

# Phylogenetic community ecology: integrating community ecology and evolutionary biology

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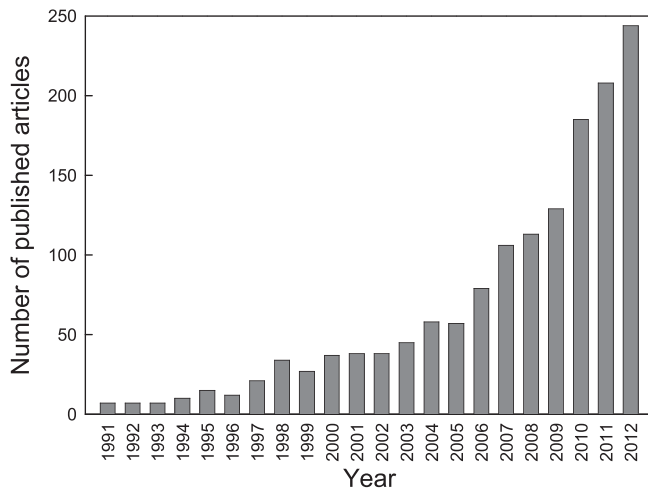
The species composition of a biological community results from the interplay between evolutionary and ecological processes (Ricklefs 1987). It depends on the availability of species in the species pool of the region where the community is located, the dispersal ability of species in the regional species pool that allows them to reach the community and the degree to which the species that have reached the community can tolerate abiotic and biotic conditions in the locality (Willis *et al.* 2010). However, evolutionary and ecological processes assembling species into biological communities have generally been studied in isolation from one another (Johnson and Stinchcombe 2007). In the face of widespread and various anthropogenic threats to biological communities worldwide, it is urgent to understand how evolutionary and ecological processes interplay to generate and maintain biodiversity patterns and species membership in biological communities across the globe.

Species diversity and assembly of biological communities are thought to be driven by three groups of processes: niche-based processes (e.g. Chase and Leibold 2003; Diamond 1975; Tilman 1982; Weiher and Keddy 1999), neutrality-based processes (Bell 2001; Hubbell 2001) and history-related processes (Ricklefs 1987; Ricklefs and Schluter 1993). Phylogenies, especially when calibrated with a dimension of time, can illuminate our knowledge of evolutionary histories of biological communities at multiple temporal and spatial scales (Pennington *et al.* 2006). At a global scale, they permit a re-evaluation of the relative roles of plate tectonics and long-distance dispersal in the assembly of regional and continental biota (Crisp *et al.* 2004). At a local scale, they permit an examination of phylogenetic relatedness of species and provide insights into the assembly of biological communities (Webb *et al.* 2002). In particular, as Cavender-Bares *et al.* (2009) point out, ‘phylogenetics helps to resolve the long-standing controversy about the relative roles of neutral vs. niche-related processes in community assembly and facilitates identification of the kinds of processes that underlie community assembly’.

The assembly of local biological communities is thought to be generally driven by two processes: filtering of species that

can persist within a community on the basis of their tolerance of the abiotic environment (Weiher and Keddy 1995) and biotic interactions among species that limit their long-term coexistence (Elton 1946; Gause 1934; Leibold 1998). The phylogenetic structure of a community can be assessed by comparing the species composition of the community with that of the regional species pool. Phylogenetic clustering should result when conserved characters determine habitat filtering, because they influence tolerance of abiotic conditions, and phylogenetic overdispersion is expected to occur if there is either filtering on convergent characters or competitive exclusion of species with similarity in conserved characters (Cavender-Bares *et al.* 2004; Webb *et al.* 2002), although competitive exclusion may also result in phylogenetic clustering (Mayfield and Levine 2010). If phylogenetic relatedness predicts ecological similarity, phylogenetic diversity should increase ecosystem productivity by maximizing total resource uptake (Pennington *et al.* 2006). A high degree of phylogenetic signal has been frequently found in plant functional traits (e.g. Donoghue 2008; Moles *et al.* 2005). Phylogenetic structure within communities can also influence phylogenetic turnover between communities, i.e. phylogenetic beta diversity (Graham and Fine 2008). Since an early attempt to perform a phylogenetic analysis of community structure (Webb 2000), the use of phylogenies to investigate patterns of community structure has blossomed (Fig. 1).

