

Phylogenetic diversity and nature conservation: where are we?

Marten Winter^{1,2}, Vincent Devictor³, and Oliver Schweiger¹

¹ Helmholtz Centre for Environmental Research – UFZ, Department of Community Ecology, Theodor-Lieser Str. 4, 06120 Halle (Saale), Germany

² German Centre for Integrative Biodiversity Research (iDiv), Deutscher Platz 5e, 04103 Leipzig, Germany

³ Institut des Sciences de l'Évolution, UMR CNRS-UM2 5554, Université Montpellier 2, Montpellier, France

To date, there is little evidence that phylogenetic diversity has contributed to nature conservation. Here, we discuss the scientific justification of using phylogenetic diversity in conservation and the reasons for its neglect. We show that, apart from valuing the rarity and richness aspect, commonly quoted justifications based on the usage of phylogenetic diversity as a proxy for functional diversity or evolutionary potential are still based on uncertainties. We discuss how a missing guideline through the variety of phylogenetic diversity metrics and their relevance for conservation might be responsible for the hesitation to include phylogenetic diversity in conservation practice. We outline research routes that can help to ease uncertainties and bridge gaps between research and conservation with respect to phylogenetic diversity.

A promising but yet ambiguous additional biodiversity component for conservation

More than two decades ago, Richard Vane-Wright *et al.* [1] proposed phylogenetic diversity (see [Glossary](#)) as an additional component for nature conservation. The idea was to integrate information on the phylogenetic positions of species as a legacy of evolutionary processes (e.g., speciation, radiation) into conservation assessments [2]. Research on the applicability of aspects of phylogenetic diversity has steadily increased since then [3,4]. Phylogenetic diversity has been repeatedly suggested to be relevant for nature conservation targets, because it can be related to processes such as extinction [5], biotic invasion [6], ecosystem functioning [7], and even ecosystem services [8].

However, despite the increasing number of studies, the scientific proof of the added value of phylogenetic diversity for nature conservation remains weak. We believe that this is one of the main reasons why phylogenetic diversity is largely neglected in conservation practice [9,10]. Here, we discuss the relevance and applicability of considering phylogenetic diversity in nature conservation.

In addition to the more general concept of conserving all components of biodiversity because of their intrinsic values, we identified four main conservation approaches that are commonly proposed as central justifications for the conservation of phylogenetic diversity: (i) the rarity

aspect; (ii) the richness aspect; (iii) phylogenetic diversity as a proxy for functional diversity; and (iv) phylogenetic diversity as a proxy for evolutionary potential. Along these lines, we emphasize that a sound conceptual justification for the added value of phylogenetic diversity is often missing. We finally highlight desirable research avenues to increase our knowledge of the role of phylogenetic diversity and of how it could potentially improve conservation in the future.

Phylogenetic diversity as an intrinsic biodiversity component

One general agreement is to conserve all components of biodiversity [11], including evolutionary information. If we lose species we will inevitably lose evolutionary information [5,12]. The concern about losing evolutionary information as a value on its own can also be seen in the context of the general motivation of nature conservation and leads to the fields of moral and ethical questions. However, it is unclear how protecting phylogenetic diversity *per se* can be an ultimate objective for modern conservation practice. Moreover, the motivations and criteria to consider phylogenetic diversity need to be clearly stated and scientifically proven. Further, it needs to be shown whether current conservation approaches do or do not automatically cover the conservation of phylogenetic diversity. In the following sections we discuss these issues in detail.

Glossary

Complementarity approach: in terms of conservation, this approach uses optimization algorithms to select a set of areas that, if protected, would represent components of biodiversity not adequately represented in existing protected areas [1]. Components could be, for example, species, regions, landscape features, evolutionary lineages, or functional characteristics.

Distinctiveness: 'distinctiveness' describes the phylogenetic relationship of a species to other extant species regardless of whether they co-occur.

Ecological keystone species: an ecological keystone species is defined as a species that is exceptionally important for the structure and functioning of the ecosystem.

