogeny of these interacting partners can also bring valuable information. For example, pollinators appear to interact with plants that are less phylogenetically related than herbivores do (Fontaine, Thébault & Dajoz, 2009).

All these studies suggest that the presence of a phylogenetic signal is common in local ecological interaction networks and that its strength often varies within networks. Although these results need further investigation, the concept that the phylogenetic signal can vary within a network is particularly interesting. It suggests asymmetries in the evolutionary forces that regulate diversification of interactions, or alternatively the presence of different constraints among compartments affecting local community assembly. Such intriguing results warrant more work to resolve better the roles of these various possibilities.

### (3) Using phylogenetic signal to understand and predict interaction network properties

A great deal of interest has been devoted to the importance of species traits, such as body size, morphology or phenology, in determining the structure of interaction networks (Brose *et al.*, 2006; Stang, Klinkhamer & van der Meijden, 2006; Olesen *et al.*, 2008; Petchey *et al.*, 2008). These determinants of network structure may themselves be partly determined by species evolutionary history, as is the case for body size (Blomberg *et al.*, 2003) or for traits involved in seed dispersal (Rezende *et al.*, 2007a). Different methods have recently begun to combine phylogeny with various species traits to study food webs and host-parasitoid networks (Ives & Godfray, 2006; Rezende *et al.*, 2009; Rohr *et al.*, 2010). Ives & Godfray (2006) found that neither host geographical range nor parasitoid feeding mode significantly affected host-parasitoid associations in the network they studied, and they did not identify any additional factors besides those linked with evolutionary history. By contrast, both Rezende *et al.* (2009) and Rohr *et al.* (2010) highlighted the combined importance of body size and phylogeny in determining the structure of the food webs. Specifically, Rohr *et al.* (2010) found that, across a sample of 12 food webs, the ratio of body size between prey and predator explained on average 20% of the interactions, and that the remaining information was linked with phylogeny. Incorporating phylogeny in studies of the structure of interaction networks thus appears to complement approaches based on species traits, possibly as a proxy for unmeasured traits that present a phylogenetic signal and that affect species interactions.

### (4) Perspectives on network phylogenetics

The application of phylogenetic information to understand ecological network structure and functioning is recent, and fundamental research avenues remain unexplored. The current methods that quantify phylogenetic signal in the structure of ecological networks are very coarse; the next generation of methods will require accounting for the

scale-dependence of the signal and for the distribution of interaction strength. Current methods quantify the phylogenetic signal for the overall network or by trophic level, but they cannot yet differentiate between distinct parts of the network. Improved methods are also needed to identify the particular types of interactions (trophic, parasitic or mutualistic) that are the most strongly related to evolutionary history. There is also a need to assess how the phylogenetic signal in interaction networks scales with space. Finally, another important issue is to disentangle the relative importance of phylogeny over other species traits (Nieberding, Jousset & Desdevises, 2010).

Given that network topology is linked to evolutionary history, phylogenetic information may also be used to predict novel interactions networks under network assembly. The identification of networks of interactions is a challenging task for empiricists and is subject to criticisms (e.g. Martinez *et al.*, 1999). Ives & Godfray (2006) proposed that phylogeny could be used to predict the location of species in an existing interaction network (i.e. which species would be its prey and predators) by comparing the phylogenetic position of this species with that of the species composing the existing interaction network. This perspective is particularly relevant to predict the structure of interactions of novel ecosystems that result from global changes (Lavergne *et al.*, 2010). For instance, species displacement associated with climate change is likely to create assemblages of species that never encountered each other before and thus that have never interacted previously.

## IV. RELATIONSHIP BETWEEN PHYLOGENETIC DIVERSITY AND ECOSYSTEM FUNCTIONING

For two decades, much effort has been placed on understanding how the composition of communities influences ecosystem functioning (Loreau *et al.*, 2001; Hooper *et al.*, 2005; see Section VIII, glossary, for definition). Working hypotheses include that the more diverse communities, i.e. with more diverse pathways to acquire and to use resources, would be more robust to species invasion (Kennedy *et al.*, 2002; Arenas *et al.*, 2006; Gerhold *et al.*, 2011), more productive (Tilman, Wedin & Knops, 1996; Hector *et al.*, 1999), and more resilient to ecosystems change (Peterson, Allen & Holling, 1998; Bellwood, Hoey & Choat, 2003). This prolific body of research (hereafter termed biodiversity and ecosystem functioning, BEF) is still trying to resolve the various mechanisms regulating the overall effects of diversity on ecosystem processes.

### (1) Phylogenetic diversity as a proxy for ecosystem functioning?

The BEF relationship is likely to be strongly related to the distribution of traits of the species within species assemblages (Loreau *et al.*, 2001; Hooper *et al.*, 2005; Reiss *et al.*, 2009), including how they are classified into functional groups (Lavorel *et al.*, 1997) based on particularly relevant



niche traits. Such classifications are however difficult to define *a priori* since myriads of traits may be involved in the ecosystem function of interest, and we often ignore the question of which are the more important traits to begin with (Violle *et al.*, 2007). As in community assembly, a comprehensive trait-based approach would be difficult to conduct and would remain open to criticisms about unmeasured traits (Cadotte, Cardinale & Oakley, 2008). Thus it may be possible to use phylogenetic diversity (see Section VIII, glossary, for definition) as a proxy of unmeasured functional diversity for the purpose of assessing its connection to ecosystem functioning (Cadotte *et al.*, 2009). As in community assembly, this assumes that phenotypic dissimilarity is correlated with evolutionary divergence time.

Pioneering work linking phylogenetic relatedness among species and ecosystem function was carried out by Maherali & Klironomos (2007) with experimental manipulation of mycorrhizal plant systems. They found that plant productivity is enhanced in communities with phylogenetically distantly related fungal species compared to closely related species. This result suggests, under the hypothesis of a strong phylogenetic signal of the traits considered, that the loss of an entire lineage could have strong negative ecological consequences since distinct lineages are likely to perform different functions.

Taking this reasoning one step further, Cadotte *et al.* (2008) explicitly compared the contribution of phylogenetic diversity, species richness and functional group richness to plant community productivity, and found that phylogenetic diversity was the best predictor of the three. Cadotte *et al.* (2009) also compared the contribution of seven different metrics of biodiversity, including phylogenetic diversity, to explain plant community productivity in the Cedar Creek experiment. Phylogenetic diversity explained, by itself, up to 41.5% of productivity and was ranked as the second best explanatory variable, following the presence of a nitrogen fixer. They concluded that phylogenetically diverse communities capture important functional diversity not reflected in the functional traits usually used in this kind of experiment (see also Flynn *et al.*, 2011). Along the same line of reasoning, Gerhold *et al.* (2011) showed that plant communities composed of species from phylogenetically distinct lineages were less likely to experience alien establishment (i.e. invasion) than communities consisting of closely related species.

