

ARTICLE

Analyses of three-dimensional species associations reveal departures from neutrality in a tropical forest

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Abstract

The study of community spatial structure is central to understanding diversity patterns over space and species co-occurrence at local scales. Although most analytical approaches consider horizontal and vertical dimensions separately, in this study we introduce a three-dimensional spatial analysis that simultaneously includes horizontal and vertical species associations. Using tree census data (2000–2016) and allometries from the Luquillo forest plot in Puerto Rico, we show that spatial organization becomes less random over time as the forest recovered from land-use legacy effects and hurricane disturbance. Tree species vertical segregation is predominant in the forest with almost all species that co-occur in the horizontal plane avoiding each other in the vertical dimension. Horizontal segregation is less common than vertical, whereas three-dimensional aggregation (a proxy for direct tree competition) is the least frequent type of spatial association. Furthermore, dominant species are involved in more non-random spatial associations, implying that species co-occurrence is facilitated by species segregation in space. This novel three-dimensional analysis allowed us to identify and quantify tree species spatial distributions, how interspecific competition was reduced through forest structure, and how it changed over time after disturbance, in ways not detectable from two-dimensional analyses alone.

KEYWORDS

forest succession, habitat association, spatial associations, species co-occurrence, vertical stratification

INTRODUCTION

A long-standing question in ecology is why, and how, many species can co-occur in relatively small areas (Chesson,

2000). A prominent mechanism is spatial segregation, through which species reduce competition with other species (Kohyama & Takada, 2009; Laurans et al., 2014; Terborgh, 1985). Spatial segregation can reflect niche partitioning along niche dimensions with a spatial component. Niche partitioning is a key factor reducing

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competition and is a well known mechanism for the maintenance of local diversity facilitating local co-occurrence (Chesson, 2000; Goldberg & Barton, 1992; Loreau & Mouquet, 1999). Reduced competition by not sharing exactly the same space or resources is, in general, advantageous for any given species. Species that occupy the same locations have, in theory, access to the same horizontal and vertical resources, and may compete directly. Such pairs of species cannot co-occur over time unless niche partitioning occurs, as predicted by the competitive exclusion principle, with the general expectation that species will become spatially segregated over time allowing local co-occurrence (Chesson, 2002). The study of plant community spatial structure is central to determining the role of deterministic and stochastic ecological processes shaping plant communities and for understanding diversity patterns over space and time (He & Legendre, 2002; Wills et al., 2006; Wright, 2002).

Spatial segregation can occur in the horizontal plane, reflecting dispersal and stochastic dynamics (Hubbell, 2001, 2006), niche partitioning along niche dimensions with a horizontal component (Kitajima & Poorter, 2008). In tropical forests, in particular, there are clear spatial associations between species and topography, soil nutrients, canopy closure, and the forest edge (Abiem et al., 2020; Harms et al., 2001; John et al., 2007; Lee et al., 2002; Lieberman et al., 1995; Russo et al., 2005). The sorting of species along these environmental gradients facilitates local coexistence by giving each species its own space within the same locality. Spatial segregation implies that some species segregate along environmental gradients (habitat specialization) in the same community, whereas others tend to co-occur. However, few studies consider the spatial organization of multiple species relative to each other. In particular, measuring spatial associations among all species present in a community is challenging, and has been rarely attempted in a species-rich tropical forest (but please refer to Taubert et al., 2015, Schmid et al., 2020).

Spatial segregation can also occur in the vertical plane, reflecting recruitment dynamics and partitioning along niche dimensions associated with plant size. Tree stature relates to different tradeoffs between species such as the growth versus survival tradeoff (Wright et al., 2010) and the early reproduction versus annual fecundity tradeoff (Wright, 2005). Species of different size have access to different levels of light and show different tolerances to shade (Poorter et al., 2005); they have different life spans (Lieberman et al., 1985), reproductive strategies (Gilbert et al., 2006), dispersal potential (Thompson et al., 2011); and are exposed to different mortality risks (Zuleta et al., 2022). Vertical stratification in tropical forests has been studied for decades (Horn, 1971; Terborgh, 1985) and clearly has a niche or life-strategy component, with some

species being reported as understory species and other species as typical canopy species.

