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Placing phylogenetic diversity back on the evolutionary track

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commentary

Placing phylogenetic diversity back on the evolutionary track

Conceptual frameworks relying on properties that are hard to measure are often challenging. A common solution is the use of proxies or surrogates for those properties. When molecular phylogenies became easily available and the conceptual framework by Webb et al. (2002) was published, many ecologists started to use phylogenies as proxy for ecological relationships. The study proposed straightforward hypotheses to infer community assembly processes by using phylogenetic information when trait information is not available, and rapidly became a seminal paper. The "phylogeny as a proxy to ecology" approach assumes that closely related species should share more similar features (e.g., ecological traits, habitats, environmental tolerances) than distantly related species, a statement that can be traced back to Charles Darwin (Webb et al. 2002). Indeed, the number of studies using this approach has quickly increased in recent years (Cianciaruso 2011), even in macroecological and biogeographical journals. Cianciaruso (2011) asked how macroecology and biogeography could benefit from phylogenetic diversity and how we could advance the theory by using novel approaches. An article recently published by Gerhold et al. (2015) presents an important contribution to answer these questions.

Gerhold et al. (2015) is a must-read paper for anyone thinking of using the "phylogeny as a proxy to ecology" approach because it highlights that phylogenies are not good proxies to ecology, and gives ideas on how ecologists and biogeographers can further connect community-level data to macroevolution. The authors challenge core assumptions that have been increasingly used in studies following the approach proposed by Webb et al. (2002). One of these assumptions is that phylogenetic clustering may be an outcome of trait clustering due to the action of environmental filters or that phylogenetic structure is mainly due to local and present-day processes. Since Webb and colleagues' paper, several ecologists have used some of their assumptions without criticism (Gerhold et al. 2015). For instance, macroecological studies have used phylogeny as a proxy (e.g., Cardillo 2011), which should be avoided considering the points made by Gerhold et al. (2015). It is important to note that other studies (e.g., Mayfield and Levine 2010) have raised some of the criticisms used by Gerhold et al. (2015), but the particular advantage of this new review is that it synthesizes the different criticisms to the "phylogeny as a proxy to ecology" approach.

But what does Gerhold et al. (2015) have to do with biogeography? Community ecologists and biogeographers have argued that community ecology and biogeography should be further integrated (Cavender-Bares et al. 2009, Cianciaruso 2011). Indeed, an attempt towards such an integration was one of the original aims of Webb et al. (2002; see their Figure 1), but it has been little explored over the years. Community ecology can benefit from biogeographic and phylogenetic approaches by putting history and evolution into the explanation for current patterns of biodiversity (e.g., community structure) as highlighted by Gerhold et al. (2015). Biogeography in turn can benefit from community ecology elucidating how local processes can feedback into regional processes, and helping explain how ecological processes shape the tree of life (i.e., phylogeny) and the current distribution of life on Earth (i.e., macroecological patterns) across evolutionary time via adaptation and other eco-evolutionary mechanisms.

Gerhold et al. (2015) argue that ecologists would improve their researches by considering phylogeny not as a mere proxy for ecology but rather by investigating how phylogenetic patterns can give insight into processes that drive species coexistence or are its outcome. Gerhold and colleagues made several points about the perils of using phylogeny as a proxy. We agree with their points. If species traits are already a proxy for functionality or species' interactions (with other species or the environment), would it be safe to use a proxy of a proxy? We believe that it would not. We argue that ecologists and biogeographers should be aware of the limitations of using phylogeny as a proxy of ecological distances, and avoid using this approach that has at least seven implicit assumptions that are weakly supported by the literature (Gerhold et al. 2015). Rather, they should think about possible historical and evolutionary explanations of their study patterns, and then elaborate clear hypotheses that may explain these patterns. Phylogeny is likely an irreplaceable tool for this purpose.

Gerhold et al. (2015) propose that phylogeny underlies the causes of current biodiversity patterns, which involves the assessment of the historical drivers of current community structure, or is a result of community assembly, which involves the evaluation of how ecological processes could scale up to broad scale patterns. Besides the future avenues highlighted by Gerhold and colleagues, some approaches have already shed light on the historical drivers of local diversity and thereby succeeded in moving towards an integration of ecology, biogeography and evolution. For instance: (1) linking alpha and beta phylogenetic diversities of local communities across distinct regions or biogeographic barriers (Graham and Fine 2008); (2) linking phylogenetic structure of local communities to characteristics of the regional phylogenetic pool (Gerhold et al. 2008, Lessard et al. 2012); (3) linking local phylogenetic structure to macro-ecoevolutionary processes such as speciation, extinction and long-distance dispersal (Davies and Buckley 2011); (4) linking beta diversity to species traits and information on biogeographic history of the study communities (Peixoto et al. 2014). These studies have built on ideas present in Webb et al. (2002), but used the phylogenetic patterns to make inferences about biogeographic processes rather than to assume that phylogenetic patterns are proxy to functional patterns.

In conclusion, Gerhold and colleagues placed phylogenies in ecology back on track by showing the limitations of currently widely used assumptions and by proposing future avenues of research for those aiming to understand biodiversity patterns through the lenses of historical and evolutionary processes. We further argue that testing clear biological hypotheses in light of the interface between community ecology and biogeography will move biodiversity science ahead by enabling us to integrate explanations of the drivers of biodiversity patterns observed at several scales.

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