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EDITORIAL

Using phylogenetics in community assembly and ecosystem functioning research

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There is a long tradition in ecology of trying to understand community assembly processes by making inferences from patterns of community structure (Diamond 1975; Connor & Simberloff 1979). Inferring process from pattern is appealing because the latter is more easily observed and quantified, especially when manipulative controlled experiments are infeasible. In such cases, our hope (albeit naïve at times) is that patterns of community structure bear *some* signature of the processes that generated them by assuming that a particular pattern is overwhelmingly the outcome of a single dominant process. However, multiple processes can often generate the same pattern. A now well-known example of the inference of processes from patterns is Joseph Connell's 'Ghost of Competition Past' (1980), which highlighted that, although coexisting competitors may tend to be niche differentiated on average, this pattern in and of itself is not proof that the observed niche differences are the result of divergent selection experienced by coevolving competitors. Connell emphasized that direct empirical support for the notion of character displacement enabling coexistence was virtually non-existent. Another classic example of inferring process from pattern relates to the intermediate disturbance hypothesis (IDH) (Connell 1978), which suggests that intermediate levels of disturbance promote the highest levels of diversity (pattern) by preventing competitive exclusion by either good competitors in undisturbed environments or rapid growers in heavily disturbed environments (process). There have been very few attempts to directly test the process leading to this pattern, and it has more recently been recognized that two alternative processes (i.e. competitive relative nonlinearity and storage effects) are capable of generating the same pattern (Chesson 2000; Shea, Roxburgh & Rauschert 2004). Such examples are important reminders that understanding community assembly requires careful understanding of how pattern and process are linked. Critical evaluation of existing research approaches an important role to play here, by pointing the way towards more productive approaches and research agendas. For instance, in response to the criticisms of Connell (1980) and others, Schluter & McPhail (1992)

developed a checklist of criteria that must be satisfied in order to demonstrate character displacement. Recent reviews highlight which items on the checklist rarely are checked off, thereby identifying productive directions for future work (Beans 2014; Stuart *et al.* 2014).

Over 35 years after Connell's publications, community phylogenetics now aimed to use patterns of phylogenetic distance or dispersion among members in a community to infer the nature and strength of the ecological processes that drive the structure of communities. With the increasing availability of genetic sequence data and phylogenetic tools, the number of studies using phylogenetic information to infer processes of community assembly has increased rapidly, growing from three papers in 2005 to 37 in 2013 (Gerhold *et al.* 2015). Webb *et al.*'s influential paper in 2002 effectively argued that if one knows something about how evolution has impacted the relevant ecological traits across a phylogeny, then one can use measures of community-level phylogenetic dispersion to understand the ecological interactions governing community assembly (e.g. table 1 in Webb *et al.* 2002). However, instead of examining how evolution impacts trait dispersion across a tree, or how community assembly processes impact trait dispersion in a community, most investigators have instead begun using phylogenetics in community ecology by first making a number of assumptions. Common assumptions include (i) that relevant ecological traits show a phylogenetic signal (i.e. more closely related species are more similar than distantly related species) and (ii) that environmental filtering leads to trait convergence, while competition leads to trait dispersion (e.g. Webb *et al.* 2002, p. 478, and see Gerhold *et al.* 2015 for a more in-depth analysis).

Despite the numerous papers highlighting the false inferences that can be made from accepting such assumptions without closer examination, and the sensitivity of conclusions to these often unsubstantiated underlying assumptions (e.g. Losos 2008; Cavender-Bares *et al.* 2009; Mayfield & Levine 2010), a rise in the use of phylogenetics in community ecology (community phylogenetics) has occurred. As the number of community ecology papers incorporating phylogenetic information grows, we need to

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increase the rigour of our scrutiny and benefit from our rich history by avoiding the pitfalls of inferring process from pattern.

The field of biodiversity and ecosystem functioning (BEF) has also tried to incorporate phylogenetic information (reviewed by Venail *et al.* 2015 in this issue), with the assumption that phylogenetic relationships among species reflect functional trait variation relevant to ecosystem functioning. BEF research has demonstrated that species richness has positive impacts on many ecosystem functions (Tilman, Reich & Knops 2006; Hector & Bagchi 2007; Zavaleta *et al.* 2010; Cardinale *et al.* 2011, 2012), but the use of species richness as the only measure of diversity leaves a great deal of unexplained variation in ecosystem functioning (Cardinale *et al.* 2011), presumably because it ignores community composition and the functional differences among species (Petchey & Gaston 2002, 2006; Petchey, Hector & Gaston 2004; Poos, Walker & Jackson 2009; Cadotte & Strauss 2011). The functional variation among species is especially difficult to define and measure due to the large number of potential traits involved, the great time and effort required to measure these traits, and the difficulty in demonstrating their ecological relevance (Petchey & Gaston 2006; Pakeman & Quested 2007; Cadotte & Strauss 2011). As a result, BEF researchers started exploring whether the evolutionary relationships among species (i.e. phylogenetic diversity) might help to explain some of the variation in ecosystem functioning that remains unexplained by species richness (Maherali & Klironomos 2007; Cadotte, Cardinale & Oakley 2008). However, the capacity to use phylogenetic diversity to predict ecological function is founded on the same set of assumptions that lay the foundation of community phylogenetics, that is, (i) traits underlying ecological functions have a phylogenetic signal (Prinzing *et al.* 2001; Losos 2008; Wiens *et al.* 2010; Cavender-Bares & Reich 2012), (ii) trait variation among species leads to functional differentiation among species, and (iii) functional differentiation in a community can enhance ecosystem functioning. To date, there are only a few studies showing an impact of phylogenetic diversity on ecosystem functioning (reviewed in Venail *et al.* 2015) and even fewer studies testing the assumptions under which phylogenetic diversity should predict ecosystem functioning.

