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Some of the Mechanisms for Coexistence of Tree Species Diversity in Tropical Forests: A Review of Effects of Tree Density Dependence

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Abstract

Tree communities contribute to maintenance of species diversity in tropical forests. Coexistence of many tree species is not without competition. Therefore, coexistence of tree species and size diversities occur sequentially or simultaneously in tropical natural forests. Understanding coexistence and competition mechanisms of tree species requires knowledge of interactions within and between species. However, many conservation efforts and strategies failed due to inability to identify and maintain functional coexistence mechanisms among tree species in the forest. Also, most trees died because of pressure on their habitats and not because of limiting growth resources. Hence, species identity, minimum distance and size of the neighbouring trees which are responsible for coexistence of competing trees in most tropical forests have not been explicitly reviewed. Therefore, this review evaluated some of the density dependent mechanisms for coexistence of tree species alpha diversity in tropical forests. Many interactive mechanisms are responsible for coexistence tree species in tropical forests. Inter- and intra-specific competitions are the most significant and both facilitate positive and negative density dependence. Therefore, switching from negative to positive density dependence may occur in some situations. Positive and negative density effects regulate species abundance and coexistence through conspecific and heterospecific structures. Aggregates of conspecific and heterospecific neighbours constitute forest spatial structure. Negative density interactions are mutually exclusive and basically ranged from effect of species identity of neighbours, distance to neighbours and tree size of the neighbours to reference trees in the community structures. Some mechanisms shorten distances for heterospecific than conspecific interactions. Conspecific structures improved survival and growth of rare tree species. Interactive mechanisms in tree community and population structures facilitate species diversity and size inequality, respectively.

Keywords

Tree Community Structure, Tree Species Diversity, Tree Species Coexistence, Tree Populations

1. Introduction

There is increasing interest in maintenance of tree species alpha diversity in tropical forests. This is because maintaining high tree species diversity presents several advantages such as ecosystem goods and services. Tropical forests harbour the greatest number of tree species and there are many interactions between individual trees. Therefore, numerous hypotheses have been proposed to explain the coexistence of high tree species alpha diversity in tropical forests. Most of these hypotheses are associated with density dependent relationship among neighbouring trees (Volkov et al., 2005; Peters, 2003; Zhu et al., 2018). Therefore, density dependence must be prevalent to be an important process in maintaining species diversity in tropical tree communities (Chave et al., 2002). This could be the reason many researchers (Harms et al., 2000; Wright, 2002; Zhu et al., 2018) emphasized the importance of effects of density-dependent in structuring of spatial patterns of tree species communities. However, there is little understanding of processes underlying density dependence because it occurs through varieties of plant ecology mechanisms. Therefore, the description of its temporal and spatial effect requires clarification. Positive and negative density dependence is a form of interaction regulating tree communities in tropical forests. Significantly, there are some misunderstandings in the role of positive and negative density dependence in the maintenance of tree species alpha diversity.

Moreover, it is not clear whether density or composition of neighbouring trees is the most effective factor regulating tree communities, apart from the density dependent self-thinning of forest trees (Peters, 2003; Hubbell et al., 2001). Self-thinning of tree stems is known to occur during stand development. Therefore, contribution of density dependence is partially recognized at forest level and presently, not at community level. At community level, the contributions of density, identity and size of neighbouring trees are yet to be confirmed. Conversely, Stoll and Newbery (2005) explained that tree community structures shape forest spatial structure in tropical forests. Hubbell et al. (2001) opined that most tropical trees are too rare to be regulated by density dependence and therefore density dependence may not promote species coexistence. Prior to these studies, there were controversies among researchers before the advent of numerical simulation of population dynamic studies because it is difficult to demonstrate these mechanisms among long-live tree species. Therefore, distance dependent and distance independent interactive mechanisms that are maintaining coexistence of high tree species alpha diversity in tropical forests were reviewed through assessment of negative and positive density dependence in conspecific and heterospecific neighbours. Possibility of switching from negative to positive density dependence was also investigated through conspecific neighbours. Therefore, the relationship between tree species diversity and size inequality in the communities of tree species was evaluated.