This Special Issue includes a collection of 10 research papers in the field of phylogenetic community ecology. These papers cover a wide range of spatial extents from an experiment in laboratory microcosms (Pu *et al.* 2014) to the globe (Brunbjerg *et al.* 2014), covering a wide taxonomic spectrum of organisms including microbial bacterivorous ciliated protists (Pu *et al.* 2014) and vascular plants (all other papers in this issue). Most of the papers investigated phylogenetic structure within biological assemblages, with five papers (i.e. Brunbjerg *et al.* 2014; González-Caro *et al.* 2014; Qian *et al.* 2014; Yang *et al.* 2014; Zhang *et al.* 2014) using net relatedness index (NRI) or nearest taxon index (NTI) as a measure of phylogenetic structure. Three papers



**Figure 1:** results of a search in the ISI Web of Science (accessed on 30 November 2013) using the key words 'phylogen\*' AND 'community ecology'.

(i.e. González-Caro *et al.* 2014; Qian *et al.* 2014; Swenson and Umaña 2014) report investigations of phylogenetic beta diversity between biological assemblages. The papers included in this issue also cover other aspects of phylogenetic community ecology such as the relationship between phylogenetic diversity and stability (Pu *et al.* 2014), the relationship between functional traits with phylogenetic signal and environmental conditions (Mi *et al.* 2014), the relationship between phylogenetic diversity of native communities and alien species invasion (Whitfeld *et al.* 2014) and the effect of disturbances on community assembly (Zhang *et al.* 2014).

Brunbjerg *et al.* (2014) investigated patterns of phylogenetic structure in coastal dune communities using a large number of sample plots ( $N = 18\,463$ ) from across the globe. They found that regional species assemblages were phylogenetically clustered relative to the global species pool, which indicates diversification within regions, and that species in local dune communities were also phylogenetically clustered regardless of whether NRI or NTI is used. In their study, species in dune communities show stronger clustering when NTI is used as a phylogenetic relatedness index, compared with the use of NRI. Because NRI measures deeper divergences in the phylogeny than does NTI, which measures tip-level divergences (Webb *et al.* 2002), a higher degree of clustering with NTI suggests recent diversifications within regions (Brunbjerg *et al.* 2014).

Brunbjerg *et al.* (2014) also found that there was significant phylogenetic signal in plant height and seed mass and that these two functional traits were negatively correlated with NRI values, suggesting that phylogenetic niche conservatism and environmental filtering interplay in generating current dune communities. Focusing on woody plants in 650 quadrats of  $20 \times 20$  m in two large forests in Southwest China (a tropical forest of 20 ha; a subtropical forest of 6 ha), Yang *et al.*

(2014) found that all seven functional traits examined showed significant phylogenetic signal and that functional traits covaried with environmental conditions. Yang *et al.* (2014) also analyzed phylogenetic structure of the forest quadrats and found opposing patterns of phylogenetic structure in the two forests: phylogenetic clustering in the subtropical forest and phylogenetic overdispersion in the tropical forest. This result is consistent with those of Kooyman *et al.* (2011) and Giehl and Jarenkow (2012) who found that woody species in subtropical and warm temperate samples were more phylogenetically clustered than those in tropical samples in Australia and South America. Mi *et al.* (2014) used four spatial statistical models to investigate the role of different mechanisms in shaping the species, phylogenetic and functional structures of woody plant assemblages in a subtropical forest of 24 ha in East China at various spatial scales, with a focus of assessing the validity of the assumption of spatial independence between species. They found inconsistent results at different spatial scales.

Similar to Mi *et al.* (2014) and Yang *et al.* (2014) who used large permanent forest plots in China to address questions of phylogenetic community ecology, Oliveira *et al.* (2014) used a permanent forest plot of  $\sim 10$  ha with different edaphic conditions in Brazil to assess the role of environmental and evolutionary processes in driving the assembly of tree and shrub species in 256 quadrats of  $20 \times 20$  m. They report that species in the forest are phylogenetically overdispersed in space and within habitat types. Specifically, closely related species tend to occur in different habitats, and close-by trees tend to be more distantly related species.

González-Caro *et al.* (2014) and Qian *et al.* (2014) both used plant assemblages distributed along elevational gradients to investigate phylogenetic structure within assemblages and phylogenetic turnover between assemblages and relate measures of phylogenetic structure and phylogenetic turnover to environmental factors. González-Caro *et al.* (2014) observed phylogenetic overdispersion in tree assemblages with lower temperatures and phylogenetic clustering in tree assemblages with higher temperatures in their dataset of 145 1-ha forest plots distributed from 200 to 3300 m elevation in New World tropical areas (Colombia). Furthermore, phylogenetic structure of the assemblages was related to the degree of seasonal flooding and seasonality in precipitation and phylogenetic beta diversity between assemblages increased with an increasing difference in temperature whereas annual precipitation was not a significant predictor of phylogenetic turnover between assemblages. In contrast to the results of González-Caro *et al.* (2014) on the relationship between phylogenetic structure and temperature, Qian *et al.* (2014) observed that angiosperm woody plant assemblages tended to be more phylogenetically clustered in lower temperature and at higher elevations in their dataset with 13 forest plots of  $32 \times 32$  m distributed from 720 to 1900 m elevation in northeastern China. The phylogenetic niche conservatism hypothesis predicts that