In the light of this growing interest in using phylogenetics in understanding community assembly and ecosystem functioning, the goals of this extended spotlight are to (i) critically re-examine the assumptions underpinning phylogenetic approaches to community ecology, (ii) chart a route forward for how to overcome the limitations of current approaches and (iii) more explicitly and mechanistically connect the dots between the processes of trait evolution, community assembly and ecosystem functioning.

To start off, Kraft *et al.* (2015) begin by re-examining the pitfalls of inferring process, namely 'environmental filtering', from patterns of species or trait variation across an environmental gradient. In community phylogenetics, for

example, numerous studies have inferred environmental filtering as an important process in community assembly from patterns of phylogenetic underdispersion. Kraft *et al.* show that, in the light of modern coexistence theory, biotic interactions have the potential to generate patterns that would normally be interpreted as evidence for environmental filtering. This paper serves as a reminder that the basic understanding of ecological processes in generating community patterns is imperative – even without incorporating the use of phylogenetics.

Gerhold *et al.* (2015) directly address the pitfalls of incorporating phylogenetics into studies of community assembly. They review and challenge all of the assumptions that are used in inferring community assembly processes from measures of phylogenetic diversity. Given the high demands of meeting these assumptions, the authors suggest that the present approach to use phylogenetic diversity as a proxy for trait diversity in understanding community assembly should be abandoned. However, they suggest that phylogenies could be more fruitfully used to understand the ways community assembly and species interactions impact evolution, and the ways in which macro-evolutionary processes impact community assembly.

While a growing number of studies have investigated whether phylogenetic distance among species predicts community structure and assembly (with mixed results), comparably few have investigated the ability of phylogenetic diversity to predict ecosystem functioning. Venail *et al.* (2015) aim to isolate and quantify the contributions of species' phylogenetic relatedness to ecosystem function from the already well-known positive contribution of species richness. They collated and re-analysed data from previous experiments manipulating plant species richness in grassland ecosystems using different statistical methods. They conclude that after controlling for variation in species richness, phylogenetic diversity is related neither to mean community biomass nor to the temporal stability of community biomass, overturning past claims about the greater importance of phylogenetic diversity as predictor of ecosystem functioning (Cadotte, Cardinale & Oakley 2008; Cadotte 2013). Furthermore, they indicate that using phylogenetic distance as a proxy for functional differentiation in ecosystem functioning research is also likely limited by the ability to meet the slough of assumptions outlined in Gerhold *et al.*'s paper. This work is a further caution against the blind use of phylogenetic diversity as a measure of functional differentiation to predict community- or ecosystem-level properties.

To finish, Münkemüller *et al.* (2015) provide a much-needed analysis of the definition of 'niche conservatism' and a quantitative, simulation-based evaluation of the performance of measures that are commonly used to test for it. They show that measures of niche conservatism – defined as a tendency for lineages to retain similar niches over time – perform very poorly when data were generated from alternative models of niche evolution. As a result, it is crucial to first determine the best-fit model of trait evolution

before selecting appropriate measures of niche conservatism. Importantly, even when the metrics (e.g. phylogenetic signal or evolutionary rate) are used appropriately, they cannot always be meaningfully interpreted without reference to metrics for other clades or traits. However, this analysis demonstrating the importance of evolutionary model selection suggests that understanding the way in which traits evolve through time is crucial for a sophisticated understanding of how phylogenetic information and trait variation are related, and therefore, how phylogenetic distance is related to community assembly and ecosystem functioning.

In conclusion, the papers in this Special Feature were able to achieve the first and second goals that we set out to accomplish which were as follows: (i) to critically re-examine the underlying assumptions of community phylogenetics, and (ii) to suggest new ways to overcome the limitations of current approaches. Münkemüller *et al.* also make some progress towards the third goal, which was to more explicitly and mechanistically connect the dots between the process of trait evolution and community assembly. However, accomplishing this goal is a larger task than can be accomplished here. Currently, almost all models of phylogenetic trait evolution fail to reflect our understanding of the processes by which traits evolve. For example, the first attempt to incorporate the impact of species interactions on evolution into phylogenetic models of trait evolution was published just a few months ago (Nuismer & Harmon 2015). While modelling the process of trait evolution on phylogenies is a difficult task, we believe it is necessary to improve our understanding of when and why phylogenetic information can be used to understand community ecology. If the next decade of research focuses on describing how ecological traits evolve along the tree of life, the merger between phylogenetics and community ecology will stand on a much firmer foundation.

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