Determinants of the spatial distribution of tree species in a neotropical forest

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2013

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

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General discussion

Carol X. Garzon-Lopez
Stochastic and deterministic processes are considered to be the main drivers of the spatial distributions of species in tropical forests (Purves & Pacala 2005, Hardy & Sonke 2004); therefore, I examined if the distribution of plant species during two life stages, i.e., adult trees and early recruitment, reflected these processes. I used these data to evaluate the relative importance of stochastic and deterministic processes in shaping the observed spatial distribution.

My study provided four main findings that contribute to our understanding of spatial species patterns in the context of species coexistence in tropical forests from a community-scale perspective. First, the spatial scale had a critical effect on habitat association studies, which could be examined using technologies such as remote sensing and modeling to reduce the effects of spatial scale. Second, adult trees were aggregated in clusters, which probably reflected the natural clumping patterns that resulted from dispersal limitation (Chapter 3). They were also significantly associated with historical and environmental variables (forest age and topography, respectively). Thus, dispersal limitation and habitat differences need to be studied simultaneously. If this is not the case, clusters that result from dispersal limitation may be mistaken for different habitats, or the dominance of species in particular habitats due to habitat preferences may be mistaken for dispersal limitation. Third, seed predation, which is part of seed limitation, depended on conspecific densities (based on Janzen–Connell hypothesis) as well as on heterospecific species densities. Furthermore, seed predation is a critical filter for species distribution because it reduces the number of seeds dispersed by specialist and generalist predator behavior to approximately 20% (Chapter 4). Fourth, seed and establishment limitations controlled the spatial distribution during the early recruitment stages (Chapter 5). However, the relative importance of these two components for dispersal limitation was dependent on the species, their local densities, and the local conditions (forest structure, predation rates, and site suitability). These findings suggest that the relative importance of stochastic and deterministic processes for controlling species distributions depend on the following: (1) the dynamic interplay of both processes, (2) the scale examined, and (3) species-specific responses to site conditions.

**Effects of spatial scale on habitat association studies**

There is an increasing recognition of the effects of spatial scale in studies of ecological patterns and processes because they are determined by spatial dynamics that act at multiple scales (Hoosbeek & Bryant 1992, Dungan et al. 2002, Lin et al. 2011). These processes have been shown to depend on factors, such as the spatial distribution of plants (Condit et al. 2000, Brown et al. 2011), seed dispersal, predation, and recruitment (Schupp & Fuentes 1995, Nathan & Muller-Landau 2000, Beckman et al. 2012) as well as the behavior of animals, their interpretation of space, and their movement patterns (Kleynhans et al. 2011, Hammond et al. 2012).
In some cases, the effects of scale has also been demonstrated previously (Wheatley & Johnson 2009) as estimators of forest diversity and structure (species-abundance distribution; Condit et al. 2000) and in conservation biology studies (bioindicators; McMahon et al. 2012). Despite all this evidence, scale is still often not included in ecological studies, which results in generalizations outside the spatial context (Wiens 1989, Rahbek 2005).

In this study, we evaluated the effects of scale during observations of plant–habitat associations, which have often been used in arguments that prove or disprove the importance of deterministic vs. stochastic processes. In these studies, the scale often varies and so do the environmental heterogeneity and species densities, which results in varying outcomes. We found a profound effect of scale (Chapter 3) on the presence of plant-habitat associations in four main areas: (1) the organism studied, which had specific characteristics in terms of body size and clumping patterns; (2) the system, which was defined by the environmental heterogeneity and species composition; (3) biotic interactions, which were determined by pathogens, predator movement patterns, and resource utilization; (4) the process, which we found had a continuous scale dependency that resulted in a change in the associations with scale. Thus, the percentages and types of habitat associations found at different scales were different but still correct, which contradicted opposing results found at other scales instead of simply demonstrating the complexity of processes controlled by the dynamic spatial structure of the forest (Figure 6.1).

Thus, ecological studies must be designed within a previously evaluated spatial context. Traditionally, the spatial explicit data used to evaluate the context are

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**Figure 6.1.** Conceptual framework of the four main areas influenced by spatial scale (rounded squares) and each of its specific properties, which should be examined and incorporated when designing ecological studies.

<table>
<thead>
<tr>
<th>Patterns and Process</th>
<th>System</th>
<th>Organism</th>
<th>Interactions</th>
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<td>- Patchiness</td>
<td>- Body size</td>
<td>- Type and characteristics of species</td>
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<td>- Continuous</td>
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<td>- Domains</td>
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<td></td>
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<td>- Characteristics</td>
<td>- Movement</td>
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</tbody>
</table>
collected in ground surveys that generate highly accurate data (Webb & Peart 2000; Lan et al. 2009; Lin et al. 2011; Hubbell, Condit, & Foster 2005) but require intensive fieldwork and thus are only performed at small scales. However, in the last decade, other less time-consuming techniques such as remote sensing have been developed, which provide accessible environmental and ecological information at small and large scales (Chapter 2), thereby supplying data at scales relevant to organisms and processes (Mayer & Cameron, 2003).