Niche conservatism: niche conservatism is a phenomenon where species ecological niches or trait characteristics tend to be unchanged along evolutionary time scales; that is, between ancestor and descendant. It is often characterized by a significantly higher ecological similarity among closely related species than expected by chance (i.e., phylogenetic signal).

Phylogenetic diversity: phylogenetic diversity is often referred to as 'evolutionary diversity' and often abbreviated as 'PD'. It is a commonly used metric [55] (See Box 2 in main text). Here, we use phylogenetic diversity as generic term. Phylogenetic diversity in general is a biodiversity measure based on evolutionary relationships between species and represents one of the components of biodiversity.

Corresponding author: Winter, M. (marten.winter@ufz.de).

Box 1. Phylogenetic tree and distances

Phylogenetic tree. A phylogenetic tree (Figure 1) is a hypothesis about evolutionary relationships among species or other entities. Evolutionary relationships are graphically represented by branches connecting nodes. An internal node represents a hypothetical common ancestor of all species originating from that node. Terminal nodes (leaves or tips) represent observed species or entities. The common ancestor of all other nodes in the tree is called the root. A clade is defined as group of species with one single common ancestor (i.e., a monophyletic group).

Branch length. The length of a branch connecting two nodes can be proportional to the evolutionary divergence between the nodes. Branch lengths are mostly based on temporal divergence (e.g., dated estimates of divergence times in geological years, based on calibrations with fossil and/or pollen records).

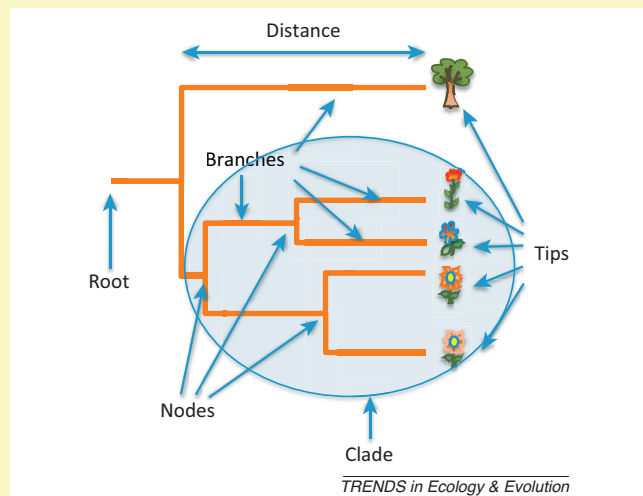


Figure 1. Theoretical phylogenetic tree of a plant community depicting the most important tree elements.

The rarity aspect

Humans usually value entities higher when they are rare. Because rare species are often the first to become extinct, rare species in addition to charismatic and ecological key-stone species have received priority protection [13]. The corresponding concept of rarity in an evolutionary framework is ‘phylogenetic rarity’, which can be measured as uniqueness or phylogenetic distinctiveness [14]. The extinction of a species from a young and species-rich clade will result in a smaller loss of evolutionary information than the extinction of a highly distinct species from an old and species-poor clade (Box 1).

However, phylogenetic distinctiveness is often correlated with rarity [5,15,16] and the protection of rare species will automatically ensure the conservation of distinct species. Thus, the added value of phylogenetic distinctiveness might be questionable. But at least two cases are evident where phylogenetic distinctiveness can help decision makers. When conservation prioritizations have to be made for a larger number of rare species, phylogenetic distinctiveness can contribute to the decision process. That is what the EDGE of Existence programme does [17], identifying species of particular conservation concern according to both rarity and phylogenetic distinctiveness. The programme has already generated conservation actions for several different threatened and evolutionarily distinct vertebrate species in over 20 countries worldwide (<http://www.edgeofexistence.org/>).

When information on the threat status of species is missing, which is the case for many species, phylogenetic distinctiveness might help to guide conservation actions [17–19]. For instance, in the global International Union for Conservation of Nature (IUCN) Red List of amphibians, 1294 species (22.5%) are not evaluated due to data deficiency but several can be identified as evolutionarily highly distinct [19].

