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On the need for phylogenetic 'corrections' in functional trait-based approaches

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Abstract There is considerable uncertainty about if, and when, phylogenetic information is needed to answer various ecological questions about trait-based ecological studies. It has been recommended that both functional and phylogenetic information should be combined, and some researchers have even suggested that functional information for species should be 'corrected' because species are not phylogenetically independent. Here, we address these issues by identifying key types of questions in functional trait-based ecology and discussing the utility of phylogenetic information for answering them, either as a correction or in combination with functional traits. Phylogenetic analyses are identified as essential to answer questions related to the evolution of adaptations to abiotic and biotic conditions. However, we argue that phylogenetic information is not always relevant for functional trait studies, and should not be incorporated into ecological analyses without clear justification. Phylogenetic relatedness between species should not be considered a bias to be corrected, but rather an evolutionary signal that allows results to be interpreted at different evolutionary scales. Furthermore, if traits are conserved, phylogeny can be used as a proxy for missing

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information on traits and functional trait diversity. We conclude by providing guidelines on when to apply, and how to interpret, results obtained using phylogenetic information for a variety of ecological questions linked to functional traits.

Keywords adaptation · functional and phylogenetic diversity · phylogenetically independent contrast · response and effect traits · limiting similarity · ecosystem services

Introduction

The last two decades have witnessed an almost exponential increase in the use and development of functional trait-based approaches in ecological research (Lavorel and Garnier 2002; McGill et al. 2006; de Bello et al. 2010). These approaches are generally based on a description of organisms in terms of their functional traits, i.e. any phenotypic attribute linked to organisms' fitness and their effects on ecosystems (Lavorel and Garnier 2002; Violle et al. 2007). The intense interest in this approach is a consequence of its potential to uncover and predict general ecological trends, not limited to narrow taxonomic groups or geographical locations. Moreover, the enormous growth of trait data-sharing and the development of online databases are allowing the use of traits for an increasing number of organisms, regions and research questions.

As trait-based approaches have become increasingly common, attention has focused on whether such data should be used without formally accounting for phylogenetic relationships between species (Westoby et al. 1995; Price 1997; Blomberg and Garland 2002; Webb et al. 2002; de Bello et al. 2005; Diniz-Filho et al. 2012). The increasing availability of detailed phylogenetic information, computing power and bioinformatic tools has facilitated a rapid expansion of studies that apply phylogenetic information and methods to community ecology (Cavender-Bares et al. 2009). However, the increasing number of available techniques to account for phylogenetic effects in trait analyses (Pillar and Duarte 2010; Pavoine et al. 2011; Diniz-filho et al. 2012) has been accompanied by a corresponding increase in uncertainty about when and how such analyses should be used. This confusion bears striking similarities with the heated discussions on the need to correct for spatial autocorrelation in geographical ecology (e.g. Diniz-Filho et al. 2003):

indeed, it became commonplace for referees to ask for correcting for spatial autocorrelation regardless of the purpose of the analyses and the nature of the data. Similarly, trait researchers are often asked to use tests for 'correcting' phylogenetic dependence between species when using functional traits, even though such tests might lead to misleading interpretations. In other words, it is not clear whether phylogenetic relatedness between species should be considered a widespread bias that must be corrected, or a signal of evolutionary effects that only needs to be considered in some cases.

The need for phylogenetic tests has been widely discussed (Westoby et al. 1995; Price 1997; Swenson 2011; Pavoine and Bonsall 2011; Gerhold et al. 2015). However, there are no specific guidelines to help researchers to identify under what circumstances they are strictly necessary, when they are less important or when they are simply unnecessary to answer given ecological questions. Here, we seek to clarify this fundamental methodological issue. Specifically, we (1) assess whether and when we can consider phylogenetic tests as necessary and as a 'correction', and (2) identify cases where functional and phylogenetic information could be combined. In doing this, we discuss the broader utility of phylogenetic tests for answering fundamental questions in trait-based ecology.