2. Aggregation and Interactions of Trees in Tropical Natural Forests

It is recognized that negative competitive interactions dominate tree populations but there are evidence that positive interactions can occur in some situations (Cavard et al., 2011). However, there is controversy on the contribution of positive density interactions to coexistence of tree species alpha diversity in tropical natural forests. Also, the factors controlling the strength of interactive mechanisms at different life stages of tree community have not been clarified. Prior to this time, positive density dependence was thought to contribute to tree species exclusion by restricting growth or mortality rate of less competitive tree species. Aubier (2020) explained that positive density dependence among the same species acting only on mortality may cause species exclusion in two species system or coexistence in multiple species system. Specifically, most evidence of positive density dependence is interspecific interaction. Therefore, there is controversy on the contribution of positive and negative density dependence to coexistence of tree species alpha diversity in tropical forests. The density dependent effects occur through direct interference, competition for resource and host-specific enemies. The direct interference takes distance to neighbouring trees into consideration.

Interactions among tree population are processes that usually extend over limited distances and evidences have shown that most tropical tree species have aggregated distributions at seedling, sapling and adult life stages (Condit et al., 2000; Harms et al., 2000). Conversely, the overall densities of tree species decline gradually from seedling to sapling to adult life stages due to plant mortality (Stoll & Newbery, 2005). This reduction in density effect also occurs at different life stages of most reproductive tree species and is attributed to negative density dependence. It is negative density dependence because it restricts growth, survival and establishment of other plants. The mortality and growth restriction occur because of high density of individuals on limited resources and can also come through occurrence of host-specific pathogenic infections or herbivory. Conversely, the gradual decline in densities of seedlings and saplings does not lead to population reduction because the gaps left by the seedling mortality are filled through recruitment of rare tree seedlings.

The role of negative density dependence on tree species alpha diversity of tropical tree community has been examined by many researchers (Condit et al., 2000; Harms et al., 2000; Wright, 2002; Peters, 2003). Harms et al. (2000) found that negative density dependent recruitment contributed significantly to increase in Shannon-Wiener diversity index from seeds to seedling in lowland forest in republic of Panama. Zhu et al. (2018) found that slow growing tree species have higher survival and sensitivity to density of conspecific neighbours at all life stages compared to fast growing tree species at some life stages. Also, the strength of conspecific neighbours effect is significantly related to tree species abundance (Zhu et al., 2018).

However, regulation of tree populations is not a function of only negative density dependence. Sometimes, high densities of plant species can modify the environment for increase in tree survival and recruitment of new species within the community. This does not indicate that there would not be competition for resources among individual in dense aggregated community but only that the dominant mechanism is positive density dependence. Positive density dependence is often referred to as Allen effects. Tree populations are not often subjected to Allen effects because they are not able to grow at high densities (Knipi & Rost, 2016). Moreover, Goldenheim et al. (2008) indicated that there is growing evidence on switching of negative to positive density dependence. The switching is dependent on environmental conditions and life history stages. The seedlings and adults of intertidal annual forb exhibited positive density dependence under physical streesful conditions high on the seashore but negative density under physically milder conditions low on the seashore. This result supported an increase in the frequency of positive interaction with increasing environmental stress. Therefore, positive density interaction may facilitate maintenance of tree species alpha diversity in tropical tree communities.

3. Tree Community Structures and Coexistence Mechanisms in Tropical Forests

There are different types of interactions among forest tree populations. The two extreme models of interaction among forest tree populations are facilitation and competition. Facilitation is positive growth interactions (Bruno et al., 2003), while competition is negative growth interactions among tree populations (Getzin et al., 2006; Hou et al., 2006), because it reduces tree growth. Example of facilitated plants is tree species that increase the survival, growth, nutrient availability and uptake use efficiency of another plant species. Although there could be switching in the mode of interaction and therefore, a competitive tree can become a facilitated plant in harsh environments.

Tree competition from neighbouring trees occurs within limited distances and therefore, it occurs either among conspecific or heterospecific trees (Maleki et al., 2015). Conspecific neighbours indicates group of trees of the same species at short distance while heterospecific neighbours indicates group of trees of different species at short distance. Conspecifics and heterospecifics facilitate and increase the importance of intra-and inter-specific competitions, respectively (Murrell & Law, 2003). Therefore, competition that occurs among trees of different species is inter-specific competition while competition that occurs among individuals of the same species is intra-specific competition. There is a controversy on whether conspecific density effects are more effective process for facilitating coexistence of tree species alpha diversity in tropical forests than heterospecifics. Zhu et al. (2018) suggested that the strength of conspecific neighbours varied with tree species life stages and shade tolerance in a tropical forest.

