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Competition analysis using neighborhood models: implications for plant community assembly rules

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ABSTRACT

Contemporary studies in plant ecology have investigated the processes and patterns underlying plant community of structure and dynamics, mainly in tropical forests. In this context, the effects of competitive interactions between trees and their neighbors on tree growth and survival in plant communities have been addressed using neighborhood models. The purpose of these efforts has been to better understand the processes that drive patterns of species abundance, which has the potential to change our understanding of the ecological and evolutionary factors involved in ecosystem dynamics. Therefore, studies concerning the competitive mechanisms that explain neighborhood interactions of plants are the subject of this short review. Two main ecological theories have received strong support in this regard: 1) environmental filtering and 2) niche complementarity. These theories are mutually compatible and act simultaneously, however, their relative importance may change depending on resource availability, type of plant community and successional stage.

Keywords: Competitive Ability, Niche Differentiation, Environmental Filtering, Plant Ecology

INTRODUCTION

A central challenge in plant ecology is to determine the key drivers of plant community assembly. Recent studies investigating the processes and patterns that drive plant community structure and dynamics have focused primarily on tropical forests, which are considered centers of biodiversity and endemism, and perform several ecosystem functions. The dynamics of tree growth and survival in these ecosystems is central to understanding and managing the forest resources (Canham et al. 2006).

The strength of interactions between species is essential to linking processes and patterns in natural plant communities. Among the processes involved in community assembly, competition has been considered important, yet its role is still an ongoing

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debate in ecology (Mayfield and Levine 2010). Competition is a key filter in determining the ecological and evolutionary success of species and is decisive in plant community assembly (Weigelt et al. 2007).

In this sense, studies using neighborhood models are currently being undertaken with the objective of understanding the role of interactions, mainly competitive interactions, on tree growth and survival in plant communities under the presupposition that they may elucidate the processes that drive patterns of species abundance. Neighborhood models of forests play a central role in determining plant community productivity (Potvin and Dutilleul 2009), and can be used to examine the nature and importance of competitive effects without the need for manipulative experiments. In addition, a neighborhood approach should lead to an understanding of whether enhanced the growth and survival can be driven by inter- or intraspecific competition (Kunstler et al. 2016).

A neighborhood approach can predict the performance of individual trees based on the characteristics of a focal tree (i.e., size, age, number, taxonomic identity, and functional traits) and the potential of depletion of local resources by neighbors. Understanding the effects of neighborhood crowding has relied on the long tradition of distance-dependent analyses of competition, in which target tree growth and survival is analyzed as a function of the size, number and/or distance of neighboring, that is, the competitor trees (Kunstler et al. 2016; Lebrija-Trejos et al. 2014; Wagner and Radosevich 1998), although studies have shown that the growth of target tree species is more sensitive to the identity of neighbors (Uriarte et al. 2004). At long last, studies using neighborhood models have the potential to change our understanding of the ecological and evolutionary factors underlying the rules of plant community assembly.

Previous studies have found that environmental filters (niche similarity) shape community assembly in Neotropical rain-forests (Kraft et al. 2008; Paine et al. 2011). On the other hand, niche complementarity has been widely put forward in the literature on community assembly as a driver of plant competition (Kraft and Ackerly 2010). Thus, the goal of this text was to review studies concerning competitive mechanisms that explain neighborhood interactions among plants. Towards this end, two main ecological theories were analyzed: environmental filtering and niche complementarity. Both theories are mutually compatible and act simultaneously, however, their relative importance can change depending on differences in resource availability, type of plant community and successional stage.

The role of environmental filters

Environmental filtering is related to the interactions between organisms and their environment, with the recognizing that not all organisms are able to successfully establish themselves and persist in all abiotic conditions; that is, the environmental conditions as a selective force (filter), previting or limiting species that lack the necessary traits for survival from persisting in habitats with a particular set of unfavorable conditions (Kraft et al. 2015). At the same time, similar abiotic conditions may result in greater interspecific competition due to phylogenetic convergence.

The closer two species are related phylogenetically, the greater will be the competition between them, due to likelihood of them possessing similar functional traits (Metz et al. 2010). According to the

Competition-Relatedness Hypothesis (Cahill et al. 2008), if traits responsible for ecological similarity are phylogenetically conserved, there will be more intense competition for resources among closely related species than between those that are more distantly related, which possess a greater dissimilarity in traits. Although, recent studies have shown that regardless of the degree of trait dissimilarity among neighbor species (or individuals), there is variation in the level of competition (Uriarte et al. 2004). For example, the age of stand of forest can promote increased in trait similarity, generally interpreted as an effect of environmental filtering, with a progressive sorting of the species best adapted to local abiotic conditions (Uriarte et al. 2010).