According to these two cases and under the assumption that rarity has a value *per se*, we see the application of phylogenetic distinctiveness of single species as a promising approach in improving current conservation practice. This position was recently reflected by the call for sound conservation of evolutionarily distinct lineages as an official motion at the last World Conservation Congress in Korea in 2012 [20].

The richness aspect

The focus on single species has a long tradition in nature conservation [17], but more recent developments highlight the importance of considering whole areas in which communities and their ecological processes can be maintained [1]. Traditional area-based conservation often relies on species richness, which has been related to ecosystem functioning (stability, productivity) [21–23]. This is a research field with important implications, but also with many remaining questions [24] and difficulties for conservation applications [25]. With these area-based approaches, again the same question arises: what would the added value of community-based phylogenetic diversity be compared with traditionally used measures?

For conservation purposes, the identification of areas with more or less phylogenetic diversity than one would expect based on species richness alone seems to be important [26–28]. Such an approach reveals areas with evolutionarily very young or old clades or with taxonomically highly clumped or overdispersed communities [29]. Forest *et al.* [26] showed that the final selection of conservation sites would differ when the criteria for selection was phylogenetic diversity or species richness. Community-based measures of phylogenetic diversity seem also particularly suitable when environmental change affects species richness differently than species community compositions [30]. Warwick and Clarke [30] showed a negative effect of environmental contamination on the phylogenetic diversity of a marine community, whereas this effect was not reflected by changes in the number of species. Such deviations of evolutionary diversity from expectations based on the number of species have also been shown repeatedly in other systems [31,32], which could make community-based measures of evolutionary diversity in principle interesting for nature conservation.

But what would the added value of conserving areas or communities of unexpectedly high phylogenetic diversity, or spending money on phylogenetically eroded areas, actually be? Unless we consider the richness in evolutionary information as a value *per se*, we need other convincing arguments. These arguments usually follow the same lines as used for conserving species richness and can be seen in the context of conserving ecosystem processes and thus providing insurance against the consequences of short-term and

long-term environmental changes. In the context of phylogenetic diversity, common arguments are to consider phylogenetic diversity as a proxy for functional diversity [33] and as a measure of evolutionary potential [26].

Phylogenetic diversity as a proxy for functional diversity

It is argued that phylogenetically distinct species are likely to also have distinct functional traits. For example, the African plant *Welwitschia mirabilis* is the only member of the family Welwitschiaceae. Due to its unique combination of life history and leaf traits, it is one of the very few plants able to survive under extreme arid conditions and thus serves as an important refuge for many desert animals. Intuitively, the loss of evolutionarily distinct species is assumed to constitute an irreversible loss of functions for entire ecosystems [34]. Thus, it is argued that preserving a high level of phylogenetic diversity (and thus of functional diversity) should be a priority target in conservation to ensure the maintenance of ecological processes at an ecologically relevant timescale [35].

Another argument for using phylogenetic diversity as a proxy for functional diversity is that comprehensive information on species traits is lacking for most taxa, whereas the rapid current methodological advances already provide us with sufficient evolutionary information for many taxa [33]. To calculate a robust measure of functional diversity, a large amount of information on different traits is needed, which is often more intricate than compiling a phylogeny. Thus, it is often argued to use phylogenetic diversity as a proxy for unmeasured functional diversity or niche dissimilarity [36,37] instead of relying on an uncertain and costly measure of functional diversity.

However, the generality of the assumption that phylogenetic diversity can indeed be used as a proxy for functional diversity is unclear [33] and has generated an increasing number of studies investigating this relationship (e.g., [38]). In fact, this argument is still anchored on the assumption that closely related species share similar traits (phylogenetic signal; [39]), whereas the traits of distantly related species differ. However, there are many examples of missing or weak phylogenetic signals in species traits, suggesting that closely related species often do not share similar traits [40–42]. Whether phylogenetic diversity correlates with functional diversity depends on the considered traits, the level of their phylogenetic conservatism, and the focal taxa and regions [7,33,39]. If the conservation goal is to conserve functional diversity, considering phylogenetic diversity might be either well suited or totally misleading. We believe that this argument cannot be used without reservation to justify the application of phylogenetic diversity measures in conservation plans.