Phylogenetic corrections in trait-environment studies

Much research has been devoted to identifying which traits make species more or less successful under given environmental conditions – broadly referred to as 'trait response' to the environment (Lavorel and Garnier 2002; de Bello et al. 2005). The main interest in this approach is the potential to predict which type of species will become more successful under future conditions imposed by land-use and climate change. Trait-response studies also try to assess to what extent environmental conditions filter species into assemblages based on their traits (environmental filtering). Trait analyses are performed at two main levels (Ackerly et al. 2002; Kleyer et al. 2012): (1) Species-level (or 'cross-species' analyses): typically performed sets of species across habitats, where trait differences among species are related to their different environmental preferences. The number of observations equals the number of species considered; and (2) Community-level; mostly performed on sets of

communities across one or more environmental gradients. In the most commonly used approach, a community trait mean, or a metric of functional diversity, is related to environmental conditions. Here, we use the term 'community' to refer to a set of coexisting species in a site, patch or territorial unit (i.e. a grid cell). The number of observations equals the number of 'communities' considered.

The potential importance of phylogeny is most intuitively understood for species level analyses, because species are, necessarily, not phylogenetically independent of each other. Closely related species are normally more similar than distantly related species in terms of both functional traits and environmental preferences. It is common for reviewers to ask researchers to take this dependency into account in their analyses. We therefore start by focusing on cross-species analyses, although much of the following reasoning applies to community-level analyses, discussed at the end of this section.

The need for phylogenetic 'correction' to answer ecological questions at the species-level strongly depends on the scale and resolution at which these questions need to be resolved. For example, researchers may be interested in whether (and which) traits have evolved as adaptations to environmental conditions (i.e. 'Are small leaf sizes reflecting an adaptation to drought or is body size bigger in cooler climate?'). Potential tests need to be made between close relatives and within lineages, to test if niche differentiation (particularly within clades) has been accompanied by the development of a specific phenotype (Diniz-Filho et al. 2009). Similar reasoning applies when researchers are interested in co-evolution of pairs of traits, or syndromes of traits (Cavender-Bares et al. 2009). Not applying a phylogenetic 'correction' to these analyses would only reveal whether a given value of a trait had been selected across all species, irrespective of their evolutionary paths, and would fail to show evolutionary changes within a clade. Ignoring phylogenetic information in such cases could therefore result in missing adaptive signals at lower hierarchical levels (i.e. species-level) and differentiation occurring towards the tips of the phylogeny. This is particularly the case when trait variation is driven by historical contingencies and/or other higher-level clade dynamics over long time scales (Diniz-Filho et al. 2009).

Another frequently asked question is: "what will be the effects of short-term environmental changes?", i.e.

which species in a given regional species pool are going to be successful and which will be driven to (local) extinction. Phylogenetic information is less important for such questions. At least, we do not recommend presenting only the phylogenetically 'corrected' results. Our reasoning is that the most important ongoing global change drivers operate on human time scales and therefore do not normally provide enough time for evolutionary processes to get 'fixed' in the phylogeny. Imagine trying to determine which plant species will increase or decrease their populations following a change in livestock grazing pressure. A test that does not account for phylogeny might indicate that species having greater specific leaf area (SLA), smaller size or nitrogen fixing will become more frequent and abundant under increased grazing pressure. This is an informative result because it identifies what kind of species, from those available in the regional pool, could be expected to increase or decrease their abundances under a given environmental change. Given that species with different traits affect ecosystem functioning in different ways, we might also potentially predict changes in ecosystem processes and services related to the new species composition (Lavorel and Garnier 2002; de Bello et al. 2010). All this would be possible without specifically accounting for evolutionary relationships between species.