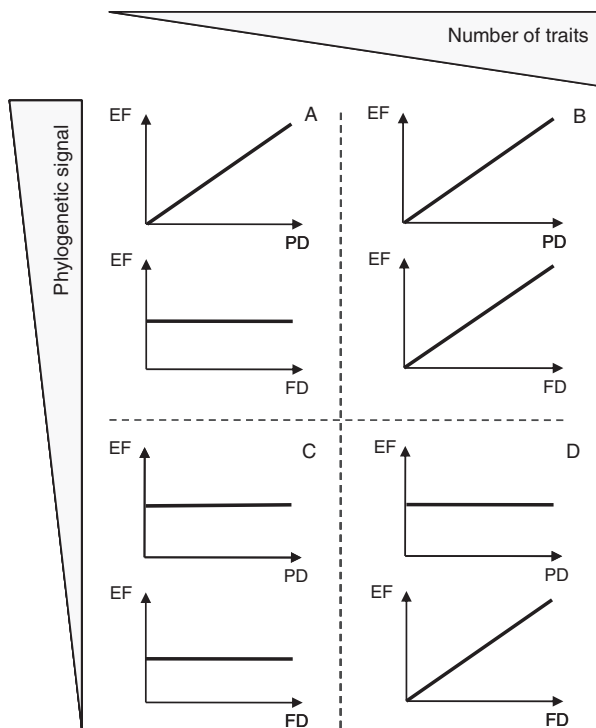
The *a posteriori* analysis of Cadotte *et al.* (2008, 2009) revealed a possibly ubiquitous relationship between phylogenetic diversity and productivity of plant communities, but it was limited by the strong co-variation between species richness and phylogenetic diversity. In an experiment with bacteria, Gravel and collaborators manipulated phylogenetic diversity and species richness independently (D. Gravel, T. Bell, C. Barbera, T. Pommier & N. Mouquet, in preparation). Combining experimental ecological and evolutionary mechanisms, they confirmed that productivity is indeed significantly related to species richness and phylogenetic diversity for their system, and that the latter is a much

stronger predictor of ecosystem functioning. However, by evolving their bacterial lineages under different environments, they were able to randomize the distribution of traits across the phylogeny, breaking the relationship between phylogenetic diversity and ecosystem functioning. They concluded that it may be misleading to use phylogenetic structure to predict ecosystem functioning without good knowledge on the evolutionary forces and ecological constraints that shaped species assemblages and trait distributions.

## (2) Perspectives: towards an ecosystem phylogenetics?

The study of 'ecosystem phylogenetics' is emerging and new experimental designs as well as appropriate statistical analyses are needed to disentangle the relative contributions of the different facets of biodiversity to ecosystem functioning. First, it would be important to understand how the relationship between phylogenetic diversity and ecosystem functioning scales with the range of phylogenetic patterns considered. There is currently no theory integrating the effects of taxonomic, functional and phylogenetic diversity on ecosystem functioning. The experimental studies conducted so far rely strongly on a marked phylogenetic signal, neglecting other patterns of trait distribution. Considering clustered, random or overdispersed distribution of species traits within the phylogeny is expected to impact the shape of the relationship between phylogenetic diversity and ecosystem functioning (illustrated in Fig. 4). Given that the level of phylogenetic signal varies also with geographic scale (as discussed in Section II), we expect the strength and the shape of the relationship between phylogenetic diversity and ecosystem functioning to follow this pattern. New experimental designs will be required as the conceptual framework matures.

A second important aspect is how much information about the phylogenetic structure of communities (abundance, tree balance, etc.) is needed to predict ecosystem functioning. Until now, BEF studies on phylogenetic diversity have only used Faith's phylogenetic diversity (PD) index that relies solely on presence/absence data, in order to predict ecosystem functioning (Cadotte *et al.*, 2008, 2010). However, the distribution of abundance along the phylogenetic tree as well as the phylogenetic distinctiveness among species within the community may be crucial since species with longer evolutionary divergence times are more likely to have diverged in resource use (Schumacher & Roscher, 2009). A more complete set of descriptors of phylogenetic relationships among species and community structure should thus be used depending on the question asked (Helmus *et al.*, 2007; Pavoine & Bonsall, 2011). Cadotte *et al.* (2010) proposed new and complementary descriptors of phylogenetic diversity in addition to Faith's PD: 'phylogenetic abundance evenness', the 'distribution of hierarchical imbalance of abundances' and 'abundance-weighted evolutionary distinctiveness'. With such metrics at hand, the question is no longer whether phylogenetic diversity promotes ecosystem functioning but rather which facet of phylogenetic diversity matters



**Fig. 4.** Four theoretical cases where the number of relevant traits for ecosystem functioning (EF) and the level of phylogenetic signal of all relevant traits vary. For each case we give the expected relationship between phylogenetic diversity (PD) or functional diversity (FD) and the level of ecosystem functioning (e.g. biomass production). If few relevant traits are considered in FD estimation but if all traits are highly conserved (A) we expect a positive relationship between PD and EF but no effect of FD on EF. If many traits are involved and if they are highly conserved (B) these two relationships should be positive. At the opposite, if few traits are involved and if all relevant traits are not conserved (C) we expect an absence of relationship between PD or FD and EF. Finally, if FD is estimated using many relevant traits that are weakly conserved (D), FD will explain EF while PD will not.

the most and what is the predictive power that we can reach using a complete view of the phylogenetic structure of communities. New experiments manipulating all components of phylogenetic diversity while keeping species richness constant are thus needed to unravel the pure effect of phylogenetic diversity and to estimate the predictive power of the complete phylogenetic structure of communities on ecosystem processes.

Once appropriate metrics are implemented, an important question is how much phylogenetic diversity influences BEF after removing the effect of functional diversity. Phylogenetic and functional diversity are interlaced, but each aspect of biodiversity contains information that needs to be partitioned better. We suggest using similar diversity metrics based on either phylogenetic or functional trees to disentangle their respective effects on ecosystem processes. The framework proposed by Cadotte *et al.* (2010) is a step in the right direction, but the question remains of whether phylogenetic

diversity still matters after removing the effect of functional diversity. This could be tested with a model comparison approach. Novel statistical methods developed for traditional BEF studies conducted at the taxonomic level were recently used (Bell *et al.*, 2009) to partition the relative contributions of species identity, interactions and community composition on ecosystem functioning (e.g. Gravel *et al.*, 2011). These methods might be adapted to understand the relative roles of the different facets of diversity.

Finally, future work should investigate thoroughly whether or not phylogenetic diversity is a more reliable (and general) predictor of ecosystem multifunctionality than functional diversity (as pioneered by Cadotte *et al.*, 2009). The choice of functional traits is critical to BEF studies, and especially for the investigation of the multifunctionality of ecosystems (Hector & Bagchi, 2007; Zavaleta *et al.*, 2010). As discussed above, phylogenetic diversity has already been shown to provide a potential integrated predictor of ecosystem functioning (Cadotte *et al.*, 2008). The next step is to explore whether by integrating numerous traits phylogenetic diversity might outperform functional diversity measures when it comes to multifunctionality. A promising avenue in this sense is the re-analysis of the multiple ecosystem processes of major BEF experiments, like the Cedar Creek long-term experiment (e.g. Zavaleta *et al.*, 2010) or the BIODEPTH project (Hector *et al.*, 1999; Spehn *et al.*, 2005).

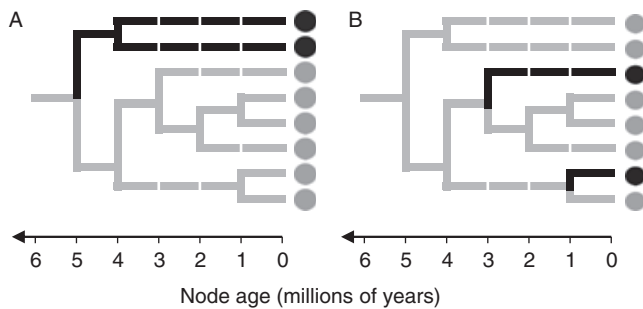
## V. VALUE OF PHYLOGENETICS IN CONSERVATION BIOLOGY

### (1) Taxonomy and systematics

For some time now, phylogenetics has contributed to the definition of conservation targets and has generated strategies for prioritizing conservation efforts (Faith, 1992; Purvis, Gittleman & Brooks, 2005). The most immediate value of phylogenetics to conservation is its influence on the definition of species, and thus on taxonomy and systematics. Species are widely regarded as a fundamental unit of biodiversity (Gaston, 1996), and their conservation is often the basis for national and international legislation (Isaac, Mallet & Mace, 2004). Phylogenetic analyses based on species' genetic sequencing have become a crucial tool in taxonomy and systematics (Godfray, 2007), accounting for the recent explosion in the numbers of recognized species in some regions and taxa (e.g. the near tripling in recognized South American amphibians since 1960, Rodrigues *et al.*, 2010). Through their influence on species identification, phylogenetic analyses also have a direct impact on the identification of priority areas for conservation, which are typically based on species as biodiversity units (e.g. Meegaskumbura *et al.*, 2002).