Phylogenetic diversity as a proxy for evolutionary potential

Another line of argument considers an evolutionary perspective in the sense of ‘evolutionary potential’; that is, species capacities to evolve in response to environmental changes [33,43,44]. From a species-centered point of view, the loss of phylogenetically distinct species might also result in the loss of evolutionary potential, which is of particular concern in the face of ongoing global change

[45,46]. However, despite an increasing body of evidence for differences in the evolutionary potential of different taxa in the context of climate change [44], diversification on islands [47], or adaptive radiations [48], it remains unclear whether the evolutionary potential depends on the phylogenetic position of a species; that is, whether it is a member of an old clade or belongs to a young clade that radiated recently [17,33,49]. Consequently, this argument cannot be used for the consideration of phylogenetic distinctiveness in species-centered conservation strategies.

From a community perspective, there are theoretical studies indicating that an increase in phylogenetic diversity of a community increases the evolutionary potential to adapt to environmental change [33,45,50,51]. If one assumes similar evolutionary potential for closely related species and larger differences among distantly related species, higher phylogenetic diversity within a community therefore should increase the chances of having some species or clades with high evolutionary potential in the community. This ‘insurance effect’ [21] would not be a simple effect of species richness [i.e., having more (of similar) species increases the chances of having successful species in unpredictable environments], but rather an effect of phylogenetic diversity itself. But as long as empirical evidence is lacking for such insurance, spending money on particular species or communities to ensure the maintenance of rather long-term and unknown processes is hard to justify.

The jungle of different indices

Even if the integration of phylogenetic diversity into conservation assessments can be justified, a major question will remain: what is the best measure and methodological approach to increase the conservation benefit compared with other, more commonly used conservation measures? Choosing the right metric of phylogenetic diversity is, in itself, not an easy task. There is a large variety of metrics and they are designed to quantify different aspects of phylogenetic diversity [52], such as the distinctiveness of single species and whole communities or phylogenetic richness [14,53,54] (Box 2). Further, some can be used more directly for priority setting in conservation, whereas others are more informative about the causes of general phylogenetic diversity patterns (Box 2).

In terms of distinctiveness of single species, metrics such as taxonomic distinctness (TD) [1] and evolutionary distinctiveness (ED) [17] were introduced. The initially purely topology-based indices reflect a branching order within a monophyletic group weighted according to its distinctiveness (number of nodes to the tree root; Box 1). Genetic distances and temporal divergence data are now increasingly available, making distance-based measures (i.e., using quantitative branch lengths rather than number of nodes; Boxes 1 and 2) more accurate. Therefore, ED can also incorporate branch lengths [17].

Many of the community-based indices are either conceptually or mathematically related or highly intercorrelated due to their dependence on covarying factors such as species richness [14,54] (e.g., phylogenetic diversity [55]) (Box 2). For conservation purposes, phylogenetic diversity or an endemism-weighted version of phylogenetic diversity

Box 2. Examples of commonly used metrics to calculate phylogenetic diversity

Phylogenetic distinctiveness of single species

Taxonomic distinctiveness (TD). Topology based; species values are calculated as the reciprocal of the number of nodes between the species and the tree root [1].

Evolutionary distinctiveness (ED). Topology based; species values are calculated as the sum of values per branch (tip to root) [17]. The branch value is its length divided by the number of descendant species.

Phylogenetic richness of communities

Phylogenetic diversity (PD). Calculated as the sum of branch lengths between root and tips for a community [55]. PD is mathematically related to species richness [14]. PD can be used as a complementary measure by identifying added evolutionary information by additional species [69].

Phylogenetic distinctiveness of communities to explore ecological processes

Average Taxonomic Distinctiveness (AvTD). Calculated as the sum of all branch lengths connecting two species averaged across all species representing the mean distance between two randomly chosen species [61]. AvTD is independent of species richness, but the extinction of closely related species will increase the index. AvTD can be applied, if the overall phylogenetic distinctiveness within a community is of interest, regardless of any comparison with other communities.

Mean pairwise distance (MPD). MPD and AvTD reflect phylogenetic structuring across the entire phylogenetic tree [70].