Referees and editors, however, could argue that additional phylogenetic 'correction' is needed to answer questions related to what type of species are going to be either successful or unsuccessful under different environmental conditions. The typical argument here is that the species used in the analyses are not independent observations. In a hypothesis-testing framework, if one is to make generalizations it certainly may be interesting to tease apart phylogenetic vs environmental effects on traits. However, this answers a completely different question from the one originally posed above. Indeed, applying phylogenetic corrections as the default practice when relating traits to environment can significantly influence results. Specifically, including phylogeny in trait analyses may result in three main scenarios (Fig. 1): (1) Traits become non-significant; (2a) The traits remain significant but both traits and niches are not phylogenetically conserved; (2b) The traits remain significant but both traits and niches are phylogenetically conserved; or (3) The traits are only significant after accounting for phylogeny.

The first scenario (traits become non-significant after accounting for phylogeny) typically indicates that both
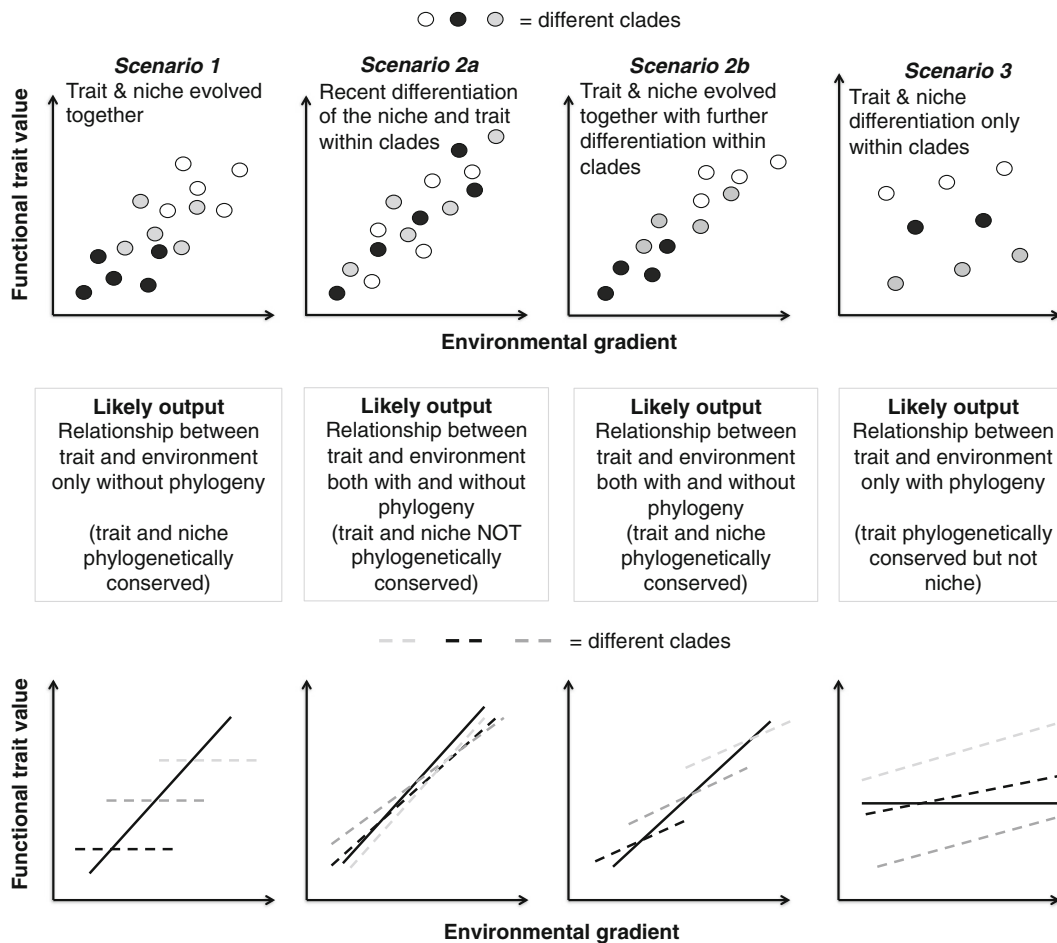
Fig. 1 Possible results when assessing the relationship between species traits and species environmental preferences. In the figure, each species is represented by one circle, with different colours indicating different clades. Solid lines show relationship between trait and environment without taking phylogeny into account.