### (2) Species prioritisation

Species are not all equivalent in terms of the amount of unique evolutionary history they represent, and that would be lost if they became extinct (Nee & May, 1997; Mace,



**Fig. 5.** The phylogenetic diversity (PD) of a set of species can be measured as the total branch length of the phylogenetic tree representing the evolutionary relationships among species. This hypothetical tree of eight species (represented by circles) has a total phylogenetic history of 26 million years. Black circles correspond to threatened species, and black branches represent the evolutionary history that would be lost if threatened species became extinct. In (A), the extinction risk is clumped in parts of the tree with long branches, corresponding to species that are evolutionarily distinctive, resulting in higher losses in phylogenetic history (lost PD = 9) than in (B), where extinction is phylogenetically random (lost PD = 4).

Gittleman & Purvis, 2003; Thuiller *et al.*, 2011, see Fig. 5). This is the case for instance for the Tuataras (*Sphenodon* spp.), two species of iguana-like reptiles that are the sole living representatives of order Sphenodontia, the sister group to nearly 8,000 snakes and lizards in the order Squamata (May, 1990). Understanding these relationships opened the door to conservation strategies that go beyond species and consider evolutionary history itself as the conservation target (Forest *et al.*, 2007; Devictor *et al.*, 2010; Thuiller *et al.*, 2011). Several metrics have been proposed to guide conservation priorities among species by quantifying their evolutionary uniqueness or distinctiveness (e.g. Vane-Wright, Humphries & Williams, 1991; Pavoine, Ollier & Dufour, 2005) and by combining evolutionary uniqueness with extinction risk (e.g. Redding & Mooers, 2006; Isaac *et al.*, 2007; Faith, 2008) or with restricted range size, abundance and endemism (Cadotte & Davies, 2010).

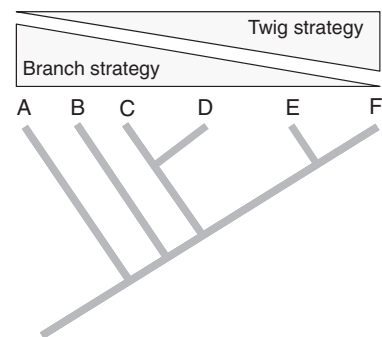
**(3) Going beyond biodiversity representation**

Conservation biology strives to preserve all components of biodiversity, either because they are intrinsically valuable (the irreplaceable products of millions of years of evolutionary history), or as a precautionary approach to ecosystem management. Incorporating phylogenetic information into conservation strategies allows for this approach to go beyond simple species representation. Phylogenetics has been used to inform priority areas for conservation by considering phylogenetic diversity, a measure of the overall evolutionary history contained in a set of taxa (e.g. Faith, 1992; Rodrigues & Gaston, 2002; Forest *et al.*, 2007; Devictor *et al.*, 2010), the expected future loss in phylogenetic diversity based on species probabilities of extinction in a given time frame (Faith, 2008; Thuiller *et al.*, 2011), and phylogenetic endemism, a measure that identifies areas where substantial amounts of

phylogenetic diversity are concentrated (Rosauer *et al.*, 2009; Cadotte & Davies, 2010).

In addition conservation biology also strives to ensure the conservation of the ecological and evolutionary processes that generate and maintain biodiversity, and the goods and services that humans obtain from nature (MEA, 2005). As such, there are some suggestions that targeting phylogenetic diversity in conservation may ultimately retain better ecosystem functioning (Section IV). Phylogenetic relationships also bear the mark of past evolutionary processes and may therefore help to guide priorities in the conservation of these processes in the future. It is still an open discussion whether these are best conserved by targeting the ‘branches’ of the phylogenetic tree (older lineages), its ‘twigs’ (new radiations, where new species have recently formed) or a combination of both (Fig. 6). On the one hand, long branches have disproportionate amounts of phylogenetic diversity, the raw material of future evolution, whereas there is much redundancy in short branches. On the other hand, short branches correspond to recent radiations, and correspond perhaps to lineages of higher ‘evolvability’ or evolutionary potential (Erwin, 1991; Mace *et al.*, 2003), and such lineages may perhaps be most likely to cope with future environmental changes. Conservation of evolvability is an attempt to conserve key elements of evolutionary processes rather than the conservation of existing static patterns (Mace *et al.*, 2003) and is central to evolutionary-based conservation strategies (Ferrière, Diekmann & Couvet, 2004).

When combined with data on species distributions, phylogenies may therefore help distinguishing between ‘museums’ of diversity—regions concentrating old lineages, where diversity has been disproportionately able to persist—from ‘cradles’—regions concentrating radiations, where diversity has been created recently, and where perhaps future speciations will be more likely (e.g. Chown & Gaston, 2000). However, there is no solid evidence that future ‘evolvability’ can be deduced from the branching patterns in the phylogenetic tree (Krajewski, 1991). Indeed, future evolutionary processes



**Fig. 6.** Two strategies for incorporating evolutionary history in conservation strategies. Lineages represent different evolutionary history. Long branches (left side of the phylogenetic tree) should be favoured in conservation strategies focusing on evolutionarily distinct species. Conversely, the twig strategy assumes that protecting recent lineages could increase evolutionary potential.



are not necessarily the same in a human-dominated world as in the past, and the fate of lineages will be determined by the fate of their species, which will in turn result from a complex combination of species-specific vulnerability traits (including population size, geographic range, genetic diversity, social behaviour, dispersal ability) that cannot directly be deduced from a phylogenetic tree (Krajewski, 1991).

Overall, while more research is needed on what drives 'evolvability', a precautionary approach would ensure the conservation of a maximum phylogenetic diversity *per se* in order to maintain as many options as possible for the future. This could be achieved by finding strategies that conserve both a maximum amount of phylogenetic diversity and the most evolutionarily distinct species (Pavoine *et al.*, 2005; Erwin, 2008), and by prioritizing regions with the highest expected loss in phylogenetic diversity in the near future based on species vulnerabilities to extinctions (Faith, 2008). Assessing changes in the geographical distribution of phylogenetic diversity in response to environmental change will also be essential to understand these potential evolutionary consequences (Lavergne *et al.*, 2010).

#### (4) Perspectives: increasing the predictive power of ecology for conservation

A key aspect of using phylogenetic information to inform conservation is that our understanding of basic ecological processes is insufficient. Thus, phylogenetic diagnostic tools can be used to identify important mechanisms driving community assembly (Section II), to identify key components of interaction networks (Section III) and to understand the relationships between diversity and function (Section IV). It could then be used to establish good management practices for protecting biodiversity in the face of global change.

For instance, phylogenetic information might help to improve predictions of species' extinction risk. Indeed, past extinctions have a strong phylogenetic signal (Nee & May, 1997; Purvis *et al.*, 2000), and it may be useful to use this to predict which clades are most at risk of future extinction (Purvis, 2008; Davies *et al.*, 2011), and in turn be useful in guiding future conservation priorities (Thuiller *et al.*, 2011). Understanding the contribution of phylogeny to the structure of interaction networks (Section III) should also help to predict the response of ecological networks to disturbances. For example, Rezende *et al.* (2007b) showed that the presence of a phylogenetic signal in mutualistic networks implies that extinction sequences are likely to be phylogenetically structured. If phylogenetically related species interact with a similar set of species, local extinction cascades are more likely to occur within phylogenetically related species too, thus putting entire clades in jeopardy in the community. The contribution of phylogenetics to the study of community ecology (Sections II and III) can therefore help to predict communities' response and susceptibility to changes in composition, for example through the addition of particular species (e.g. in biological invasions), as well as to assess the reliability of the model used to forecast the geographical distribution of species responses to global change (Lavergne *et al.*, 2010).