Mean nearest taxon distance (MNTD). Calculated as the mean of the branch lengths connecting each species to its closest relative [70]. MNTD reflects the phylogenetic structure of the tips of the tree.

Net Relatedness Index (NRI)/Nearest Taxon Distance (NTI). Represent the standardized effect size of MPD and MNTD accounting for the effects of species richness via repeated random resampling from a source pool based on a null model [70]. NRI and MPD assess relatedness deeper in the phylogenetic tree (i.e., an evolutionarily older pattern). NTI and MNTD reflect fine-scale relatedness [36,70].

Rao's Quadratic Entropy (QE). Based on the Simpson index and can account for abundances [62]. Without abundances, QE is mathematically similar to AvTD.

[56] are particularly suited for a complementarity approach. But the added value of indices that are mathematically highly dependent on species richness is obviously limited unless they can detect deviations from the expectations based on species richness [26,27]. To prevent any phylogenetic diversity metric from being a merely modified version of species richness, one can analyze the residuals from the relationship of the chosen index and species richness [57,58] or apply null models [42]. In doing so, areas with unexpectedly high or low phylogenetic diversity can be identified independent of the effects of species richness [59]. However, this approach is not free from arbitrary choices (e.g., the shape of the statistical relationship to estimate residuals or the design of the null model [60]).

Alternatively, various indices that are mathematically independent of species richness are commonly used in comparative ecological studies. They mostly reflect the phylogenetic distinctiveness of entire communities, such as the Average Taxonomic Distinctiveness (AvTD) [61], or other conceptually related measures, such as Rao's Quadratic Entropy [62], the Phylogenetic Species Variability

measure (which is $1 - \text{AvTD}$ [53]), the Net Relatedness Index, and the Nearest Taxon Index [36] (Box 2). These indices are more informative about causes of general phylogenetic diversity patterns and ecological processes (e.g., community assembly, resistance against species invasions). For instance, positive, negative, or no relationship with species richness can be interpreted in an ecological sense [14] (e.g., as environmental filtering or phylogenetic overdispersion [36]). Despite the obvious advantage of using richness-independent indices, it inevitably leads to the violation of set monotonicity [14]. In other words, such indices can increase when closely related species go extinct. The conservation implications of using these indices are therefore not necessarily straightforward.

Overall, the suitability of any metric for conservation purposes obviously depends on the question addressed (e.g., species-based or community-based approach) and on the available data (Box 2). Although bioinformatic tools have been developed to calculate a large variety of phylogenetic diversity metrics (e.g., [52]), we, however, believe that conservationists still lack a comprehensive guideline to determine which measure is suitable for which conservation goal. It is even likely that research on the technical issues related to metric development has been mostly conducted from a purely academic point of view and has largely failed to address the practical needs of conservationists. This might be an additional reason for the obvious hesitation to include the evolutionary perspective in nature conservation.

The need for a solid conceptual basis and reliable guidance

If we accept rarity and richness to represent values deserving protection on their own, as has long been done by conservationists for the species- and area-centered approaches, phylogenetic diversity has the potential to enrich modern conservation practice. It can help by the identification and prioritization of species in need of protection and it can improve the spatial planning of conservation areas by the identification of locations with high levels of phylogenetic diversity in addition to species-rich areas, which are not necessarily congruent.

However, in our opinion, the justification for preserving phylogenetic diversity as a proxy for functional diversity or evolutionary potential has so far largely failed. Our current knowledge of the benefits to the (future) functioning of ecosystems and securing evolutionary potential remains equivocal. If such justifications are wanted by conservationists and policymakers, current knowledge will not convince them to apply the concept of phylogenetic diversity because it still depends on many assumptions, uncertainties, and varying messages. Without better justification, pretending that increasing phylogenetic diversity is a target of conservation interest will remain highly questionable. Note that we do not say that phylogenetic diversity has no potential to provide benefits to nature conservation. But this can only be the case when it is well embedded in a sound conceptual framework and the justifications quoted for its usage are plausible and verified. This will be possible only if we increase our understanding of the relevance of phylogenetic diversity for ecosystems, what can be important for

conservation practice, and how this can be best implemented. In this respect, we think the research agenda on phylogenetic diversity should focus on the following four main directions.