Dashed lines show relationships between trait and environment taking phylogeny into account (i.e. within clades). Ecological niche refers to species preferred environmental conditions. See section 'Phylogenetic corrections in trait-environment studies' for further details.

species traits and species environmental preferences (i.e. niche) are phylogenetically conserved. We use the term 'phylogenetically conserved' to indicate that closely related species are more functionally similar than evolutionary distant species (Webb et al. 2002; Cavender-Bares et al. 2009; Münkemueller et al. 2015). Species niche refers here to the environmental and ecological conditions at the sites where the species is more frequently found or where it grows better (which corresponds to the beta-niche concept proposed by Silvertown et al. 2006 and the Grinnellian niche sensu Soberón 2007). Such a non-significant result could occur, for example, if legumes prefer highly grazed sites, or if a clade that prefers a given grazing regime (say abandonment) contains species that are tall

and have a low SLA compared to species in other clades. As such, although there is a replacement of clades with different traits across the study gradient, phylogenetic correction would most likely lead to loss of the signal of the association between traits and the environmental gradient – metaphorically throwing the baby out with the bathwater. The loss of signal certainly provides important information, but critically it does not invalidate the predictions that abandonment of grazing regimes will initially favour (within a given regional pool of species), tall, tough-leaved species without nitrogen fixing abilities. It also does not invalidate the fact that certain traits have evolved in different lineages with different preferred environmental conditions; for example, all species in a clade being ruderal

species with specific traits. Therefore, interpretations of the adaptive value of traits under this scenario (traits not related to environment after accounting for phylogenetic relationships between species) could prove misleading (cf. Klimeš 2008). The results may be due to a lack of differentiation within clades in terms of both traits and niche, but a differentiation in terms of niche and traits could have occurred early in evolution.

The second scenario (the relationship between traits and the environment remains significant after accounting for phylogeny) can occur in two cases (Fig. 1). In scenario 2a, environmental preferences and traits are not strongly phylogenetically conserved (i.e. closely related species do not share often the same environmental niche and trait values) and environmental changes will probably not exclude many lineages, but may cause a functional replacement between species within and between clades. In scenario 2b, environmental preferences and traits are strongly phylogenetically conserved (i.e. closely related species often share the same environmental niche and trait values), and environmental changes will therefore often exclude some lineages.

The third scenario (some traits have a significant relationship with an environmental gradient, but only after accounting for the phylogeny) could happen, for example, when species growing in both grazed and ungrazed conditions are characterized by a wide variety of trait values and there are no obvious differences between habitats. If some traits become significant only after applying phylogenetic information, then differences between habitats are observable only in changes between more closely related species, i.e. within clades, for example, as a replacement of congeneric species with different traits along environmental gradients (Hoffmann and Franco 2009). This would imply a recent adaptation to either one or both habitats – one that would remain hidden if the evolutionary relationships between species were not taken into account.

Clearly, phylogenetic tests can provide insights into important questions about the relationship between traits and environmental preferences, providing a very useful mechanistic view on the evolutionary processes responsible for the observed patterns. Moreover, these tests can sometimes indicate what type of changes can be expected under some environmental scenarios (within and/or between clades). However, the scenario in which results become non-significant after accounting for phylogenetic relationships does not invalidate the predictions of trait-environment patterns within a region. The key

point is that tests conducted with and without phylogeny focus on different questions. On this basis, functional trait researchers should not feel obliged to always include phylogenetic analyses. That said, as a rule of thumb it might be useful to apply both tests, always presenting the results without phylogenetic 'correction' and, where appropriate, including the results of further tests on the effects of phylogenetic conservatism on traits and environmental preferences. Since these additional tests provide different information, they may generate insights into ecological and evolutionary questions that are not the main objective of a study. Special attention is deserved for the case of groups of closely related species which are usually very difficult to distinguish (for example species within the *Alchemilla vulgaris* group or *Taraxacum* sect. *ruderalia*) and have very similar functional traits and niche preferences within the group. Having, for example, four *Taraxacum* species in a dataset (in the sometimes unlikely case that plant ecologists are able to distinguish them), will results in the over-representation of the information of this clade into the analyses. In this case, treating the whole group as a single species or applying phylogenetic corrections, although with the risk shifting the focus from between-clades to within-clades differentiation, are options to be seriously considered.