In this study, I applied a reliable, less costly, and replicable method to capture and process digital images to identify and map adult tree species. The use of this method in a multiscale ecological study provided useful information about the specific properties of the organism, system, its biotic interactions, and the process observed as well as the areas influenced by the selection of spatial scales, which should be included in studies of plant–habitat associations (Figure 6.1).

**Spatial aggregation of species**

Patterns of species aggregations influence and are influenced by the structure of a forest and its ecological processes (Plotkin et al. 2002). These patterns alone can provide data, which can be combined with other factors to aid the understanding of mechanisms that lead to species coexistence (Plotkin et al. 2000). These data are an initial critical step when looking at spatially structured ecological processes. Chapter 3 shows how all the studied species were aggregated, although the aggregation characteristics (e.g., clump size and density) varied with the species, scale, and location examined. This has important implications in the study of spatial patterns because it suggests that the selection of the study area in terms of the location, size, and species studied is critical for the outcome and can lead to inaccurate generalizations.

For example, I found that the adult species distributions were significantly associated with specific environmental conditions, where the results depended on the location and the scale of the area examined (Chapter 4). Voormisto et al. (2004) found the same variation among sites at the same scale using palm species. This analysis of the habitat associations of palms and the topography suggested significant plant–habitat associations at each site, but these associations lost significance due to site-specific characteristics when considering various sites (Voormisto et al. 2004).

**Plant–habitat associations during the adult stages: Stochastic or deterministic patterns?**

The observation of plant–habitat associations has often been used in arguments to prove or disprove the importance of deterministic processes. Each of these processes is considered to control species distributions, and if they control species coexistence, either process should be tractable during the adult stages. Chapter 3 shows that the studied species distributions were associated with the site proper-
ties, although these associations were changed, in terms of significance and the type of association (positive or negative), depending on the scale and locations of the samples. Although the differences in findings generally indicated the importance of one process over the other (Svenning et al. 2009, Harms et al. 2001), our findings suggested that the strengths of plant–habitat associations depended on unchanging site conditions and the interplay among several site-specific circumstances combined with species-specific properties. Thus, the different percentages and types of habitat associations found at one scale were still correct and did not contradict opposing results found at another scale, instead of simply demonstrating the complexity of the processes controlled by the dynamic spatial structure of the forest.

**Transport: Seed limitation through dispersal and predation**

Seed limitation is key to species survival, allowing species to “move” to a less competitive/safer site and colonize new areas (Nathan & Muller-Landau 2000). Seed limitation encompasses seed production, seed dispersal, and seed predation, which together generate and shape the initial species distribution. In this study, the effects of seed predation on the spatial distribution of plant species were sufficiently strong to be tractable in the adult distribution at the entire island scale (Chapter 3). Natural clumping had to be included in the analysis to ensure a more realistic analysis of the species distribution as well as historical variables that had significant effects on the spatial distributions of species. This is an interesting outcome because historical variables (forest age) generate differences in the forest structure and provide evidence of dispersal events and colonization (Svenning 2001).

In this study, dispersal allowed species to reach areas of low adult conspecific densities, yet seed predation reduced the seed availability in 80% of the population. During the early stages of recruitment, the forest age and tree density affected seed dispersal, predation, and more importantly, the seed germination through density-dependent effects (Chapter 5). Furthermore, density-dependence affected the seed survival through conspecific densities ; there was also a clear effect of heterospecific densities through generalist predator behavior (Chapter 4). These findings indicate the importance of dispersal allowing seeds to reach sites far from their parents, which highlights the striking effect of seed predation as a critical and complex filter on the initial distribution of species. These processes are critical for shaping spatial distributions of species, which are increasingly important in conditions where the species densities and/or functional similarity increase and the environmental heterogeneity decrease.

**Settling: Seed survival and establishment**

Site properties are hypothesized to impose a strong filter during species establishment (Mangan et al. 2010). In Chapter 5, it was shown that establishment limita-
tions (site properties) did not significantly affect the spatial distribution of species recruitment because they did not significantly affect seed germination, unless the effects of tree density and forest age were included. Even in these cases, the effects varied among species (Chapter 5). This variation agreed with the variation found in 14 species in French Guiana where seeds (in seed traps) and establishment limitations (in seedlings plots) were measured (Norden et al. 2009). It was demonstrated that seed dispersal and site conditions helped to explain the distribution of species, although there was high interspecific variation in the relative importance of each type of limitation.