## VI. CONCLUSIONS

(1) Despite the fact that both changes in genotype frequencies (evolution) and species abundances (ecology) arise by interactions between individuals and the environment (Fussmann *et al.*, 2007), evolutionary and ecological processes have been largely studied in isolation from each other. Ecophylogenetics is rapidly becoming a key concept that lies at the crossroads of ecology, biogeography and macroevolution in ways that extend beyond the simple use of phylogenetic information in community ecology as begun almost ten years ago (Webb *et al.*, 2002). This new and fast-growing field is promoting the incorporation of evolution and historical contingencies into the ecological research agenda through the widespread use of phylogenetic data. In its short history, it has already had important impacts on a wide variety of fields by providing a fertile ground to reconcile evolutionary, ecological and functional approaches into a more integrative ecology.

(2) Ecophylogenetics brings together biologists interested in community and ecosystem ecology, evolution, phylogeny, biogeography and conservation biology. This offers an opportunity for creating 'an atmosphere of creativity that embraces the merging of disciplines, the application of novel tools and independence from established paradigms', as proposed by Whitham *et al.* (2006, p. 519) in their research program establishing the basis for a new framework for community and ecosystem genetics.

(3) Ecophylogenetics has advanced our understanding of how evolutionary history contributes to shape extant species distributions. We have outlined some of the areas where significant advances have been made recently, illustrated caveats, and proposed future research directions. Particularly important are the design of appropriate null models against which phylogenetic structure can be compared, and the incorporation of different spatial and temporal scales of community organisation.

(4) Ecophylogenetics started with an approach based on a phylogeny-as-proxy paradigm and greatly simplified its implications by focusing on clustering *versus* overdispersion patterns. Multiscale and multidimensional analyses of variation in niche and trait evolution should be made on the basis of hierarchical models and statistics. This partitioning will help gain an understanding about complex aspects of the evolutionary context of community structure that can go far beyond the competition *versus* environmental filter dualism that phylogenetic community ecology began with.

(5) Ecophylogenetics has improved our understanding of ecological network complexity. A strong phylogenetic signal between network constituents has revealed how much evolutionary history is important in shaping these complex interactive systems, as well as their properties (complexity, stability, functioning). Early results suggest that the strength of the phylogenetic signal varies among networks, implying that the degree of evolutionary binding will depend on the type of interaction considered (trophic, parasitism or mutualism). Although this is a promising avenue for future



research, a strong effort is now needed to assemble the data required to study this new area fully.

(6) Ecophylogenetics may also help ecology to become a more predictive science in fields such as ecosystem science and conservation biology (Belovsky *et al.*, 2004). For instance, by linking the distribution of species traits within a phylogeny to ecosystem functioning (Cadotte *et al.*, 2008) or by improving conservation strategies and the reliability of the model used to forecast the geographical distribution of a species response to global change (Lavergne *et al.*, 2010). Major challenges in this field will be to produce a theory integrating the effect of taxonomic, functional and phylogenetic diversity to ecosystem functioning, to adapt the phylogenetic perspective to the concept of multifunctionality, and to translate the phylogenetic approaches of conservation biology into tools that can be easily implemented by managers.

(7) One of the main challenges of ecophylogenetics remains conceptual. Whereas phylogenetic distance has been proposed as a proxy for niche similarity, phylogenetic community structure also sheds light on the underlying evolutionary and biogeographical processes (Leibold *et al.*, 2010). These two complementary views highlight the fact that macroevolutionary history constrains community assembly, which itself constrains diversification (Hutchinson, 1965; Johnson & Stinchcombe, 2007). What ecophylogenetics has achieved best is to stress how much a consistent theoretical framework is still lacking [despite some work in the right direction (Vellend, 2010)], ranging from local coexistence to macroevolution and ecosystem functioning in order to interpret efficiently observed phylogenetic and ecological patterns, and to implement tools of applied relevance in conservation biology.

## VII. ACKNOWLEDGEMENTS

This contribution was written collectively by the participants of the symposium PhyloCom-Montpellier-2010 funded by the French Ecological Society, the Institut des Sciences de l'Evolution de Montpellier, the Centre d'Ecologie Fonctionnelle et Evolutive and the University of Montpellier 2. We thank our two anonymous reviewers for their thoughtful comments. N.M. was supported by the CNRS and by a research grant ANR-09-JCJC-0110-01-BACH. N.M., V.D., C.N.M., S.L., D.M. and W.T. were supported by a research grant ANR-09-PEXT-01102-546-EVORANGE. N.M., C.N.M., S.L. and T.M. were supported by a research grant ANR-07-BDIV-014-DIVERSITALP. M.A.L. was supported by NSF and by NCEAS. V.D. was supported by a FRB grant FABIO.

## VIII. GLOSSARY

**Community assembly rules:** processes by which a community acquires its structure and composition. Includes

competition, dispersal, environmental filtering (i.e. species sorting along environmental gradients) and colonization events.

**Community phylogenetic structure:** patterns of species relatedness within and among communities that are significantly different from what would be expected in a random assembly of species. In general, it refers to phylogenetic overdispersion (or phylogenetic clustering): when individuals in a community are more (or less) distantly related to each other than expected from a random draw of same size from the regional pool of species.

**Ecological similarity:** the degree to which any two species resemble each other in the way they use the environment, in the identity of the species they interact with, in their ecological traits, or in the types of environment that they occupy. Similarity is usually measured as the inverse or the complement of dissimilarity, which can be calculated as a multi-dimensional distance between species from a trait or an environmental matrix that characterizes each species.

**Ecosystem functioning:** the collective organization of the biotic community through intraspecific and interspecific interactions, and through abiotic interactions with the environment, which is at the basis of primary and secondary productivity, nutrient cycling, soil development, water budgeting, and other ecosystem function. In biodiversity experiments, ecosystem functioning is often measured as the productivity or biomass of plants.

**Evolutionary convergence:** a situation where two contemporaneous species are more similar than were their respective ancestors at a given time in the past. Evolutionary convergence can occur in very distant lineages undergoing common selective pressures. For instance, similar strategies of carnivorous plants appeared independently in distant lineages of angiosperms (e.g. orders Caryophyllales and Ericales), in stressful, nutrient-poor environments.

**Interaction networks:** a description of interaction links between species found in a community. The links can be any interaction type, such as competition, predation, mutualism, etc. An interaction network is usually characterized through different measures including for instance the average number of links per species (complexity), the nestedness in species interactions and the modularity (network structural heterogeneity).

**Null model:** a hypothesis made in the absence of the mechanism that one wishes to test in order to draw statistically meaningful comparisons (Gotelli & Graves, 1996). A null model is always 'null' with respect to something. For example, there is a long history of null models in community ecology to test for the significance of competition in structuring ecological communities. Species can be shuffled randomly across sites, conserving the total number of occurrences of each species but changing the total number of species for each site; alternatively, occurrences can be shuffled randomly within sites keeping the species richness constant in each site but changing the total number of occurrences for each species. The choice of an adequate null

model to test a particular null hypothesis is very delicate and, ideally, should be validated using simulated datasets.