Similar considerations to the scenarios discussed above apply to community-level analyses. Here, the question of how traits relate to the environment is formulated in terms of whether the environment selects communities with certain trait values, often referring this selection effect as 'environmental filtering' (Götzenberger et al. 2012). Various potential tests could be used to address this question. For example, researchers might assess changes in mean trait values or functional trait diversity for several communities across environmental gradients (Pillar and Duarte 2010; Pavoine et al. 2011). Alternatively, researchers could compare indices of beta functional diversity between communities to assess the influence of abiotic conditions on functional replacement between sites (Swenson 2009; de Bello et al. 2010).

Several authors have suggested that accounting for phylogeny is important for community-level analyses of functional traits (Diniz-Filho et al. 2009; Pillar and Duarte 2010; Pavoine et al. 2011). However, few tests have so far been proposed and there is a clear need to further develop methodology. Regardless of analytical advances, we would argue that the decision to apply

phylogenetic tests is again dependent on the level of answer required. Consider a situation where the percentage of coniferous species (with certain shared traits) increases along an aridity or coldness gradient while the proportion of deciduous species decreases (cf. Ackerly et al. 2002). This would be the case if both environmental preferences and traits are phylogenetically conserved (scenario 1 above), and would indicate early differentiation (in both traits and niches) between these groups. Accounting for phylogeny would risk that the test will not show the replacement of functionally different species along the gradient, but would instead indicate that there is no apparent environmental filtering within lineages. This would lead to the misleading conclusion that environmental filtering is not important for community assembly. It follows that researchers should not feel obliged to account for phylogeny in studies of community trait composition if evolutionary trait patterning is outside the scope of the study. However, for questions related to beta diversity there are cases where phylogenetic information could be useful. For example, when information on various important traits expected to be phylogenetically conserved is missing (Swenson 2009; see further below).

Combining phylogeny and traits

In the previous section we challenged the view that phylogenetic information should be uncritically and systematically used for correcting functional trait data. We now identify and discuss the types of questions that could potentially benefit from combining functional and phylogenetic information together. Two main areas of study could, in principle, benefit from such an approach: first, the study of community assembly rules, i.e. the mechanisms underlying species coexistence; second, predicting ecosystem functions and services from the type of species present in a community. In general, phylogenetic information becomes important to complement the information on traits, i.e. to take into account information not accounted by the traits measured and/or when trait information is largely missing (Cadotte et al. 2013). Because of the complexity of dealing with multiple traits and their combinations, potentially important or complex traits could be easily overlooked or remain unmeasured, while uninformative traits could be included in analyses. Phylogenetic information, in this sense, can provide additional information

to that provided by the few traits that have been measured. Indeed, phylogenetic differences between species have been used as a surrogate of functional trait differences between species, particularly to account for missing or complex trait information (Cavender-Bares et al. 2009; Swenson and Enquist 2009; Gerhold et al. 2015).

Species coexistence

There has been a recent surge of interest in the effects of traits on species coexistence, considerably augmenting the literature on functional trait diversity in the last decade (Gotzenberger et al. 2012). Functional traits reveal ecological differentiation between species, and thus represent one of the most relevant components of biodiversity from which the processes governing community assembly can be inferred (Swenson and Enquist 2009). A growing body of literature suggests that species need to be functionally different to coexist, as functionally distinct species are able to use different niches and therefore minimize interspecific competition (Gotzenberger et al. 2012).