- (i) We still need a solid conceptual basis for the added value of measures of phylogenetic diversity compared with the more traditional measures such as rarity, threat status, species richness, and other existing metrics reflecting the state of species and communities. In particular, we need to know under which conditions a clear link between phylogenetic diversity and functional uniqueness and diversity can be assumed and what the likely consequences for species survival and ecosystem functioning would be. Further, we also need to know more about the short-, intermediate-, and long-term importance of evolutionary potential at the species, community, and ecosystem level. We suggest building on research evaluating the relevance of phylogenetic diversity for ecosystem functioning [37,63–65] and the link between past evolution and recent population dynamics [66]. Those promising research fields provide already some insights on the role of evolutionary information for ecosystem functioning and population trends.
- (ii) We also call for a comprehensive guideline through the jungle of available phylogenetic diversity indices, with particular respect to the needs of conservationists – which index helps to protect what?
- (iii) Instead of using phylogenetic diversity as a new silver bullet, scientists should always communicate clearly on the advantages and disadvantages of the metrics and the reliability and feasibility of suggested spatial settings. This approach is necessary to increase the acceptance of scientific results and recommendations by conservationists.
- (iv) The importance of adding any evolutionary aspect to protected-area planning should be assessed quantitatively. For spatial planning in nature conservation, optimization procedures are frequently applied [13] and it should be an easy exercise to include different aspects of phylogenetic diversity. We suggest the use of species-based and community-based measures of phylogenetic diversity alongside species richness in such optimization tools [67]. Also, including other facets of diversity, such as functional diversity, should be encouraged whenever possible. This would result in maximization of the set of species to be conserved and in the identification of high evolutionarily and functionally distinct communities or regions, and can contribute to the conservation of ecological processes. We believe that, ultimately, the application (not only the recommendation) of such an approach would be a major step forward for modern conservation praxis rather than using abstract ideas on the potential importance of phylogenetic diversity [29].

It took some decades before already accepted scientific knowledge on the effects of climate change on biodiversity were accepted by decision makers and converted into relevant policy and conservation actions. But climate change has obvious effects on biodiversity, whereas the

potential benefits of phylogenetic diversity for nature conservation are still ambiguous. Will we ever see a national park designated on the basis of phylogenetic diversity? Maybe, but only if phylogenetically distinct species or areas with high phylogenetic diversity are explicitly considered to be of conservation interest. The existence of the already mentioned EDGE programme might be regarded as a first sign in this direction. One will learn from such initiatives whether two decades of agony [1] have been enough for a concept to mature and be applied in practice.

Acknowledgments

We are grateful to Ingolf Kühn for comments on earlier drafts and thank Walter Durka, Stefan Michalski, and the team at the EEF symposium ‘Evolutionary history, ecosystem function and conservation biology: new perspectives’ [68] for fruitful discussions. We also acknowledge the helpful and detailed comments and suggestions from three anonymous reviewers and Paul Craze.