**Phylogenetic conservatism:** in a wide sense it is the ‘tendency of species to retain ancestral ecological characteristics’ (Wiens & Graham, 2005; Wiens *et al.*, 2010). It can be due to strong stabilizing selection, lack of additive genetic variation for niche-related traits, phenotypic constraints due to pleiotropy (when a single gene influences multiple phenotypic traits) and gene flow hampering local adaptation in ecologically marginal populations. If this also applies for complex syndromes, then niche-related traits should evolve more slowly than neutral expectations based on estimated species divergence times. Ecological studies usually refer to *niche conservatism* to describe conservatism of traits strictly related to the environment where they live, and to *trait conservatism* to describe conservatism on characteristics such as life-history traits or any other species characteristics. This term has been used in very different ways in the literature of phylogenetic community ecology, leading to a debate on how it should be measured.

**Phylogenetic diversity:** the amount of evolutionary history represented in the species of a particular community (Faith, 1992). Commonly used measures of phylogenetic diversity are the total branch length of a phylogenetic tree that contains all species present in a community, or the sum of pairwise distances between species weighted by their relative abundances. See Pavoine & Bonsall (2011) for a framework of phylogenetic diversity indices.

**Phylogenetic signal:** a statistical pattern whereby related species tend to resemble each other more than species taken at random from a phylogeny (Blomberg & Garland, 2002; Losos, 2008). A phylogenetic signal can be compared to two scenarios: (i) the absence of signal (i.e. no association between phenotypic or niche similarity and phylogenetic relatedness) or (ii) the signal expected under a Brownian motion model in which evolution occurs by small changes, which are random in direction at each interval. Testing for a phylogenetic signal is usually performed through a randomization of species among the tips of the phylogeny. Blomberg *et al.* (2003)’s  $K$  index became popular as a quantitative means of testing whether traits are more or less similar between closely related species than expected under Brownian motion (which corresponds to  $K = 1$ ). Data on communities (i.e. the co-occurrence of species in different sites) is not needed in order to look for phylogenetic signals among a group of species; only lists of species and traits are required. In a network context, phylogenetic signal quantifies the extent to which closely related species tend to share a similar position in the network and/or interact with similar species.

## IX. REFERENCES

ARENAS, F., SANCHEZ, I., HAWKINS, S. J. & JENKINS, S. R. (2006). The invasibility of marine algal assemblages: role of functional diversity and identity. *Ecology* **87**, 2851–2861.

AVISE, J. (2009). Phylogeography: retrospect and prospect. *Journal of Biogeography* **36**, 3–15.

BARTISH, I. V., HENNEKENS, S., AIDOU, A., HENNION, F. & PRINZING, A. (2010). Species pools along contemporary environmental gradients represent different levels of diversification. *Journal of Biogeography* **37**, 2317–2331.

BASCOMPTE, J. (2009). Disentangling the web of life. *Science* **325**, 416–419.

BELL, T., LILLEY, A. K., HECTOR, A., SCHMID, B., KING, L. & NEWMAN, J. A. (2009). A linear model method for biodiversity-ecosystem functioning experiments. *American Naturalist* **174**, 836–849.

BELLWOOD, D. R., HOEY, A. S. & CHOAT, J. H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* **6**, 281–285.

BELOVSKY, G., BOTKIN, D., CROWL, T., CUMMINS, K., FRANKLIN, J., MALCOLM, J., HUNTER, L., JOERN, A., LINDENMAYER, D., MACMAHON, J., MARGULES, C. & SCOTT, J. (2004). Ten suggestions to strengthen the science of ecology. *BioScience* **54**, 345–351.

BERSIER, L. F. & KEHRLI, P. (2008). The signature of phylogenetic constraints on food-web structure. *Ecological Complexity* **5**, 132–139.

BLOMBERG, S. P. & GARLAND, T. J. (2002). Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology* **15**, 899–910.

BLOMBERG, S. P., GARLAND, T. & IVES, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.

BROSE, U., JONSSON, T., BERLOW, E. L., WARREN, P., BANASEK-RICHTER, C., BERSIER, L. F., BLANCHARD, J. L., BREY, T., CARPENTER, S. R., BLANDENIER, M. F. C., CUSHING, L., DAWAH, H. A., DELL, T., EDWARDS, F., HARPER-SMITH, S., JACOB, U., LEDGER, M. E., MARTINEZ, N. D., MEMMOTT, J., MINTENBECK, K., PINNEGAR, J. K., RALL, B. C., RAYNER, T. S., REUMAN, D. C., RUESS, L., ULRICH, W., WILLIAMS, R. J., WOODWARD, G. & COHEN, J. E. (2006). Consumer-resource body-size relationships in natural food webs. *Ecology* **87**, 2411–2417.

CADOTTE, M. (2009). Ecophylogenetics. In *Encyclopedia of Earth* (ed. C. J. CLEVELAND), Environmental Information Coalition, National Council for Science and the Environment, Washington, DC. available at <http://www.eoearth.org/article/Ecophylogenetics?topic=49508>. (Retrieved 1 March 2012).

CADOTTE, M. W., CARDINALE, B. J. & OAKLEY, T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences* **105**, 17012–17017.

CADOTTE, M. W., CAVENDER-BARES, J., TILMAN, D. & OAKLEY, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE* **4**.

CADOTTE, M. W. & DAVIES, T. J. (2010). Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions* **16**, 376–385.

CADOTTE, M. W., DAVIES, T. J., REGETZ, J., KEMBEL, S. W., CLEVELAND, E. & OAKLEY, T. H. (2010). Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters* **13**, 96–105.

CAIDARELLI, G., HIGGS, P. G. & MCKANE, A. J. (1998). Modelling coevolution in multispecies communities. *Journal of Theoretical Biology* **193**, 345–358.

CATTIN, M. F., BERSIER, L. F., BANASEK-RICHTER, C., BALTESSPERGER, R. & GABRIEL, J. P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature* **427**, 835–839.

CAVENDER-BARES, J., KEEN, A. & MILES, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* **87**, S109–S122.

CAVENDER-BARES, J., KOZAK, K. H., FINE, P. V. A. & KEMBEL, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters* **12**, 693–715.

CHASE, J. M. & LEIBOLD, M. A. (2003). *Ecological Niches. Linking Classical and Contemporary Approaches*. The University of Chicago Press, Chicago.

CHAVE, J. (2004). Neutral theory and community ecology. *Ecology Letters* **7**, 241–253.

CHAVE, J., CHUST, G. & THÉBAUD, C. (2007). The importance of phylogenetic structure in biodiversity studies. In *Scaling Biodiversity* (eds D. STORCH, P. MARQUET and J. BROWN), pp. 150–167. Cambridge University Press, Cambridge.

CHOWN, S. L. & GASTON, K. J. (2000). Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution* **15**, 311–315.

COHEN, J. E., BEAVER, R. A., COUSINS, S. H., DEANGELIS, D. L., GOLDWASSER, L., HEONG, K. L., HOLT, R. D., KOHN, A. J., LAWTON, J. H., MARTINEZ, N., OMALLEY, R., PAGE, L. M., PATTEN, B. C., PIMM, S. L., POLIS, G. A., REJMANEK, M., SCHOENER, T. W., SCHOENLY, K., SPRULES, W. G., TEAL, J. M., ULANOWICZ, R. E., WARREN, P. H., WILBUR, H. M. & YODZIS, P. (1993). Improving food webs. *Ecology* **74**, 252–258.

DAVIES, T. J., BARRACLOUGH, T. G., CHASE, M. W., SOLTIS, P. S., SOLTIS, D. E. & SAVOLAINEN, V. (2004). Darwin’s abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 1904–1909.

DAVIES, T. J., SMITH, G. F., BELLSTEDT, D. U., BOATWRIGHT, J. S., BYTEBIER, B., COWLING, R. M., FOREST, F., HARMON, L. J., MUASYA, A. M., SCHRIRE, B. D., STEENKAMP, Y., VAN DER BANK, M. & SAVOLAINEN, V. (2011). Extinction risk and diversification are linked in a plant biodiversity hotspot. *PLoS Biology* **9**, e1000620.