On the other hand, the coexistence of the species within a community can define competitive ability, which is related to differences in functional traits (fitness differences), independent of variation in the density of competitive interactions (Lasky et al. 2014). Fitness differences, which are reflected in competitive ability, favor the predominance of one competitor over another regardless of abundance, and can cause competitive exclusion in the absence of niche differences (Chase and Leibold 2003; Mayfield and Levine 2010).

However, local resource partitioning (environmental filters) by itself may not have a strong effect on tree survival and growth, owing to the evidence of species coexistence on a regional scale. It is likely, however, that other types of stabilizing niche differences, such as those of other spatial or temporal scales or processes (limited dispersal), or different traits (niche complementarity), may also a play a significant role (Kunstler et al. 2012). In fact, neighborhood interactions can be modeled better by hierarchical trait effects than by phylogenetic similarity (Chi et al. 2015; Kunstler et al. 2012; Uriarte et al. 2010).

The role of niche complementarity

The occurrence of neighbors may increase resource limitation due to asymmetric competition between focal and neighboring trees, thus reducing growth rates by varying degrees depending on the competition tolerance different of the species involved (Chi et al. 2015). The strengths of competitive interaction between species increases as niche distance decreases (niche complementarity), measured as absolute trait distance; that is, interspecific competition can promote trait diversification, thereby increasing dissimilarity among species (Kunstler et al. 2016).

In the absence of a strong spatial effect, some species with similar niches will act to promote species diversity through density dependent effects, and this diversity can reflect a variety of neighborhood dependent, with the life history traits and tradeoffs determining the position of each species in the community (Uriarte et al. 2004). Greater trait differences weaken the negative density effects of neighbors and promote stable coexistence of functionally diverse neighbors (Lasky et al. 2014). In other words, if neighborhood competition is driven mainly by trait similarity, then a broad distribution of trait values will be favored on a local scale, thereby increasing functional diversity. The coexistence of species with diverse traits is possible due environmental heterogeneity (i.e. creation of microhabitats) and the expression of trait differences among species (Chesson 2000), or due to disturbances that create a mosaic of successional stages (Kunstler et al. 2016).

Several functional traits may reflect the competitive ability of trees species. For example, results of studies on forest dynamics, especially in tropical forests, addressing functional traits have shown that successional stage can direct fundamental competitive abilities that guarantee growth and survival (Kunstler et al. 2016). In others words, during the process of gap formation in tropical forests, the possession of competitive abilities (tradeoff of traits of focal tree) favorable to conditions of increased light can be a determinant in the maintenance of an individual within a community. Plants can modify their growth pattern to minimize the interception of light by neighbors (Clark and Bullock 2007). A study performed in Puerto Rico using census data from the 16-ha Luquillo Forest Dynamics Plot, found that the conspecific or group effects were important for the survival of pioneer light-demanding species and non-pioneer species but not for late-successional species (Uriarte et al. 2004).

Models incorporating multi-trait distance as a predictor should be able to more accurately detect species niche similarities (Kunstler et al. 2012). However, these similarities (according to the traits) are not necessarily evidence for greater competition (Lebrija-Trejos et al. 2014). In a recent study using growth data from more than 3 million trees in over 140,000 plots across the world, competition within species was found to be stronger than among species, yet increased trait dissimilarity among species can have little influence in weakening competition (Kunstler et al. 2016).

Final remarks

The focus on neighborhood analysis can clarify the role of competition in plant community assembly, both in interspecific or intraspecific studies (Weigelt et al. 2007), as well as in evaluation of competition between adults and saplings (Metz et al. 2010). However, it is necessary to understand that the neighborhood interactions (competition) alone cannot completely explain patterns of richness and abundance of plants, and may fail to capture and measure the effects of infrequent events, particularly in highly diverse tropical forests (Uriarte et al. 2004). According to neutral theory (Hubbell 2001), patterns of relative abundance in tropical forests are non-equilibrium (neutral) assemblages that experience continuous taxonomic turnover with little coevolution between competitors (Hubbell et al. 2001). In other words, interspecific differences in competitive effects can be relatively unimportant in explaining patterns of diversity and relative abundance in forests, because the capacity of persistence and coexistence of species exist independently of their functional traits. In this sense, some studies have found moderate support for a model that assumed functional equivalence of competitors with regard to survival (Uriarte et al. 2004).

Neighborhood models have revealed various mechanisms or processes that have important roles in plant community assembly. For example, the role of positive species interactions (facilitation) (Bulleri et al. 2015) or behavior of common natural enemies (Paine et al. 2012) can determine a species distribution and abundance. In this sense, the rules for plant community assembly are a combination of dynamic processes (e.g., limited dispersal, positive species interactions, natural enemies, among others) and environmental heterogeneity (Canham et al. 2004). Although neighborhood competitive interactions show a prominent role in the patterns of distribution and abundance of plant species in tropical forests, it is important to understand that both competitive ability (environmental filters) and niche difference (niche complementarity) determine the outcome of competition (coexistence theory).

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