Most studies on tree species spatial distribution typically focus on “space” as being either the two-dimensional horizontal dimension or the vertical dimension, but not both. As a result, we do not know, at a given scale, the relative importance of the horizontal dimension versus the vertical dimension for the co-occurrence of species. Here, we introduce a novel three-dimensional spatial analysis that considers horizontal and vertical associations among tree species simultaneously. Associations can be positive (species aggregate in space) or negative (species segregate in space) or random (species are not particularly close to or far from each other). To describe such associations in space, we estimate the crown overlap between each pair of neighboring trees to capture processes that result in species aggregating or segregating in space. The measured spatial aggregation/segregation can reflect processes happening at a range of spatial scales, from the sorting along environmental gradients to fine-scale processes at the few-meters scale. We use data from four censuses spanning 16 years (2000–2016) from the tree communities in the Luquillo Forest Dynamics Plot (LFDP), Puerto Rico. Our goals were to:

1. Classify the spatial associations (i.e., tendency for species i to aggregate with or segregate from species j) between each pair of common species in Luquillo, considering both horizontal and vertical dimensions.
2. Determine the relationship between a species' dominance (abundance and basal area) and its ability to segregate successfully from other species.

METHODS

Study site

The LFDP is a 16-ha tropical wet forest located in the Luquillo Experimental Forest in northeast Puerto Rico (Thompson et al., 2002). The plot is 500 m N–S and 320 m E–W and is divided into four hundred 20 m × 20 m subplots. The plot can be divided into disturbance areas that have had contrasting land-use histories and suffered different intensities of natural hurricane disturbances. The northern two-thirds of the LFDP (the high-disturbance area) experienced logging and small-scale farming until 1934 (Thompson et al., 2002). The southern third of the plot (the low-disturbance area), in contrast, only experienced small-scale selective logging. The LFDP experienced disturbance by major hurricanes including Hurricanes Hugo (1989) and Georges (1998) that caused widespread damage to the forest canopy and

above-background levels of tree mortality (Canham et al., 2010; Uriarte et al., 2004; Zimmerman et al., 2010). As a result of the previous land-use history, the southern, less human-disturbed part of the plot is dominated by late-successional high wood density species that are more resistant to winds and hurricanes. The northern, more-human-disturbed part of the plot has more abundant pioneer and low wood density species that suffer more damage during strong storms and hurricanes (Zimmerman et al., 1994). The association between land-use history, species distribution, and species differences in response to hurricanes, means that the southern part of the plot has a low intensity of disturbance when compared with the northern part of the plot (Zimmerman et al., 2010). From this point forwards, the southern part of the LFDP will represent the low-intensity disturbance area and the northern part of the plot the high-intensity disturbance area. Because the studied plot has two areas with contrasting land-use histories and levels of damage by natural disturbance, we applied the spatial analysis separately to each area.

In the LFDP all trees ≥ 1 cm of diameter at 130 cm from the ground (aka diameter at breast height, dbh) have been measured for diameter, identified, and mapped approximately every 5 years since 1990 (Hogan et al., 2016; Thompson et al., 2002). Here we included four censuses carried out in 2000, 2005/2006, 2010/2011 and 2015/2016. Areas experiencing high-intensity disturbance (northern two third of the plot) contain a high abundance of pioneer and secondary forest species such as *Casearia arborea* Rich. (Salicaceae), *Schefflera morototoni* Aubl. (Araliaceae), and *Cecropia schreberiana* Miq. (Urticaceae) (Thompson et al., 2002). Areas experiencing low-intensity disturbance (southern one-third of the plot) are dominated by late-successional species such as *Dacryodes excelsa* Vahl. (Burseraceae), *Manilkara bidentata* A.Chev. (Sapotaceae), *Guarea guidonia* (Meliaceae), and *Sloanea berteriana* Choisy ex DC. (Elaeocarpaceae) (Hogan et al., 2016; Swenson et al., 2006; Thompson et al., 2002; Zimmerman et al., 2010). A palm, *Prestoea acuminata* (Wild.) H.E.Moore (Arecaceae), is the dominant species in both portions of the plot but has a higher relative abundance in areas experiencing high-intensity disturbance (Thompson et al., 2002).

Spatial analyses to determine species associations

We quantified the spatial association of a given pairs of species (designated species i and j) by quantifying crown overlap between all pairs of individuals of those species. The following subsections explain how we: calculated observed overlaps, calculated expected overlaps,

calculated the intensity and direction of each association by comparing the observed overlaps with the expected overlaps, how we classified species–species associations into four types or categories, and determine relationship between species' dominance and spatial segregation.