- DAYAN, T. & SIMBERLOFF, D. (2005). Ecological and community-wide character displacement: the next generation. *Ecology Letters* **8**, 875–894.
- DEVICTOR, V., MOUILLOT, D., MEYNARD, C., JIGUET, F., THULLER, W. & MOUQUET, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters* **13**, 1030–1040.
- DIAMOND, J. M. (1975). Assembly of species communities. In *Ecology and Evolution of Communities* (eds M. L. CODY and J. M. DIAMOND), Harvard University Press, Cambridge, Mass.
- DIAMOND, J. M. & CASE, T. J. (1986). *Community Ecology*. Harper and Row, New York.
- DROSSEL, B., HIGGS, P. G. & MCKANE, A. J. (2001). The influence of predator-prey population dynamics on the long-term evolution of food web structure. *Journal of Theoretical Biology* **208**, 91–107.
- EASTMAN, J. M., PAINE, T. & HARDY, O. J. (2011). SPACoDi 0.10: a program for spatial & phylogenetic analysis of community diversity. *Bioinformatics* **27**, 2437–2438.
- EMERSON, B. C. & GILLESPIE, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution* **23**, 619–630.
- ENGBRECHT, B. M. J., COMITA, L. S., CONDIT, R., KURSAR, T. A., TYREE, M. T., TURNER, B. L. & HUBBELL, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* **447**, 80–82.
- ERWIN, T. L. (1991). An evolutionary basis for conservation strategies. *Science* **253**, 750–752.
- ERWIN, D. H. (2008). Extinction as the loss of evolutionary history. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11520–11527.
- FAITH, D. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**, 1–10.
- FAITH, D. P. (2008). Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. *Conservation Biology* **22**, 1461–1470.
- FELSENSTEIN, J. (1985). Phylogenies and the comparison method. *The American Naturalist* **125**, 1–15.
- FERRIERE, R., DIEKMANN, U. & COUVET, D. (2004). *Evolutionary Conservation Biology*. Cambridge University Press, Cambridge.
- FLYNN, D., MIROTCHEV, N., JAIN, M., PALMER, M. & NAEEM, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. *Ecology* **98**, 1573–1581.
- FONTAINE, C., THÉBAULT, E. & DAJOZ, I. (2009). Are insect pollinators more generalist than insect herbivores? *Proceedings of the Royal Society of London Series B* **276**, 3027–3033.
- FOREST, F., GRENYER, R., ROUGET, M., DAVIES, T. J., COWLING, R. M., FAITH, D. P., BALMFORD, A., MANNING, J. C., PROCHES, S., VAN DER BANK, M., REEVES, G., HEDDERSON, T. A. J. & SAVOLAINEN, V. (2007). Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **445**, 757–760.
- FRECKLETON, R. P., HARVEY, P. H. & PAGEL, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* **160**, 712–726.
- FRECKLETON, R. P. & JETZ, W. (2009). Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society B: Biological Sciences* **276**, 21–30.
- FUSSMANN, G. F., LOREAU, M. & ABRAMS, P. A. (2007). Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* **21**, 465–477.
- GASTON, K. J. (1996). *Biodiversity: A Biology of Numbers and Difference*. Oxford, Blackwell.
- GERHOLD, P., PARTEL, M., TACKENBERG, O., HENNEKENS, S. M., BARTISH, I., SCHAMINEE, J. H. J., FERGUS, A. J. F., OZINGA, W. A. & PRINZING, A. (2011). Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *American Naturalist* **177**, 668–680.
- GILLESPIE, R. (2004). Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**, 356–359.
- GIVNISH, T. J., MILLAM, K. C., MAST, A. R., PATERSON, T. B., THEIM, T. J., HIPPI, A. L., HENS, J. M., SMITH, J. F., WOOD, K. R. & SYTSM, K. J. (2009). Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences* **276**, 407–416.
- GODFRAY, H. (2007). Linnaeus in the information age. *Nature* **446**, 259–260.
- GOTELLI, N. J. & ENTSMINGER, G. L. (2003). Swap algorithms in null model analysis. *Ecology* **84**, 532–535.
- GOTELLI, N. J. & GRAVES, G. R. (1996). *Null Model in Ecology*. Smithsonian Institution Press, Washington, DC.
- GRAFEN, A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* **326**, 119–157.
- GRAHAM, C. H. & FINE, P. V. A. (2008). Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters* **11**, 1265–1277.
- GRANT, B. R. & GRANT, P. R. (1996). High survival of Darwin's finch hybrids: effects of beak morphology and diets. *Ecology* **77**, 500–509.
- GRAVEL, D., BELL, T., BARBERA, C., BOUVIER, T., POMMIER, T., VENAIL, P. & MOUQUET, N. (2011). Experimental niche evolution alter the strength the diversity-productivity relationship. *Nature* **469**, 89–94.
- GRIME, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* **17**, 255–260.
- GROSS, T., RUDOLF, L., LEVIN, S. A. & DIECKMANN, U. (2009). Generalized models reveal stabilizing factors in food webs. *Science* **325**, 747–750.
- HARDY, O. J. (2008). Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology* **96**, 914–926.
- HARDY, O. J. & SENTERRE, B. (2007). Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *Journal of Ecology* **95**, 493–506.
- HECTOR, A. & BAGCHI, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188–190.
- HECTOR, A., SCHMID, B., BEIERKUHNEIN, C., CALDEIRA, M. C., DIEMER, M., DIMITRAKOPOULOS, P. G., FINN, J. A., FREITAS, H., GILLER, P. S., GOOD, J., HARRIS, R., HÖGGER, P., HUSS-DANELI, K., JOSHI, J., JUMPPONEN, A., KÖRNER, C., LEADLEY, W., LOREAU, M., MINNS, A., MULDER, C. P. H., O'DONOVAN, G., OTWAY, S. J., PEREIRA, J. S., PRINZ, A., READ, D. J., SHERER-LORENZEN, M., SCHULZE, E.-D., SIAMANTZIOURAS, A.-S. D., SPEHN, E. M., TERRY, A. C., TROUBIS, A. Y., WOODWARD, F. I., YACHI, S. & LAWTON, J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1126.
- HELMUS, M. R., BLAND, T. J., WILLIAMS, C. K. & IVES, A. R. (2007). Phylogenetic measures of biodiversity. *American Naturalist* **169**, E68–E83.
- HOMMOLA, K., SMITH, J. E., QIU, Y. & GILKS, W. R. (2009). A permutation test of host–parasite cospeciation. *Molecular Biology and Evolution* **26**, 1457–1468.
- HOOPER, D. U., CHAPIN, F. S., EWEL, J. J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J. H., LODGE, D. M., LOREAU, M., NAEEM, S., SCHMID, B., SETALA, H., SYMSTAD, A. J., VANDERMEER, J. & WARDLE, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.
- HUBBELL, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- HUTCHINSON, G. E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *The American Naturalist* **93**, 145–159.
- HUTCHINSON, G. E. (1965). *The Ecological Theater and the Evolutionary Play*. Yale University Press, Yale.
- INGS, T. C., MONTROYA, J. M., BASCOMPTE, J., BLUTHGEN, N., BROWN, L., DORMANN, C. F., EDWARDS, F., FIGUEROA, D., JACOB, U., JONES, J. I., LAURIDSEN, R. B., LEDGER, M. E., LEWIS, H. M., OLESEN, J. M., VAN VEEN, F. J. F., WARREN, P. H. & WOODWARD, G. (2009). Ecological networks—beyond food webs. *Journal of Animal Ecology* **78**, 253–269.
- ISAAC, N. J. B., MALLETT, J. & MACE, G. M. (2004). Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology & Evolution* **19**, 464–469.
- ISAAC, N. J., TURVEY, S. T., COLLEN, B., WATERMAN, C. & BAILLIE, J. E. (2007). Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE* **2**, e296.
- IVES, A. R. & GODFRAY, H. C. J. (2006). Phylogenetic analysis of trophic associations. *American Naturalist* **168**, E1–E14.
- JOHNSON, M. T. J. & STINCHCOMBE, J. R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology & Evolution* **22**, 250–257.
- KEMBEL, S. W. (2009). Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters* **12**, 949–960.
- KENNEDY, T. A., NAEEM, S., HOWE, K. M., KNOPS, J. M. H., TILMAN, D. & REICH, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature* **417**, 636–638.
- KRAFT, N. J. B., VALENCIA, R. & ACKERLY, D. D. (2008). Functional traits and niche-based tree community assembly in an amazonian forest. *Science* **322**, 580–582.
- KRAJEWSKI, C. (1991). Phylogeny and diversity. *Science* **254**, 918–919.
- LAVERGNE, S., GARNIER, E. & DEBUSSCHE, M. (2003). Do rock endemic and widespread plant species differ under the Leaf-Height-Seed plant ecology strategy scheme? *Ecology Letters* **6**, 398–404.
- LAVERGNE, S., MOUQUET, N., RONCE, O. & THULLER, W. (2010). Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics* **41**, 321–350.
- LAVOREL, S. & GARNIER, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**, 545–556.
- LAVOREL, S., MCINTYRE, S., LANDSBERG, J. & FORBES, T. D. A. (1997). Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution* **12**, 474–478.
- LEGENDRE, P. (2000). Comparison of permutation methods for the partial correlation and partial Mantel tests. *Journal of Statistical Computation and Simulation* **67**, 37–73.
- LEGENDRE, P., DESDEVISES, Y. & BAZIN, E. (2002). A statistical test for host-parasite coevolution. *Systematic Biology* **51**, 217–234.
- LEGENDRE, P., GALZIN, R. & HARMELIN-VIVIEN, M. L. (1997). Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* **78**, 547–562.