Phylogeny has been increasingly used to study trait-based assembly processes because, if traits are phylogenetically conserved, phylogenetic diversity can be used as a proxy of functional diversity. The use of phylogenetic differences in place of functional differences relies on the assumption that the ecological differences between species are proportional to the amount of time since they diverged from a common ancestor, supported by a Brownian motion model of evolution (Webb et al. 2002). However, this assumption is often not substantiated (Webb et al. 2002; Prinzing et al. 2008; Pavoine et al. 2013; Gerhold et al. 2015), and we therefore do not recommend the use of phylogeny instead of traits to answer questions related to species coexistence. Moreover, as noted by Swenson and Enquist (2009), while phylogenetic diversity may be a good general proxy for ecological similarity between species, it has a reduced capacity to reveal the functional mechanisms behind species coexistence, especially when coexisting species simultaneously converge on different traits. Another risk of focusing only on phylogenetic information is that traits could be conserved because of evolutionary adaptations to different environments overriding the effects of trait differentiation within clades. Thus, phylogenetic patterns alone are generally considered as little use as proxies of community assembly (Gerhold et al. 2015).

Phylogeny can, however, serve as a general proxy of a trait that has not been measured, or of a 'bundle' of traits. For example, the type of mycorrhiza is seldom included among measured traits, even though this trait could be essential to understand interactions between plants species. Here, the phylogenetic relatedness might correspond to similar mycorrhiza infections, for example in Ericoids. Another example is provided by Orchids, which have special types of mycorrhiza (or, in general, dependence on fungi) and also depend on specific pollinators (determined by a special type of polinaria). In such cases, using phylogeny allows researchers to analyze, through a proxy, important (phylogenetically conserved) traits that are usually not measured, or which are not available for many species. As species interactions typically operate via multiple traits, a combination of key measured traits and phylogeny may better assure that different axes of differentiation between species are being considered. Phylogeny can also sometimes be used to complete missing trait information in a dataset (Penone et al. 2014).

A researcher might be interested in the evolutionary effect of species interactions. In this sense, a negative correlation between phylogenetic and functional diversity in certain habitats could indicate the effect of past competition on present day coexistence (Prinzing et al. 2008). Thus, phylogeny could be useful to tease apart the effect of past vs present day patterns on species interactions and evolution. Theoretically, the combination of phylogeny with trait information could provide insights into the interplay between local coexistence and macroevolution (Gerhold et al. 2015), for example, through competition among close relatives triggering displacement and diversification of characters. However, phylogenetic information is less useful if trait information is available for most species and the question is focused on whether the species present in a community need to be different to coexist.

Ecosystem functioning

There has been recent emphasis on ecosystem processes/services as a way to economically value ecosystems and promote their sustainable use. This, in turn, has drawn attention to the ways in which different organisms contribute to the delivery of such services (Hooper et al. 2005; Díaz et al. 2013). Indeed, there is a growing consensus among researchers that the quantification of the traits present in biotic communities can

greatly contribute to ecosystem service assessment and management (de Bello et al. 2010). Consequently, several studies have been implemented to assess the effect of mean trait values and trait diversity on ecosystem processes (see review by de Bello et al. 2010). The effect of species on ecosystems cannot be directly modulated by their number (Hooper et al. 2005), or by their phylogenetic origin. There must be some traits, or trait syndromes that cause different species to have different impacts (Hooper et al. 2005). If the traits that cause major effects on ecosystems are known, and trait information is available for most of the species in the study system, then we see no strong reason for accounting for phylogeny. The questions typically being asked in these trait-based approaches relate to what kind of processes will be affected by a change in species composition. In this sense the temporal scale of the question is ecological rather than evolutionary – although it might not be always the case for all organisms with short life cycle.