Observed overlaps between the crowns of each pair of species

We estimated crown area and vertical position from general allometric equations relating tree diameter to height and crown dimensions (Zambrano et al., 2019): $\log_{10}(\text{height}) = -0.1318 \times (\log_{10}(\text{dbh}))^2 + 0.8888 \times \log_{10}(\text{dbh}) + 0.2708$ for all individuals; $\log_{10}(\text{tree crown radius}) = 0.6598 \times \log_{10}(\text{dbh}) - 0.3918$ for dicots; $\log_{10}(\text{tree crown radius}) = \log_{10}(0.1762) + 0.8233 \times \log_{10}(\text{dbh})$ for palms. Previous results for the LFDP suggest that this size-dependent definition of “interaction” or “proximity” is a more relevant representation of spatial associations than a fixed distance threshold (Zambrano et al., 2019, 2020). The horizontal position of each crown was centered at the coordinates of that tree determined during the tree censuses, as if all trunks were perfectly straight. Appendix S1 explores the sensitivity of our methods to the height allometries (Appendix S1: Figure S1), the crown radius allometries (Appendix S1: Figure S2), and the assumption of perfectly straight trunks (Appendix S1: Figure S3).

Based upon the relative location of the trees and the size of their crown estimated from allometric equations we estimated the overlap between each pair of crowns (c_1 and c_2) as A = the area of intersection of the two crowns projected into the horizontal plane. If c_1 was taller than c_2 , we assumed that c_1 shaded c_2 by A m², and c_2 shaded c_1 by 0 m². Conversely, if c_2 was taller than c_1 , we assumed that c_1 shaded c_2 by 0 m² and c_2 shaded c_1 by A m². This is not completely precise, but it is sufficiently accurate for our analyses (Appendix S1: Figures S4–S6). This simplification was needed for practical reasons, as it reduced by several orders of magnitude the computational time required for our calculations.

In total, we calculated between $\sim 71,000$ and $\sim 390,000$ non-zero individual-level overlaps, depending on the disturbance level (represented by the northern versus southern areas of the plot) and census. We then summed the individual-level crown overlaps across all individuals for each pair of common species, to calculate pairwise species-level overlaps. Common species were defined as those that, when listed in rank order by number of individuals, accumulated at least 90% of the total number of individuals during at least one census, in at least one disturbance area. There were 44 common species (out of 145 in total),

which yielded 1892 possible pairs of species, but we only observed between 843 and 1497 non-zero species-level pairwise associations (i.e., crowns did overlap for some individuals of these species pairs), depending on the census and disturbance level. These associations between common species accounted for 80.0%–84.7% of all the surface of crown overlap between pairs of individuals in the forest, depending on the disturbance level and census.

Species-level overlaps were calculated both directionally and non-directionally: species i shades species j in a given area ($A_{i>j}$, in m^2), and species j shades species i in a different area, $A_{j>i}$. Without considering who shades who, both overlap $A_{i\leftrightarrow j} = A_{i>j} + A_{j>i}$. When species i is consistently taller than j , we will expect $A_{i>j} \gg A_{j>i}$ but, in general, both species can shade each other by similar amounts if they are common and tend to grow relatively close together in similar horizontal spatial locations. If both species tend to occupy different positions in the horizontal space (e.g., topographic positions), they will not shade each other, regardless of their relative heights and abundances ($A_{i\leftrightarrow j} \approx 0$, which implies $A_{i>j} \approx 0$ and $A_{j>i} \approx 0$).

Expected overlaps between the crowns of each pair of species at the community level

Small or large overlaps between two species, per se, do not mean much in terms of their associations or differences/similarities in preferences or spatial distribution. For example, two very abundant species will overlap with each other more frequently than two rare species, just by chance, even if they do not associate with each other in any meaningful way. To identify meaningful associations, we compared the observed species-level overlaps with the expectations from a null model. The process of how to build and interpret our null model is described in detail in Appendix S2. The null model breaks the spatial (three-dimensional) associations between any two species by randomizing the location of individual trees in the horizontal and the vertical dimensions. Diversity, relative abundances, individual crown areas, and spatial aggregation within species, were all kept as observed. The horizontal randomization involves torus translations for each species independently. This breaks the horizontal location of species with respect of each other while respecting the horizontal aggregation within each species, which may be caused by dispersal limitation or other causes unrelated to species–species interactions or species-level niche preferences. The vertical randomization of the location of the individual crowns is a simple permutation of all the heights of all the individuals in the forest (all species combined). This randomization breaks any relationship between the height and crown area of individual trees. We did not permute heights internally to each species independently, as differences in

size between species are a major force structuring forests and a pattern of interest.