- LEIBOLD, M. A., ECONOMO, E. P. & PERES-NETO, P. (2010). Metacommunity phylogenetics: separating the roles of environmental filters and historical biogeography. *Ecology Letters* **13**, 1290–1299.
- LEIBOLD, M. A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J. M., HOOPES, M. F., HOLT, R. D., SHURIN, J. B., LAW, R., TILMAN, D., LOREAU, M. & GONZALEZ, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**, 601–613.
- LOEUILLE, N. (2010). Influence of evolution on the stability of ecological communities. *Ecology Letters* **13**, 1536–1545.
- LOEUILLE, N. & LOREAU, M. (2005). Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 5761–5766.
- LOEUILLE, N. & LOREAU, M. (2009). Emergence of complex food web structure in community evolution models. In *Community Ecology* (eds H. A. VERHOEF and P. J. MORIN), pp. 163–178. Oxford University Press, Oxford.
- LOREAU, M., NAEEM, S., INCHAUSTI, P., BENGTTSSON, J., GRIME, J. P., HECTOR, A., HOOPER, D. U., HUSTON, M. A., RAFFAELLI, D., SCHMID, B., TILMAN, D. & WARDLE, D. A. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808.
- LOSOS, J. B. (1990). A phylogenetic analysis of character displacement in caribbean anolis lizards. *Evolution* **44**, 558–569.
- LOSOS, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* **11**, 995–1003.
- LOSOS, J. B., GLOR, R. E., KOLBE, J. J. & NICHOLSON, K. (2006). Adaptation, speciation, and convergence: a hierarchical analysis of adaptive radiation in Caribbean Anolis lizards. *Annals of the Missouri Botanical Garden* **93**, 24–33.
- MACARTHUR, R. H. & LEVINS, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* **101**, 377–387.
- MACE, G. M., GITTLEMAN, J. L. & PURVIS, A. (2003). Preserving the tree of life. *Science* **300**, 1707–1709.
- MAHERALI, H. & KLIRONOMOS, J. N. (2007). Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* **316**, 1746–1748.
- MARTINEZ, N. D., HAWKINS, B. A., DAWAH, H. A. & FEIFAREK, B. (1999). Effects of sample effort on characterization of food-web structure. *Ecology* **80**, 1044–1055.
- MATTHEWS, B., NARWANI, A., HAUSCH, S., NONAKA, E., PETER, H., YAMAMICHI, M., SULLAM, K. E., BIRD, K. C., THOMAS, M. K., HANLEY, T. C. & TURNER, C. B. (2011). Toward an integration of evolutionary biology and ecosystem science. *Ecology Letters* **14**, 690–701.
- MAY, R. M. (1973). Qualitative stability in model ecosystems. *Ecology* **54**, 638–641.
- MAY, R. (1990). Taxonomy as destiny. *Nature* **347**, 129–130.
- MAYFIELD, M. M. & LEVINE, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* **13**, 1085–1093.
- MCGILL, B. J., ENQUIST, B. J., WEIHER, E. & WESTOBY, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21**, 178–185.
- MCKANE, A. J. (2004). Evolving complex food webs. *European Physical Journal B* **38**, 287–295.
- MCPEEK, M. A. & BROWN, J. M. (2000). Building a regional species pool: diversification of the Enallagma damselflies in eastern North America. *Ecology* **81**, 904–920.
- MEA (2005). The Millennium Ecosystem Assessment. available at www.MAweb.org (Accessed 2005)
- MEEGASKUMBURA, M., BOSSUYT, F., PETHIYAGODA, R., MANAMENDRA-ARACHCHI, K., BAHIR, M., MILINKOVITCH, M. C. & SCHNEIDER, C. J. (2002). Sri Lanka: an amphibian hot spot. *Science* **298**, 379.
- MONTOYA, J. M., PIMM, S. L. & SOLE, R. V. (2006). Ecological networks and their fragility. *Nature* **442**, 259–264.
- MORLON, H., SCHWILK, D. W., BRYANT, J. A., MARQUET, P. A., REBELO, A. G., TAUSS, C., BOHANNAN, B. J. M. & GREEN, J. L. (2011). Spatial patterns of phylogenetic diversity. *Ecology Letters* **14**, 141–149.
- MÜNKEMÜLLER, T., DE BELLO, F., MEYNARD, C. N., GRAVEL, D., LAVERGNE, S., MOUILLOT, D., MOUQUET, N. & THUILLER, W. (in press). From diversity indices to community assembly processes: a test with simulated data. *Ecography*.
- NEE, S. & MAY, R. M. (1997). Extinction and the loss of evolutionary history. *Science* **288**, 328–330.
- NIEBERDING, C., JOUSSELIN, E. & DESDEVISES, Y. (2010). The use of co-phylogeographic patterns to predict the nature of host–parasite interactions, and vice versa. In *The Biogeography of Host-Parasite Interactions* (eds S. MORAND and B. KRASNOV), pp. 631–641. Oxford University Press, Oxford.
- OLESEN, J. M., BASCOMPTE, J., ELBERLING, H. & JORDANO, P. (2008). Temporal dynamics in a pollination network. *Ecology* **89**, 1573–1582.
- OLLIER, S., COUTERON, P. & CHESSEL, D. (2006). Orthonormal transform to decompose the variance of a life-history trait across a phylogenetic tree. *Biometrics* **62**, 471–477.
- PAVOINE, S., BAGUETTE, M. & BONSALE, M. B. (2010). Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecological Monographs* **80**, 485–507.
- PAVOINE, S. & BONSALE, M. B. (2011). Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews* **86**, 792–812.
- PAVOINE, S., LOVE, M. S. & BONSALE, M. B. (2009). Hierarchical partitioning of evolutionary and ecological patterns in the organization of phylogenetically-structured species assemblages: application to rockfish (genus: *Sebastes*) in the Southern California Bight. *Ecology Letters* **12**, 898–908.
- PAVOINE, S., OLLIER, S. & DUFOUR, A. B. (2005). Is the originality of a species measurable. *Ecology Letters* **8**, 579–586.
- PAVOINE, S., VELA, E., GACHET, S., DE BELAIR, G. & BONSALE, M. B. (2011). Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *Journal of Ecology* **99**, 165–175.
- PETCHEY, O. L., BECKERMAN, A. P., RIEDE, J. O. & WARREN, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 4191–4196.
- PETERSON, G., ALLEN, C. R. & HOLLING, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems* **1**, 6–18.
- PURVIS, A. (2008). Phylogenetic approaches to the study of extinction. *Annual Review of Ecology, Evolution, and Systematics* **39**, 301–319.
- PURVIS, A., AGAPOW, P., GITTLEMAN, J. & MACE, G. (2000). Nonrandom extinction and the loss of evolutionary history. *Science* **288**, 328–330.
- PURVIS, A., GITTLEMAN, J. & BROOKS, T. (2005). *Phylogeny and Conservation*. Cambridge University Press, Cambridge.
- REDDING, D. & MOERS, A. (2006). Incorporating evolutionary measures into conservation prioritization. *Conservation Biology* **20**, 1670–1678.
- REISS, J., BRIDLE, J. R., MONTOYA, J. M. & WOODWARD, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution* **24**, 505–514.
- REVELL, L. J., HARMON, L. J. & COLLAR, D. C. (2008). Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* **57**, 591–601.
- REZENDE, E. L., ALBERT, E. M., FORTUNA, M. A. & BASCOMPTE, J. (2009). Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters* **12**, 779–788.
- REZENDE, E. L., JORDANO, P. & BASCOMPTE, J. (2007a). Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. *Oikos* **116**, 1919–1929.
- REZENDE, E. L., LAVABRE, J. E., GUIMARAES, P. R., JORDANO, P. & BASCOMPTE, J. (2007b). Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* **448**, 925–926.
- RICKLES, R. E. (1987). Community diversity: relative roles of local and regional processes. *Science* **235**, 167–171.
- RODRIGUES, A. S. L. & GASTON, K. J. (2002). Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation* **105**, 103–111.
- RODRIGUES, A. S. L., GRAY, C. L., CROWTER, B. J., EWERS, R. M., STUART, S. N., WHITTEN, T. & MANICA, A. (2010). A global assessment of amphibian taxonomic effort and expertise. *BioScience* **60**, 798–806.
- ROHR, R. P., SCHERER, H., KEHRLI, P., MAZZA, C. & BERSIER, L. F. (2010). Modeling food webs: exploring unexplained structure using latent traits. *The American Naturalist* **173**, 170–177.
- ROSAUER, D., LAFFAN, S. W., CRISP, M. D., DONNELLAN, S. C. & COOK, L. G. (2009). Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology* **18**, 4061–4072.
- ROSSBERG, A. G., MATSUDA, H., AMEMIYA, T. & ITOH, K. (2005). An explanatory model for food-web structure and evolution. *Ecological Complexity* **2**, 312–321.
- RUNDEL, H. D. & NOSIL, P. (2005). Ecological speciation. *Ecology Letters* **8**, 336–352.
- SCHLUTER, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- SCHUMACHER, J. & ROSCHER, C. (2009). Differential effects of functional traits on aboveground biomass in semi-natural grasslands. *Oikos* **118**, 1659–1668.
- SPEHN, E. M., HECTOR, A., JOSHI, J., SCHERER-LORENZEN, M., SCHMID, B., BAZELEY-WHITE, E., BEIERKUHNEIN, C., CALDEIRA, M. C., DIEMER, M., DIMITRAKOPOULOS, P. G., FINN, J. A., FREITAS, H., GILLER, P. S., GOOD, J., HARRIS, R., HOGBERG, P., HUSS-DANELL, K., JUMPPONEN, A., KORICHEVA, J., LEADLEY, P. W., LOREAU, M., MINNS, A., MULDER, C. P. H., O'DONOVAN, G., OTWAY, S. J., PALMBORG, C., PEREIRA, J. S., PFISTERER, A. B., PRINZ, A., READ, D. J., SCHULZE, E. D., SIAMANTZOURAS, A. S. D., TERRY, A. C., TROUMBIS, A. Y., WOODWARD, F. I., YACHI, S. & LAWTON, J. H. (2005). Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs* **75**, 37–63.
- STANG, M., KLINKHAMER, P. G. L. & VAN DER MEIJDEN, E. (2006). Size constraints and flower abundance determine the number of interactions in a plant-flower visitor web. *Oikos* **112**, 111–121.
- THUILLER, W., LAVERGNE, S., ROQUET, C., BOULANGEAT, I. & ARAUJO, M. B. (2011). Consequences of climate change on the tree of life in Europe. *Nature* **470**, 531–534.
- TILMAN, D., WEDIN, D. & KNOPS, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720.
- VANE-WRIGHT, R., HUMPHRIES, C. & WILLIAMS, P. (1991). What to protect—systematics and the agony of choice. *Biological Conservation* **55**, 235–254.
- VELLEND, M. (2010). Conceptual synthesis in community ecology. *Quarterly Review of Biology* **85**, 183–206.