According to niche theory (Bruno et al., 2003), tree species within the same niche space are more competitive than those in different niche spaces. Therefore, competition intensity is often higher in conspecific than heterospecific neighbours. Hence, trees that are surrounded by neighbours of the same species often exhibit low growth and survival (Comita et al., 2010). Conspecifics constrains locally abundant species and encourage proliferation of less abundant tree species and therefore, facilitate coexistence of tree species through many processes. This may be the reason the long distance conspecifics are not common in tropical forests. Negative density dependence was stronger among conspecifics than heterospecifics, especially for two species systems (Chesson, 2000). On the other hand, Comita et al. (2010) reported that rare tree species exhibited more slow growth from the presence of conspecific neighbours than less abundant tree species on Barro Colerado Island. Furthermore, Zhu et al. (2018) reported that fast-growing species had higher mortality in conspecific than slow-growing tree species at all life stages. Also, growth restriction was greater in fast-growing tree species in the presence of conspecifics than in slow-growing species at most life stages. Furthermore, Zhu et al. (2018) reported that fast-growing tree species had higher mortality in conspecific than slow-growing species at all stages. However, growth restriction was greater in fast-growing tree species in the presence of conspecific than slow-growing species at most life stages. Therefore, density dependence in conspecific regulates species abundance in alpha diversity of tree community. These indicated that conspecifics density effects are more pronounced in maintaining coexistence mechanisms of tree species alpha diversity in tropical forests.

The overall effect a tree has on another involves a range of mechanisms that operates over different distances (Murrell & Law, 2003). However, the minimum distance required for negative density dependence to enhance tree species alpha diversity has not been quantified in most tropical forests. However, Bhandari et al. (2021a) stated that the intensity of competition on indivdual tree varies with distance of the competitors and their sizes. Hence, distance and size of neighbouring trees are synonymous and critical in the estimation of competition for tropical forest trees. The optimum neighbourhood distance for optimum tree growth could be investigated in tropical forests. However, optimum neighbourhood distance to examine the conspecific and heterospecific density effects on tree growth needs to be considered. Therefore, determination of optimum distance and number of competitors may help to decide the appropriate plot size for studying the effect of competition on individual trees growth in tropical natural forest (Bhandari et al., 2021a). It was demonstrated that competition within approximately 7 metres distance from the base of the reference trees was optimal in predicting growth model of competitors in Eucalypts Forest (Bhandari et al., 2021a). In another study, competitors within approximately 10 metres from the base of the reference tree were required for optimum diameter growth (Bhandari et al., 2021b). These indicated that distance for optimum tree growth may not be the same for tropical natural forests.

Some tropical tree species adopt allelopathy, herbivory and pest facilitation to restrict recruitment and growth of other trees and therefore, these have shown to be negative density dependent mechanisms (Wright, 2002; Murrell & Law, 2003). Allelopathy is when plant species produce chemical that inhibit the growth of heterospecifics. These have short distance effects (Sharma et al., 2000) and therefore shorten distance between heterospecifics. Therefore, negative density dependent recruitment of seedling is an important mechanism contributing to the alpha diversity of tropical tree communities. The density dependent mechanisms occur through direct interference, competition for resource and host-specific enemies. Therefore, host-specific enemies such as specialist herbivores, seed predator and disease infestation could lengthen the distance between conspecific beyond heterospecific interactions. Host-specifc pests reduce recruitment near reproductive adults (Wright, 2002).

Condit et al. (1992) compared distances between reproductive adults for con-conspecifics and heterospecifics and found that recruits were more concentrated near conspecific adults and concluded that recruitment and dispersal limitations cause proliferation of recruits near conspecifics. Also, Hubbell et al. (1999) concluded independently that dispersal limitation and hence recruitment limitation are common phenomena among competing tree species.

