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Consequences of phylogenetic conservativeness and functional trait similarity on aboveground biomass vary across subtropical forest strata

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ABSTRACT

Phylogenetically close and/or functionally similar species are generally assumed to compete more strongly than phylogenetically distant and functionally dissimilar species in a community. However, how coexisting species with different extents of variation in their phylogeny and functional traits determine community function such as aboveground biomass across forest strata remains an unresolved question. We hypothesize that phylogenetically close and functionally similar species of overstorey, but phylogenetically distant and functionally dissimilar species of understorey drive high aboveground biomass in structurally-complex subtropical forests. Multiple linear regression models were used to test the consequences of phylogenetic distances and functional traits of tree species, and environmental factors on aboveground biomass in a subtropical forest in Eastern China. Overstorey aboveground biomass was driven by functional evenness ($\beta = -0.21$), phylogenetic species evenness ($\beta = -0.27$) and phylogenetic diversity ($\beta = 0.31$). Understorey aboveground biomass was driven by functional richness ($\beta = 0.25$), functional dispersion ($\beta = -0.21$), soil nutrients ($\beta = -0.17$) and topography ($\beta = 0.36$). Whole-community aboveground biomass was best predicted by functional divergence ($\beta = 0.36$), functional dispersion ($\beta = -0.38$), phylogenetic diversity ($\beta = 0.24$) and soil nutrients ($\beta = -0.20$). Our results suggest that understorey aboveground biomass is great for groups of phylogenetically distant species having high functional richness due to specific functional strategy shared by all the species. By contrast, high overstorey aboveground biomass is related with groups of phylogenetically close species having low functional trait diversity (i.e. high functional trait similarity) due to the evolutionary relatedness. The mechanism at the whole-community level might result from the mixed effects of overstorey evolutionary relatedness and understorey functional trait diversity. This study highlights that disentangling the effects of evolutionary diversity and functional trait diversity across forest strata may be helpful for better understanding of ecological mechanisms for predicting aboveground biomass in a subtropical forest.

1. Introduction

Earlier ecologists, including Charles Darwin (1859), suggested that species belonging to the same genus would compete more intensely than species belonging to different genera (Simberloff, 1970; Valiente-Banuet and Verdú, 2007). The general notion is that phylogenetically close or functionally similar species would compete more strongly than phylogenetically distant or functionally dissimilar species, and may be less likely to coexist due to competitive exclusion (Cavender-Bares et al., 2009; Lyu et al., 2017). More recently, the same general notion has been revisited as the competition-relatedness hypothesis (Cahill et al., 2008) or the phylogenetic limiting similarity hypothesis (Violle et al., 2011) for the understanding of biodiversity, community structure and functions (Cadotte et al., 2008; Cavender-Bares et al., 2009; Lyu et al., 2017). Therefore, phylogenetic diversity and/or functional trait dissimilarity are frequently considered as the main drivers of aboveground biomass or productivity across different ecosystems (Cadotte et al., 2009; Flynn et al., 2011; Paquette and Messier, 2011; Yuan et al., 2016). To date, direct tests for community assembly hypotheses on ecosystem function remain rare in (sub-) tropical forests, and not much is known about whether and how evolutionary diversity and functional trait dissimilarity drive aboveground biomass across each individual forest stratum (i.e. overstorey and understorey).

Functional trait dissimilarity and phylogenetic or evolutionary

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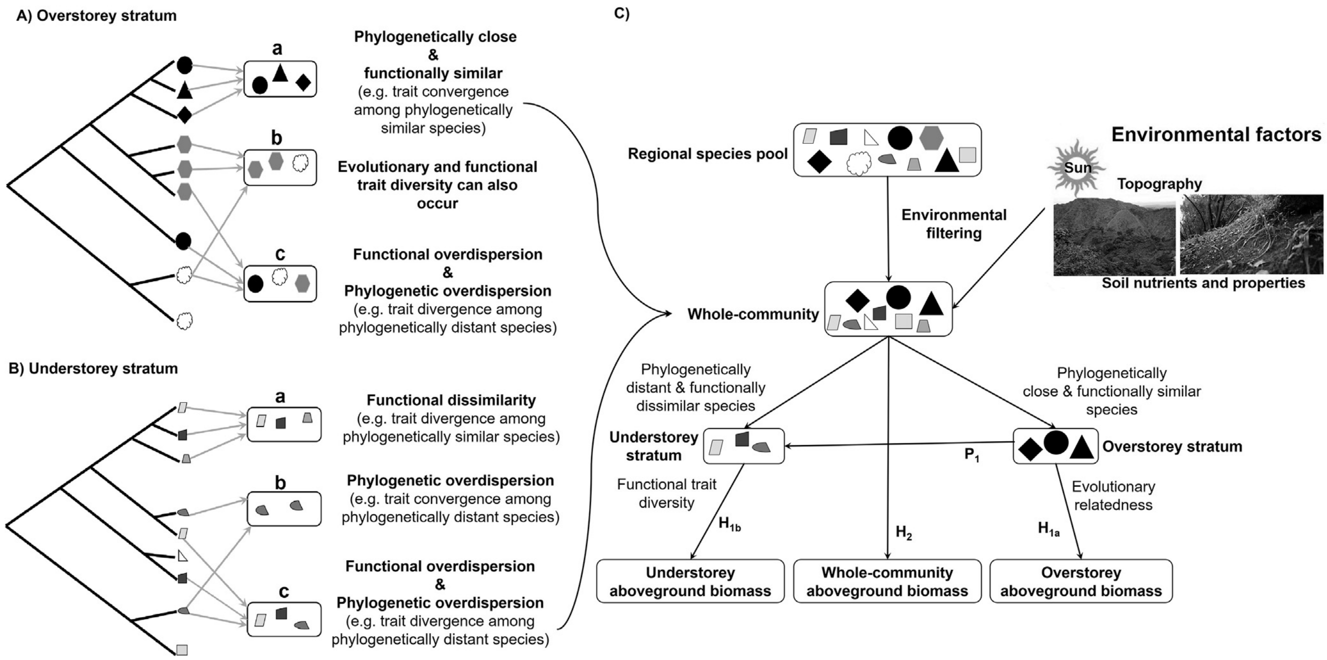