Intensity and direction of species–species associations

Deviations from the null model indicate whether species establish stronger or weaker associations than expected for their dbh, abundance, and horizontal within-species aggregation. We quantified these associations between species using standardized effect sizes (SES), comparing the observations of crown overlap with 999 null expectations: $SES = (\text{observed} - \text{mean}_{\text{null}}) / \text{SD}_{\text{null}}$. In cases when the observed overlaps and all 999 expected overlaps were exactly zero, we defined $SES = 0$ (meaning no changes from the expected). SES were calculated for $A_{i>j}$, $A_{j>i}$, and $A_{i\leftrightarrow j}$, as $SES_{i>j}$, $SES_{j>i}$ and $SES_{i\leftrightarrow j}$ respectively. $SES_{i>j} > 0$ means that i shades j more than expected by chance, $SES_{i>j} < 0$ means that i shades j less than expected by chance, and so on. $SES_{i\leftrightarrow j} > 0$ means that both species overlap more than expected by chance and $SES_{i\leftrightarrow j} < 0$ that they overlap less than expected by chance, regardless of who shades whom. $SES_{i>j}$ and $SES_{j>i}$ are independent of each other: both can be zero, or low, or one can be low and the other high, or vice versa, or both can be high. Their values depend on how the species are organized in space. $SES_{i\leftrightarrow j}$, in contrast, is not independent from $SES_{i>j}$ and $SES_{j>i}$: when $SES_{i>j}$ and/or $SES_{j>i}$ are low, then $SES_{i\leftrightarrow j}$ will be low.

In addition to calculating SES for the observed overlaps between species, we calculated SES for the null values of $A_{i>j}$, $A_{j>i}$ and $A_{i\leftrightarrow j}$ as well. The SES of null values are just the scaled null values: $SES^{\text{null}} = (\text{null} - \text{mean}[\text{null}]) / \text{SD}(\text{null})$. These values will be denoted $SES_{i>j}^{\text{null}}$, $SES_{j>i}^{\text{null}}$ and $SES_{i\leftrightarrow j}^{\text{null}}$. $SES_{i>j}^{\text{null}}$, $SES_{j>i}^{\text{null}}$ and $SES_{i\leftrightarrow j}^{\text{null}}$ serve as a reference to define appropriate SES thresholds to keep the Type I error rate at a predefined level when categorizing the associations between species, as explained in the following section.

Assessing the type and strength of species–species three-dimensional associations

Based on $SES_{i>j}$, $SES_{j>i}$ and $SES_{i\leftrightarrow j}$ values, we classified each pair of species into four association types: (1) horizontal segregation (two species tend to occupy different horizontal locations); (2) horizontal aggregation and vertical segregation (two species tend to occupy similar horizontal locations, but occupy different positions in the vertical dimension); (3) three-dimensional aggregation (two species tend to occupy the same locations both in

the horizontal and vertical space); and (4) random association (two species associate approximately as expected by the null model). The operational definitions for each association type were as follows:

1. We assigned a given spatial association between two species to the “horizontal segregation” class if $SES_{i \leftrightarrow j} < Q(p = 0.05, SES_{i \leftrightarrow j}^{null})$, where $Q(p = 0.05, SES_{i \leftrightarrow j}^{null})$ is the 5% quantile in the distribution of $SES_{i \leftrightarrow j}^{null}$. By this definition, if associations in the empirical forest are similar to the associations in the null forests, we will have a 5% of associations assigned to the “horizontal segregation” category just by chance.
2. We assigned a given spatial association between two species to the “horizontal aggregation and vertical segregation” class if $SES_{i > j} > Q(p = v_{ij}, SES_{i > j}^{null})$ and $SES_{j > i} < Q(p = 1 - v_{ij}, SES_{j > i}^{null})$, where v_{ij} is a value between 0 and 1 chosen in a way that, for this particular pair of species i and j , only 5% of null associations exceeded both thresholds simultaneously. In other words, we assigned an association to this category only when $SES_{i > j}$ was very high and $SES_{j > i}$ was very low simultaneously, adjusting symmetrical thresholds to not to exceed a 5% Type I error rate. By this definition, if associations in the empirical forest are similar to the associations in the null forests, we will have 5% of associations assigned to the “horizontal aggregation and vertical segregation” category just by chance.
3. We assigned a given spatial association between two species to the “three-dimensional aggregation” class if $SES_{i > j} > Q(p = w_{ij}, SES_{i > j}^{null})$ and $SES_{j > i} > Q(p = w_{ij}, SES_{j > i}^{null})$, where w_{ij} is a value between 0 and 1 chosen in a way that, for this particular pair of species i and j , only 5% of null associations exceeded both thresholds simultaneously. In other words, we assigned an association to this category only when $SES_{i > j}$ and $SES_{j > i}$ were high simultaneously, adjusting the same relative threshold to not to exceed a 5% Type I error rate. By this definition, if associations in the empirical forest are similar to the associations in the null forests, we will have a 5% of associations assigned to the “three-dimensional aggregation” category just by chance.
4. We assigned to the “random association” category all pairs of species that did not fulfill the conditions for the three categories above. By this definition, if associations in the empirical forest are similar to the associations in the null forests, we will have 85% of

associations assigned to the “random” category just by chance (100% – 5% – 5% – 5%).

To determine variation in species–species associations between disturbance level and for each census, we estimated the proportion of species in each of these association types. Disturbance-related and time-related changes in the direction of the different types of species associations were assessed visually (please refer to Figures 1 and 2 and Zambrano et al., 2021).

Relationship between species’ dominance and spatial segregation

For this analysis, we grouped together all censuses and both disturbance levels. To determine the relationship between species dominance and their tendency to segregate from other species, we calculated:

1. The overall relative abundance (%) of each species.
2. The overall relative basal area (%) of each species.
3. The total number of associations involving horizontal or vertical segregation in which each species was involved. This was calculated for common species only (those that together accumulated 90% of individuals or more).

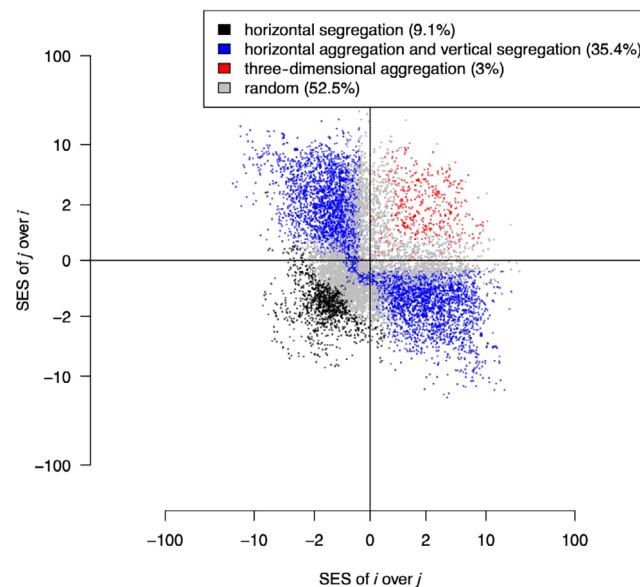


FIGURE 1 Diagram depicting the types of species associations. The points represent all pairs of species at all census times and disturbance levels, covering the conceivable association space in the Luquillo Forest Dynamics Plot forest. Gray points represent random associations, black points represent horizontal segregations, blue points represent horizontal aggregations combined with vertical segregations, and red points represents three-dimensional aggregations. SES, standardized effect sizes