4. Spatial Segregation in the Tree Community Structures of Tropical Forests

Conspecific and heterospecific interactions shape the forest spatial structures. Tree interaction in conspecific and heterospecific structures causes negative density dependent effects in tropical natural forests. However, variation in negative density dependence of conspecifics and heterospecifics is not explicitly clear. Understanding the mechanisms controlling tree interactions is essential to separate conspecifics from heterospecifics. However, interactions within conspecific and heterospecific structures have been argued to be independently responsible for coexistence of tree species alpha diversity in tropical forests (Wright, 2002). The cause of variation may include Jansen-Connell effects. Effects of heterospecific in the maintenance of tree species diversity were justified by Jaazen-Connell effects (Wright, 2002). Janzen-Connell effects are when host-specific pests or pathogen infestation cause mortality and reduce recruitment near conspecific reproductive adults. Therefore, seeds that disperse farther from the parent tree are more likely to escape mortality from host-specific predators or pathogen infestations (Volkov et al., 2005). This spatially structure mortality of seedlings has negative effects on population growth of locally abundance tree species and hence, create opportunity for recruitment of less abundant tree species, through forest gap creation. Also, coexistence of tree species diversity is achieved in heterospecific interaction when it occurs over shorter distances than conspecific interaction (Murrell & Law, 2003).

Although, Stoll and Newbery (2005) pointed that significant negative effects of conspecific interaction were only found in some common species and not found in rare species. However, Wright (2002) emphasized that niche differences and Jansen-Connell effects may control the coexistence of many rare tree species in tropical tree community structures. He further concluded that the differences in the strength of the conspecific neighbours were not explained by the degree of spatial clumping or relative size distributions. Therefore, competition causes local segregation among tree community structures. The extent of the spatial segregation determines the occurrence of coexistence or competition exclusion of tree species. Coexistence occurs when local spatial segregation is great enough to create an advantage for the rare trees species while exclusion occurs when local spatial segregation is insufficient to permit coexistence of rare species (Murrell & Law, 2003).

Stoll and Newbery (2005) reported that trees with heterospecific neighbours had significantly higher absolute growth rates (32.4 cm^2 basal area) than trees with conspecific neighbours (14.7 cm^2 basal area) from 1986 to 1996. Stoll and Newbery (2005) reported further that negative effects of large conspecific neighbours on seedling establishment and survival are significantly stronger than large heterospecific canopy trees. Moreover, Wang et al. (2021a) reported that average diameter-at-breast height of most intra-species competitor trees was greater than those of inter-species competitors. Hence, inter- and intra-specific competitions for tree growth resources have been mostly recognized to be responsible for species coexistence and exclusion effects among forest tree populations, respectively (Hou et al., 2006; Wang et al., 2021b). Conversely, it is important to note that inter-specific can switch to inter-specific competition during forest development. Wang et al. (2021a) concluded that dominant tree species composition determine the mode of competition in community structures. Furthermore, Bhandari et al. (2021b) reported that large and near competitors have higher competitive stress than small and distant competitors.

Spatial species diversity is evaluated by tree mingling indices which measures the probability that the reference tree and the nearest neighbouring trees are conspecific or heterospecific (Aguirre et al., 2003; Zhang et al., 2021). Spatial size inequality is evaluated by diameter differentiation and Gini coefficient. Therefore, conspecific and heterospecific interaction plays an important role in size structure and contributes to the maintenance of tree species diversity (Stoll & Newbery, 2005). Hence, investigating the spatial species diversity and size inequality will help to understand the coexistence mechanisms of tree species in tropical forest structure. This is because high species diversity is critical for maintaining stable forest ecosystem (Loreau et al., 2001). Competition effects are mechanisms for maintaining high tree species diversity in a natural forest but have negative effect on population size. However, high population size and coexistence of high tree species could occur sequentially or simultaneously in tropical forest structure. Therefore, it is required to understand the mechanisms that maintain coexistence of high tree species diversity in tropical forest for effective conservation and decision making on silvicultural treatment. Natural processes can be mimic through silvicultural system of selective thinning and enrichment planting (Aguirre et al., 2003).

5. Size Structure and Coexistence of Tree Species Diversity in Tropical Forests

It was suggested that competition limit population size and tree species diversity but more than 100 mechanisms have been postulated that confirmed how forest dynamics delay or prevent competition exclusion (Wright, 2002). Therefore, competition affects only population size and not species diversity in tropical natural forests. Size symmetry is often attributed to mode of competition among tree populations (Metsaranta & Lieffers, 2008). The shape expression of size variation in tree population is referred to as size symmetry. Asymmetric and symmetric models are recognized as two extreme expressions of resource competition in plant populations (Weiner, 1990). Competition for limiting resources in a population causes size inequality and fitness reduction among the competing trees. Size inequality is the variation in size due to competition. Therefore, size symmetry of tree varies with available resource (Schwinning & Weiner, 1998). Size hierarchy is an advance stage of size inequality, where two or more peak are expressed in a distribution. Also, asymmetric and symmetric models may be represented by distance functions that differ in shape or scale (Ledermann & Stage, 2001).