References

- 1 Vane-Wright, R.I. *et al.* (1991) What to protect?—Systematics and the agony of choice. *Biol. Conserv.* 55, 235
- 2 Erwin, T.L. (1991) An evolutionary basis for conservation strategies. *Science* 253, 750–752
- 3 Purvis, A. *et al.*, eds (2005) *Phylogeny and Conservation*, Cambridge University Press
- 4 Bininda-Emonds, O.R.P. *et al.* (2000) The calculus of biodiversity: integrating phylogeny and conservation. *Trends Ecol. Evol.* 15, 92–94
- 5 Purvis, A. *et al.* (2000) Nonrandom extinction and the loss of evolutionary history. *Science* 288, 328–330
- 6 Winter, M. *et al.* (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proc. Natl. Acad. Sci. U.S.A.* 106, 21721–21725
- 7 Srivastava, D.S. *et al.* (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* 15, 637–648
- 8 Faith, D.P. *et al.* (2010) Ecosystem services: an evolutionary perspective on the links between biodiversity and human well-being. *Curr. Opin. Environ. Sustainabil.* 2, 66–74
- 9 Mace, G.M. and Purvis, A. (2008) Evolutionary biology and practical conservation: bridging a widening gap. *Mol. Ecol.* 17, 9–19
- 10 Santamaria, L. and Mendez, P.F. (2012) Evolution in biodiversity policy - current gaps and future needs. *Evol. Appl.* 5, 202–218
- 11 United Nations (1992) *Convention on Biological Diversity*, p30 United Nations
- 12 Mace, G.M. *et al.* (2003) Preserving the tree of life. *Science* 300, 1707–1709
- 13 Arponen, A. (2012) Prioritizing species for conservation planning. *Biodivers. Conserv.* 21, 875–893
- 14 Schweiger, S. *et al.* (2008) A comparative test of phylogenetic diversity indices. *Oecologia* 157, 485–495
- 15 Redding, D.W. and Mooers, A.O. (2006) Incorporating evolutionary measures into conservation prioritization. *Conserv. Biol.* 20, 1670–1678
- 16 Mi, X.C. *et al.* (2012) The contribution of rare species to community phylogenetic diversity across a global network of forest plots. *Am. Nat.* 180, E17–E30
- 17 Isaac, N.J.B. *et al.* (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE* 2, e296
- 18 Redding, D.W. *et al.* (2010) Evolutionary distinctiveness, threat status, and ecological oddity in primates. *Conserv. Biol.* 24, 1052–1058
- 19 Isaac, N.J.B. *et al.* (2012) Phylogenetically-informed priorities for amphibian conservation. *PLoS ONE* 7, e43912
- 20 Zoological Society of London (2012) *M019 - Halting the Loss of Evolutionarily Distinct Lineages*, p. 2 International Union for Conservation of Nature
- 21 Balvanera, P. *et al.* (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156
- 22 Bouvier, T. *et al.* (2012) Contrasted effects of diversity and immigration on ecological insurance in marine bacterioplankton communities. *PLoS ONE* 7, e37620