Nevertheless, there may be some benefits of using phylogenetic analyses, particularly when combined with functional diversity (Cadotte et al. 2013) and specifically when an ecosystem process is expected to be affected by multiple traits (some of which might be unknown or unmeasured). Ecosystem functions are typically affected by a variety of traits (de Bello et al. 2010) and focusing on the few traits available or measured could therefore prove of limited utility (Gerhold et al. 2015). The potential utility of considering phylogeny is based on the assumption that some unmeasured traits underlying processes are phylogenetically conserved. This may sometimes be the case, given that phylogeny has proven to be a good indicator of ecosystem functioning (Cadotte et al. 2012). As mentioned above, phylogeny can be useful when the values of key functional traits are characteristic of few clades. For example, it has long been recognized that legume species have specific effects on ecosystems. For this reason many studies have expressed functional composition in terms of 'functional groups', e.g. grasses, forbs, and legumes (van der Putten et al. 2001). These taxonomic labels were, in essence, defining functional groups in phylogenetic terms (though some groups, such as forbs, are paraphyletic). Various small phylogenetic groups share functionally important traits that are missing in most other lineages (e.g. characteristic combinations of mechanical and chemical anti-herbivore defence, i.e. stinging trichomes in many Urticaceae, fig-wasp pollination in the genus *Ficus*, etc.). One option would be to measure and

include many traits in the analyses (provided that these are known). However, this often results in too many predictors or too many traits that are irrelevant for most of the species in the analysis. Consequently, the weight of important traits (as Westoby's LHS, i.e. the leaf, height seed scheme; Westoby 1998) will be diluted among the many traits that are only important for a small minority of the study species. Phylogenetic relatedness might provide a solution for these cases, where functional similarity is determined by a trait that is highly important for a limited phylogenetic group.

Conclusions

When used in combination with trait-based approaches, phylogenetic information can generate new insights and strengthen hypothesis testing, especially when the focus of research is uncovering evolutionary trends of communities or ecosystem functioning. Nevertheless, it should not be always included. Rather, phylogenetic comparison analyses should only be applied if the question asks for it. More generally, phylogenetic relatedness between species should not be considered a bias to be corrected, but a signal that allows results to be interpreted in relation to adaptation to environmental change. When trait information is missing for many species and traits are conserved, phylogeny can also be used to provide robust proxies for missing or unmeasured trait data. When assessing evolutionary mechanisms behind present and short-term trait-environment patterns it might be useful to consider phylogeny, but phylogenetically 'corrected' results do not invalidate results obtained without phylogeny – they just highlight different aspects and evolutionary scales.

In summary, phylogeny is clearly essential for understanding the evolutionary paths of adaptations to abiotic and biotic conditions. However, such understandings are often peripheral to many of the most pressing ecology questions, which focus on predicting trait shifts across environmental gradients over short (ecological) time scales. In conclusion, we strongly argue that phylogeny should only be included in statistical analyses with a convincing justification and motivation. In this sense, researchers need to move away from the concept of phylogenetic 'correction' and 'bias' and towards a concept of incorporating phylogenetic signal or structure as a source of information. Adopting such a perspective will considerably strengthen the burgeoning field of functional trait-based ecology, generating new insights and leading to a better understanding of the mechanisms underlying environment–trait patterns.

References

Ackerly DD, Knight CA, Weiss SB, Barton K, Starmer KP (2002) Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* 130: 449–457

Blomberg SP, Garland T (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J Evol Biol* 15: 899–910

Cadotte MW, Dinnage R, Tilman D (2012) Phylogenetic diversity promotes ecosystem stability. *Ecology* 93: S223–S233

Cadotte M, Albert CH, Walker SC (2013) The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecol Lett* 16: 1234–1244

Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecol Lett* 12: 693–715

de Bello F, Lepš J, Sebastia MT (2005) Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *J Appl Ecol* 42: 824–833

de Bello F, Lavorel S, Díaz S, Harrington R, Cornelissen JHC, Bardgett RD, Berg MP, Cipriotti P, Feld CK, Hering D, da Silva PM, Potts SG, Sandin L, Sousa JP, Storkey J, Wardle DA, Harrison PA (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers & Conserv* 19: 2873–2893

Díaz S, Purvis A, Cornelissen JHC, Mace GM, Donoghue MJ, Ewers RM, Jordano PPearse WD (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol & Evol* 3: 2958–2975