Consequently, species in my study appeared to have different requirements depending on their life stages, as previously reported by Comita et al. (2007). This suggests that species respond to deterministic processes. However, for these types of processes to shape the spatial distribution of species, a site must have high environmental heterogeneity and low conspecific densities to overcome the effects of stochastic processes.

Transport or settling: How do stochastic and deterministic processes interact?

As mentioned earlier, stochastic and deterministic processes are proposed as the main drivers of species distributions. In addition, there is a growing body of literature that highlights the importance of specific mechanisms within both processes as drivers of the distribution and coexistence of species (Mari et al. 2008), such as Janzen–Connell patterns (Janzen 1970, Connell 1978), resource competition (Tilman 1980), and predator movement strategies (Mari et al. 2008), which include spatially structured processes that can be summarized in previously stated areas: (1) organism-specific characteristics and requirements; (2) interactions through competition and predation; (3) the system and spatial context in terms of environmental heterogeneity and species composition; and (4) patterns and processes in an open system at a selected scale (Figure 6.1).

Based on the results of this study, particularly those reported in Chapters 4 and 5, I propose a set of stochastic and deterministic processes that interact to control species recruitment, thereby determining the distributions of species, which include the mechanisms mentioned earlier (Figure 6.2). The deterministic processes include two variables: species-specific traits and site properties. First, species-specific properties will limit variables such as clumping patterns, seed production, and resource requirements, which interact with the site conditions to promote recruitment. Second, site properties such as environmental heterogeneity and species composition will impose a filter, which will promote competition among individuals of the same species or species with similar requirements.

The stochastic components include two variables: seed dispersal and predation. Seed dispersal is a critical step in species recruitment because it limits the potential distribution of plants. In this study, we focused on seed arrival rather than the
process of dispersal; thus, our estimates corresponded to the seed densities after dispersal (Figure 6.2), which were generally correlated with the distribution of adults. Predation, the second variable, is controlled by the characteristics of the interacting organisms, i.e., predator–seed, and the condition under which this interaction occurs (Nathan & Muller-Landau 2000, Mari et al. 2008, Beckman et al. 2012). The effects of specialist predators can be estimated based only on presence of the focal species, whereas the effects of generalist predators will be modified by the presence of the seeds of other species (Chapter 4), which highlights the importance of predator specificity and the species composition on recruitment. Although species traits are critical for the spatial patterns observed, this did not occur through a fixed set of requirements, as proposed by niche differentiation, instead it was due to a set of circumstances (spatial context, dispersal events, and biotic interactions) that strengthened either stochastic (Figure 6.2; high environmental heterogeneity, predator specificity, and seed density) or deterministic (Figure 6.2; low environmental heterogeneity, predator specificity, and high seed density) effects.

In conclusion, the spatial distribution of species is not constant and determined only by the environment. Instead, it is the result of dynamic combinations of changes (in space and time): (i) environmental heterogeneity, (ii) species movements (through dispersal and predator behavior), and (iii) the plant community
composition and densities. Thus, the forces driving these spatial patterns depend on combinations of factors while our ability to observe them depends on the scale. In addition, large-scale single species studies (>500 ha) are extremely rare; therefore, this study represents the first investigation to use this approach.

**Directions for future work**

What are the effects of species loss on ecosystem functioning? What are the effects of fragmentation on biodiversity maintenance? These are some questions researchers are asking, alarmed by the rapid decline in species diversity and ecosystem connectivity. Thus, understanding the processes that facilitate diversity maintenance and species coexistence is of critical importance. Currently, technology provides us with a set of tools that allow us to observe ecosystems from multiple perspectives, thereby allowing integrative analyses of the processes that facilitate diversity maintenance and species coexistence.

Throughout this thesis, I have attempted to identify the processes controlling species distributions from the perspective of spatial dimensions. First, I demonstrated the utility of species mapping through high-resolution aerial images to study ecological processes in the tropical forest. Second, I provided evidence for the importance of including scale in ecological studies. Third, my large-scale spatial analyses provided insights into the complexity of interactions, the criticality of species characteristics, and the spatial context for species distributions and coexistence. Future studies of this type should consider the spatial scale as well as the characteristics of organisms and their interactions to provide an informed and complete view of the complexity of the forest.

Human activities such as colonization and hunting are known to have consequences for species coexistence (Wright 2003, Beckman 2007). This study suggests that particular species characteristics at the community scale should be carefully considered as critical determinants of species distributions and diversity maintenance because each species loss may have enormous consequences for ecosystem functioning.