Although negative density dependence dominates the processes of population dynamic in tropical natural forests, there are evidences that positive density dependence can trigger size inequality in high tree density ecosystems (Chu et al., 2009). There are evidences of competition for tree growth resources in high tree density ecosystem. There is intrinsic difference between competition symmetry for above-ground and below-ground tree growth resources, inspite both express size inequality. Hou et al. (2006) found size dependent effects in mixed species forest in Northern China which detect both asymmetric and symmetric inter-specific competitions between some tree species. The size dependence expressed large tree in the canopy layer and reduced fitness of small trees in the understory. These indicated that inter-specific competition enhances intrinsic different combination of tree size inequality and spatial arrangement of tree species. However, species mingling is often omitted in most studies on spatial structure of natural forest because of different spatial arrangement of tree species (Hui et al., 2018). However, there is need to establish critical competition threshold for different combination of tree species and sizes in the tropical natural forests. Combination of competition and tree diversity indices at spatial scale would help to understand coexistence mechanism among tree species (Keren et al., 2020). These interactions determine the size inequality and species mingling in tree community structures (Hui et al., 2018). Therefore, it is important to investigate interaction among neighbouring trees of different species and sizes so as to understand the mechanisms of their coexistence (Keren et al., 2020). Forest spatial structure is controlled by competitive interaction among neighbouring trees of different species and sizes. Therefore, spatial structure is described by regularity of tree locations, species mingling and size differentiation. Hence, size symmetry in tree population can be described by size hierarchy and degree of size inequality (Weiner & Solbrig, 1984).

Spatial structure of species and size of trees contribute to structural diversity of natural forests and therefore control many ecological functions and services (Metsaranta & Lieffers, 2008). However, quantification of the effects of species diversity on ecosystem functioning is difficult. The effect of tree species diversity on size hierarchy of tropical natural forests could be investigated as substitute to ecological functions and services. Therefore, Forrester et al. (2016) demonstrated that effects of individual tree species on ecosystem function are dependent partly on their size. Keren et al. (2020) emphasized also that mid-sized and large tree determine the ecosystem functions and services in the forest, in many situations. Forest structure is described by spatial structure of its components plant stems, plant diversity and their abundance (Miren et al., 2004). Spatial structure is one of the characteristic attributes of structural diversity of forest (Von Gadow & Hui, 2015; Zhang et al., 2021). There is no direct relationship between structural diversity and mode of competition of forest stand because of tree species mingling. Therefore, quantification of relative local community inter- and intra-specific interactions is important but difficult.

6. Correlation between Tree Species Mingling and Size Inequality

There is great loss of biodiversity due to variability of climate. Therefore, it is important to reduce biodiversity losses through appropriate conservation management and strategies. Understanding the mechanisms to maintaining high tree species diversity in tropical forest is essential for the mitigation and adaptation of climate change (Wang et al., 2021a, 2021b). Natural and mixed species forests are widely advocated for climate change mitigation and adaptation because of their ecosystem stability and high potential of ecosystem services (Forrester et al., 2016). Structure of forest is spatially and temporally dynamic and therefore, effective prediction of structural diversity is difficult. Correlation of spatial species diversity and size inequality may show different spatial patterns in the same forest ecosystem. However, the dominant correlation determines the functional mechanism in the forest ecosytem (Wang et al., 2020). Interaction between conspecific and heterospecific structure facilitate the correlation between spatial species diversity and size inequality in tropical forests (Wang et al., 2020).

7. Conclusion

A large variety of negative density dependent mechanisms contribute to tree species regulation and coexistence in tropical communities. Community composition and diversity are maintained through conspecifics' and heterospecifics' negative density mechanisms. Conspecific structures contribute to the increase in species diversity through negative density dependence. The distribution of conspecifics and heterospecifics determines the community structures of tropical forests. Conspecific may be switched to heterospecific structures in tropical tree communities through density dependent effects. Coexistence of tree species in tropical forest is the result of several processes interdependent on each other. Therefore, switching from conspecific to heterospecific interactions and negative to positive density dependence occur in some situations. Coexistence of tree species alpha diversity can not be understood without the knowledge of competitive interaction through the species identity and mingling.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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