Fig. 1. An example patterns for functional trait diversity and evolutionary diversity when traits are conserved or labile on the phylogeny. (A) Individual species are represented by the shapes of symbols at the tips of the phylogenetic tree, the colors of the symbols indicate different traits, and rectangles represent species assemblage within a stratum. In this example (Fig. 1A), the similar trait is conserved on the phylogeny, such that phylogenetically close species tend to have the same traits (colors), i.e. phylogenetically close and functional similar species. Environmental filtering selects for species with similar traits (a in Fig. 1A) causing evolutionary relatedness and functional similarity. Functional trait diversity and evolutionary diversity that is no different from random expectation can also occur (b in Fig. 1A), such that less phylogenetically close and functionally similar species. Interspecific competition limits similarity between co-occurring species resulting in different traits (c in Fig. 1A) causing functional or phylogenetic overdispersion. (B) Functional dissimilarity in a stratum where a variety of traits are conserved on the phylogeny (a in Fig. 1B), such that phylogenetically close species tend to have the different traits (colors). Phylogenetic overdispersion (b in Fig. 1B) could be clustered in functional trait diversity, such that phylogenetically distant species tend to have the same traits. Both phylogenetic and functional overdispersion can also be expected (c in Fig. 1B), such that phylogenetically distant species tend to have the different traits. Note that these patterns (shown in Fig. 1A and B) can be interchangeably used for overstorey and understorey strata, but here we just present examples related to our expectations across forest strata. (C) Conceptual framework showing how changes in aboveground biomass are regulated by evolutionary diversity and functional trait diversity across forest strata and whole-community. Species pool having different symbols and colors represent different species and traits dissimilarity, respectively, while the size of the symbols represents the overstorey (big size) and understorey (small size) species. H_{1a}, H_{1b}, H_2 and P_1 indicate proposed hypotheses, prediction or questions (see introduction section).

diversity have often been treated as the two sides of the same coin, based on the assumption that functional traits are phylogenetically conserved (Cadotte et al., 2009; Paquette et al., 2015; Yuan et al., 2016). However, the relationships may be not that simple possibly due to the convergence in traits among phylogenetically distant species or divergent selection among phylogenetically close species (Fig. 1A and B), or vice versa (Wiens and Graham, 2005). In simple words, it is theoretically plausible that the decrease (i.e. the trait convergence) and increase (i.e. the trait divergence) of functional trait dissimilarity depend on the extent of habitat selection *versus* limiting similarity due to biotic interactions within communities (de Bello, 2012). On the one hand, phylogenetically close species are likely to assemble due to environmental filtering, and evolutionary relatedness and/or functional trait similarity are expected if traits are phylogenetically conserved (Fig. 1A) (Webb, 2000). On the other hand, it is possible that niche differentiation or ecological fitting mediates community assembly, and hence phylogenetic overdispersion and/or functional trait dissimilarity are expected (Fig. 1B) (Cavender-Bares et al., 2009).

Functional, evolutionary and ecological similarities of tree species might be fundamentally different across forest strata. Natural communities are assembled by niche-related, neutral and historical processes, where coexisting species are selected based on their functional traits, ecological similarity and evolutionary history (e.g. Cavender-Bares et al., 2009). More specifically, tree species with contrasting functional strategies are generally assembled in different vertical layers, probably due to the trait convergence and divergence across forest strata in complex natural forests (Rüger et al., 2012; Ali and Yan, 2017b; Ali et al., 2018). Since whole-community species are selected from the regional species pool through natural assembly processes based on their functional traits and ecological similarity (Fig. 1C), how do evolutionary and functional trait dissimilarity measures explain variation in aboveground biomass at each individual forest stratum in natural communities? It is expected that evolutionary relatedness would drive aboveground biomass at overstorey stratum, probably due to environmental filtering of phylogenetically close species with similar physiological or functional tolerances (Webb et al., 2002). By contrast, phylogenetic overdispersion can result from competition or other processes such as complementarity and facilitation among phylogenetically distant species in the resource-limited environment (Cavender-Bares et al., 2009), such as in the understory stratum of the forest. At this juncture, it is expected that functional trait dissimilarity would drive aboveground biomass at understorey stratum, probably due to the niche complementarity (Ali and Yan, 2018).

We have previously reported that whole-community aboveground biomass is driven by the high functional trait diversity of understorey but low functional trait diversity of overstorey in a subtropical forest (Ali et al., 2018). This study aims to investigate whether the evolutionary and functional trait dissimilarity have differential consequences on aboveground biomass across forest strata along local environmental gradients in a natural subtropical forest. Specifically, we ask three major questions with the corresponding hypotheses and predictions. (1) How do evolutionary and functional trait dissimilarity indices affect aboveground biomass across each individual forest stratum? We hypothesize that phylogenetically close and functionally similar species