evolutionary adaptation to novel temperature environments is rare, and descendent species tend to remain within the environments of their ancestors (Miller *et al.* 2013). Because angiosperms originated in tropical environments (Takhtajan 1969), one would expect to find increasing phylogenetic clustering in community assemblages along a gradient from ancestral, warm to derived, cold environments (Miller *et al.* 2013). Thus, the finding of Qian *et al.* (2014) is consistent with the prediction of the phylogenetic niche conservatism hypothesis on the relationship between phylogenetic relatedness and temperature. Their finding is also consistent with the finding of Li *et al.* (2014) for alpine plant assemblages along an elevational gradient in the Hengduan Mountains Region, southwestern China, and the finding of Qian *et al.* (2013) for angiosperm tree assemblages along latitudinal gradients in North America. Interestingly, Culmsee and Leuschner (2013) also observed that angiosperm tree assemblages in Malesia were more phylogenetically overdispersed at higher elevations (with lower temperatures), and Bryant *et al.* (2008) found that angiosperm assemblages in Colorado Rocky Mountains, USA, tend to be more phylogenetically overdispersed at higher elevations. These findings, together with that of González-Caro *et al.* (2014), are contrary to the relationship between phylogenetic structure and temperature predicted by the phylogenetic niche conservatism hypothesis. The mechanisms that have resulted in the opposing patterns of phylogenetic structure along elevational gradients in different regions provide an interesting challenge for future investigation.

Unlike González-Caro *et al.* (2014) and Qian *et al.* (2014) who investigated, among other things, phylogenetic turnover between plant assemblages along elevational gradients, Swenson and Umaña (2014) studied phylogenetic turnover of vascular plants among 18 islands in Central America (the Lesser Antillean). Their results show a major influence of environmental heterogeneity on the assembly of the island floras and that spatial distance is not a significant predictor of compositional dissimilarity of plant species between islands.

The relationships of biodiversity with ecosystem stability and productivity have been a focal research subject of ecologists in the past two decades (e.g. Cardinale *et al.* 2012; Hooper *et al.* 2012) but few studies on this topic have taken into account species evolutionary history. In the only study of this collection addressing the relationship between phylogenetic diversity and productivity, Pu *et al.* (2014) used 12 bacterivorous ciliated protist species as a model to investigate whether phylogenetic diversity can affect temporal stability of biomass after controlling for species diversity. Their results show that increasing phylogenetic diversity promotes temporal stability of community biomass, which supports the utility of species phylogenetic knowledge for predicting ecosystem functions and their stability.

Ecologists have been increasingly interested in investigating the effect of disturbances, either caused by natural

processes or by human activities, on phylogenetic structure of biological communities (e.g. Knapp *et al.* 2008; Letcher *et al.* 2012; Santos *et al.* 2010). Zhang *et al.* (2014) conducted a review of the literature on this topic and provided a case study using a data set with 301 sites from the boreal forest region of Alberta, Canada. Their literature synthesis suggests that phylogenetic diversity is inconsistently related to disturbance; their case study leads to the same conclusion. Specifically, phylogenetic diversity is not related to disturbance extent in any consistent way, species richness is not correlated with phylogenetic diversity, and patterns of phylogenetic relatedness are inconsistent across plant growth forms and anthropogenic disturbance types. Whitfeld *et al.* (2014) used 24 oak forests in Minnesota, USA, to assess the effects of resident plant species richness, phylogenetic diversity and abiotic characteristics on the abundance of the introduced species *Rhamnus cathartica*. Sites with higher plant phylogenetic diversity harbor less *R. cathartica*, even in the case where species diversity is not significantly related to the abundance of *R. cathartica*.

The 10 research articles of this collection cover various aspects of phylogenetic community ecology. We appreciate Nathan G. Swenson for his leading role in setting the scope of this issue, inviting authors to contribute and getting several manuscripts reviewed. We are grateful to Bernhard Schmid for handling two manuscripts and editing this article and to over 20 reviewers who provided comments that have substantially improved the quality of many papers included in this collection. Last but not least, we thank the authors of the 10 research articles for their contributions to this Special Issue.

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