- 23 Hooper, D.U. *et al.* (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, U105–U129
- 24 Cardinale, B.J. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature* 486, 59–67
- 25 Srivastava, D.S. and Vellend, M. (2005) Biodiversity-ecosystem function research: is it relevant to conservation? *Annu. Rev. Ecol. Evol. Syst.* 36, 267–294
- 26 Forest, F. *et al.* (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445, 757–760
- 27 Sechrest, W. *et al.* (2002) Hotspots and the conservation of evolutionary history. *Proc. Natl. Acad. Sci. U.S.A.* 99, 2067–2071
- 28 de Carvalho, R.A. *et al.* (2010) Drafting a blueprint for functional and phylogenetic diversity conservation in the Brazilian cerrado. *Nat. Conserv.* 8, 171–176
- 29 Rodrigues, A.S.L. *et al.* (2005) Integrating phylogenetic diversity in the selection of priority areas for conservation: does it make a difference? In *Phylogeny and Conservation* (Purvis, A. *et al.*, eds), pp. 101–119, Cambridge University Press
- 30 Warwick, R.M. and Clarke, K.R. (1995) New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol. Prog. Ser.* 129, 301–305
- 31 Heino, J. *et al.* (2005) The relationship between species richness and taxonomic distinctness in freshwater organisms. *Limnol. Oceanogr.* 50, 978–986
- 32 Knapp, S. *et al.* (2008) Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecol. Lett.* 11, 1054–1064
- 33 Mouquet, N. *et al.* (2012) Ecophylogenetics: advances and perspectives. *Biol. Rev.* 87, 769–785
- 34 Bracken, M.E.S. and Low, N.H.N. (2012) Realistic losses of rare species disproportionately impact higher trophic levels. *Ecol. Lett.* 15, 461–467
- 35 Cadotte, M.W. *et al.* (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087
- 36 Webb, C.O. *et al.* (2002) Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505
- 37 Flynn, D.F.B. *et al.* (2011) Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. *Ecology* 92, 1573–1581
- 38 Devictor, V. *et al.* (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–1040
- 39 Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* 11, 995–1003
- 40 Freckleton, R.P. *et al.* (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* 160, 712–726
- 41 Fritz, S.A. and Purvis, A. (2010) Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proc. R. Soc. Lond. B: Biol. Sci.* 277, 2435–2441
- 42 Kluge, J. and Kessler, M. (2011) Phylogenetic diversity, trait diversity and niches: species assembly of ferns along a tropical elevational gradient. *J. Biogeogr.* 38, 394–405
- 43 Lankau, R. *et al.* (2011) Incorporating evolutionary principles into environmental management and policy. *Evol. Appl.* 4, 315–325
- 44 Lavergne, S. *et al.* (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu. Rev. Ecol. Evol. Syst.* 41, 321–350
- 45 Sgro, C.M. *et al.* (2011) Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.* 4, 326–337
- 46 Thuiller, W. *et al.* (2011) Consequences of climate change on the tree of life in Europe. *Nature* 470, 531–534
- 47 Losos, J.B. and Ricklefs, R.E. (2009) Adaptation and diversification on islands. *Nature* 457, 830–836
- 48 Ackerly, D.D. *et al.* (2006) Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology* 87, S50–S61
- 49 Krajewski, C. (1991) Phylogeny and diversity. *Science* 254, 918–919
- 50 Meynard, C.N. *et al.* (2011) Beyond taxonomic diversity patterns: how do alpha, beta and gamma components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Global Ecol. Biogeogr.* 20, 893–903
- 51 Bellwood, D.R. *et al.* (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol. Lett.* 6, 281–285
- 52 Kembel, S.W. *et al.* (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464
- 53 Helmus, M.R. *et al.* (2007) Phylogenetic measures of biodiversity. *Am. Nat.* 169, E68–E83
- 54 Vellend, M. *et al.* (2010) Measuring phylogenetic biodiversity. In *Biological Diversity: Frontiers in Measurement and Assessment* (Magurran, A.E. and McGill, B.J., eds), pp. 193–206, Oxford University Press
- 55 Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10
- 56 Rosauer, D. *et al.* (2009) Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Mol. Ecol.* 18, 4061–4072
- 57 Davies, T.J. and Buckley, L.B. (2011) Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 366, 2414–2425
- 58 Fritz, S.A. and Rahbek, C. (2012) Global patterns of amphibian phylogenetic diversity. *J. Biogeogr.* 39, 1373–1382
- 59 Mouillot, D. *et al.* (2011) Protected and threatened components of fish biodiversity in the Mediterranean Sea. *Curr. Biol.* 21, 1044–1050
- 60 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. *J. Ecol.* 96, 914–926
- 61 Warwick, R.M. and Clarke, K.R. (1998) Taxonomic distinctness and environmental assessment. *J. Appl. Ecol.* 35, 532–543
- 62 Rao, C.R. (1982) Diversity and dissimilarity coefficients - a unified approach. *Theor. Popul. Biol.* 21, 24–43
- 63 Cadotte, M. *et al.* (2012) Phylogenetic diversity promotes ecosystem stability. *Ecology* 93, S223–S233
- 64 Dinnage, R. (2009) Disturbance alters the phylogenetic composition and structure of plant communities in an old field system. *PLoS ONE* 4, e7071
- 65 Dinnage, R. *et al.* (2012) Diversity of plant evolutionary lineages promotes arthropod diversity. *Ecol. Lett.* 15, 1308–1317
- 66 Lavergne, S. *et al.* Are species' responses to global change predicted by past niche evolution? *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* (in press)
- 67 Diniz-Filho, J.A.F. and Pires de Campos Telles, M. (2006) Optimization procedures for establishing reserve networks for biodiversity conservation taking into account population genetic structure. *Genet. Mol. Biol.* 29, 207–214
- 68 Rolland, J. *et al.* (2011) Using phylogenies in conservation: new perspectives. *Biol. Lett.* 8, 692–694
- 69 Faith, D.P. *et al.* (2004) Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conserv. Biol.* 18, 255–261
- 70 Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.* 156, 145–155