Diniz-Filho JAF, Bini LM, Hawkins BA (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol Biogeogr* 12: 53–64

Diniz-Filho JAF, Rodríguez MA, Bini, LM, Olalla-Tárraga MA, Cardillo M, Nabout JC, Hortal J, Hawkins BA (2009)

Climate history, human impacts and global body size of Carnivora (Mammalia: Eutheria) at multiple evolutionary scales. *J Biogeogr* 36: 2222–2236

Diniz-Filho JAF, Bini LM, Rangel TF, Morales-Castilla I, Olalla-Tarraga MA, Rodriguez MA, Hawkins BA (2012) On the selection of phylogenetic eigenvectors for ecological analyses. *Ecography* 35: 239–249

Gerhold P, Cahill JF, Winter M, Bartish IV, Prinzing A (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Funct Ecol* 29: 600–614

Götzenberger L, de Bello F, Brathen KA, Davison J, Dubuis A, Guisan A, Leps J, Lindborg R, Moora M, Pärtel M, Pellissier L, Pottier J, Vittoz P, Zobel K, Zobel M (2012) Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biol Rev (Cambridge)* 87: 111–127

Hoffmann WA, Franco AC (2009) The importance of evolutionary history in studies of plant physiological ecology: examples from cerrados and forests of central Brazil. *Brazil J Pl Physiol* 20:247–256

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol Monogr* 75: 3–35

Kleyer M, Dray S, de Bello F, Lepš J, Pakeman RJ, Strauss B, Thuiller W, Lavorel S (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? *J Veg Sci* 23: 805–821

Klimeš L (2008) Clonar splitters and integrators in harsh environments of the Trans-Himalaya. *Evol Ecol* 22: 351–367

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* 16: 545–556

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21: 178–185

Münkemueller T, Boucher F, Thuiller W, Lavergne S (2015) Phylogenetic niche conservatism – common pitfalls and ways forward. *Meth Ecol Evol* 29: 627–639

Pavoine S, Bonsall MB (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biol Rev (Cambridge)* 86: 792–812

Pavoine S, Vela E, Gachet S, de Belair, G, Bonsall MB (2011) Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *J Ecol* 99: 165–175

Pavoine S, Gasc A, Bonsall MB, Mason NWH (2013) Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? *J Veg Sci* 24: 781–793

Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM, Young, BE, Graham CH, Costa GC (2014). Inputation of missing data in life-history trait datasets: which approach performs the best? *Meth Ecol Evol* 5: 961–970

Pillar VD, Duarte LDS (2010) A framework for metacommunity analysis of phylogenetic structure. *Ecol Letters* 13: 587–596

Price T (1997) Correlated evolution and independent contrasts. *Philos Trans, Ser B* 352: 519–529

Prinzing A, Reiffers R, Braakhekke WG, Hennekens SM, Tackenberg O, Ozinga WA, Schaminee JHJ, van Groenendael JM (2008) Less lineages – more trait variation: phylogenetically clustered plant communities are functionally more diverse. *Ecol Lett* 11: 809–819

Silvertown J, Dodd M, Gowing D, Lawson C, McConway K (2006) Phylogeny and the hierarchical organization of plant diversity. *Ecology* 87: S39–S49

Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecol Letters* 10: 1115–1123

Swenson NG (2009) Phylogenetic Resolution and Quantifying the Phylogenetic Diversity and Dispersion of Communities. *PloS ONE* 4

Swenson NG (2011) Phylogenetic Beta Diversity Metrics, Trait Evolution and Inferring the Functional Beta Diversity of Communities. *PloS ONE* 6

Swenson NG, Enquist BJ (2009) Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology* 90: 2161–2170

van der Putten WH, Vet LEM, Harvey JA, Wackers FL (2001) Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends Ecol Evol* 16: 547–554

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 CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annual Rev Ecol Syst* 33: 475–505

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Pl & Soil* 199: 213–227

Westoby M, Leishman MR, Lord JM (1995) On missinterpreting the 'phylogentic correction'. *J Ecol* 83: 531–534