- VERDU, M. & VALIENTE-BANUET, A. (2011). The relative contribution of abundance and phylogeny to the structure of plant facilitation networks. *Oikos* **120**, 1351–1356.
- VIOLLE, C., NAVAS, M. L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. & GARNIER, E. (2007). Let the concept of trait be functional! *Oikos* **116**, 882–892.
- WEBB, C. O. (2000). Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist* **156**, 145–155.
- WEBB, C. O., ACKERLY, D. D., MCPEEK, M. A. & DONOGHUE, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**, 475–505.
- WESTOBY, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213–227.
- WHITHAM, T. G., BAILEY, J. K., SCHWEITZER, J. A., SHUSTER, S. M., BANGERT, R. K., LEROY, C. J., LONSDORF, E. V., ALLAN, G. J., DIFAZIO, S. P., POTTS, B. M., FISCHER, D. G., GEHRING, C. A., LINDROTH, R. L., MARKS, J. C., HART, S. C., WIMP, G. M. & WOOLEY, S. C. (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* **7**, 510–523.
- WIENS, J. J., ACKERLY, D. D., ALLEN, A. P., ANACKER, B. L., BUCKLEY, L. B., CORNELL, H. V., DAMSCHEN, E. I., DAVIES, T. J., GRYNES, J. A., HARRISON, S. P., HAWKINS, B. A., HOLT, R. D., MCCAIN, C. M. & STEPHENS, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**, 1310–1324.
- WIENS, J. J. & GRAHAM, C. H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* **36**, 519–539.
- WILLIAMS, R. J. & MARTINEZ, N. D. (2000). Simple rules yield complex food webs. *Nature* **404**, 180–183.
- ZAVALETA, E. S., PASARI, J. R., HULVEY, K. B. & TILMAN, G. D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 1443–1446.
- ZURELL, D., BERGER, U., CABRAL, J. S., CALABRESE, J., JELTSCH, F., MEYNARD, C. N., MÜNKEMÜLLER, T., NEHRBASS, N., PAGEL, J., REINEKING, B., SCHRÖDER, B. & GRIMM, V. (2010). The virtual ecologist approach: simulating data and observers. *Oikos* **119**, 622–635.

(Received 5 July 2011; revised 20 January 2012; accepted 14 February 2012; published online 20 March 2012)