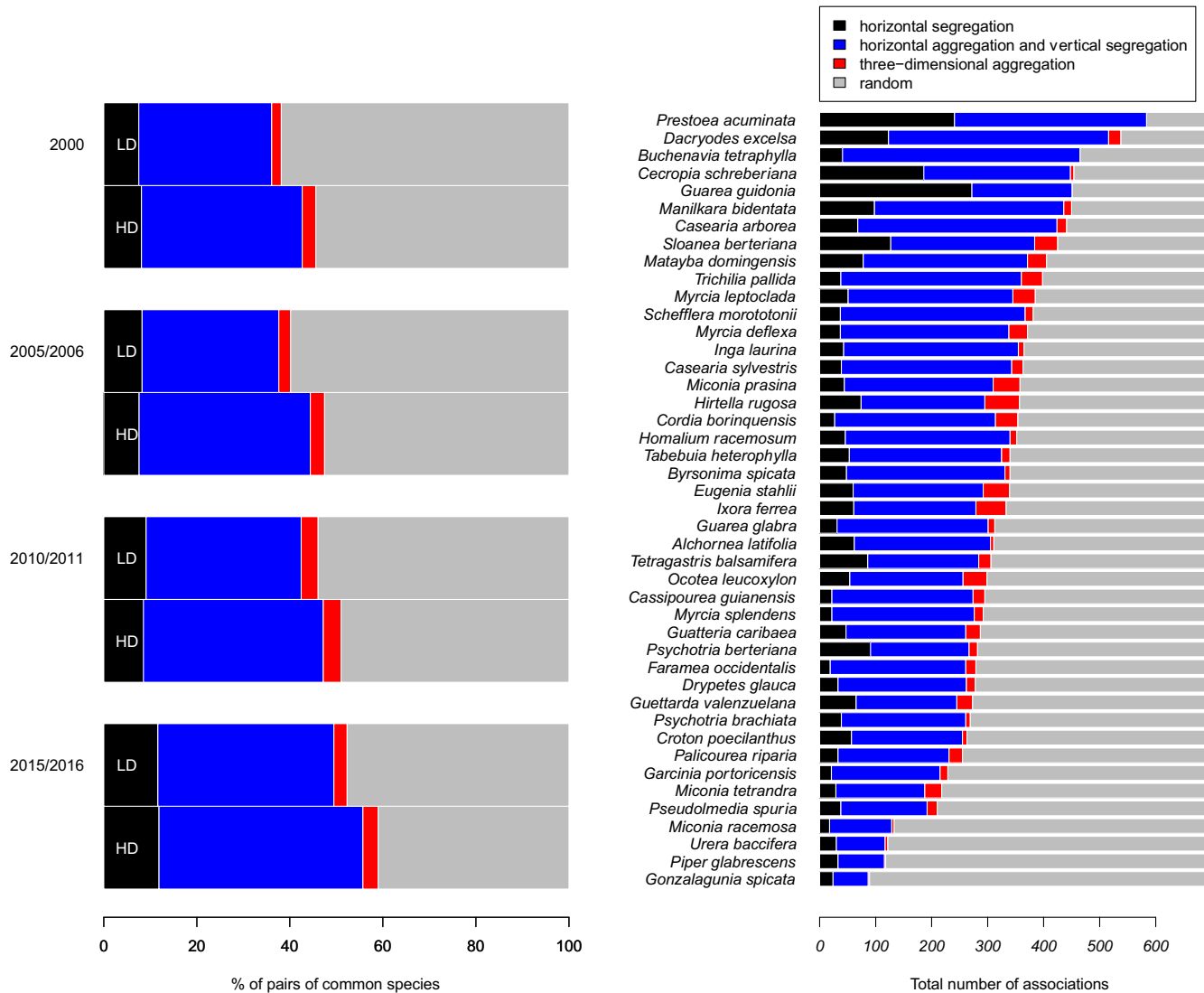


FIGURE 2 Left panel: the frequency of each type of association between common species each censuses year in the southern part of the Luquillo Forest Dynamics Plot low-disturbance area (LD) and high-disturbance area (HD). Right panel: number of species–species associations involving common species (those that together accumulated at least 90% of the individuals during at least one census in at least one disturbance level)

4. The mean $|SES|$ of all the associations in which each species was involved. Greater mean $|SES|$ implies fewer random associations on average. This value was calculated for all species, including common and uncommon species.

We correlated the relationship between the metrics of dominance (abundance, basal area) and the metrics of spatial organization (number of segregations and mean $|SES|$) using Pearson's correlations.

RESULTS

At the community level and when considering only common species, random associations were the most

common type of association (Figure 1), especially in the low-intensity disturbance area (southern part of the LFDP). The percentage of species random associations ranged between 41% and 62% (Figure 2, left panel), well below the theoretical expectation of 85%. The number of random associations tended to decrease slightly over time in both forest disturbance areas (Figure 2a). The species association that combined horizontal aggregation and vertical segregation was the predominant non-random association (29%–44% vs. 5% expected by chance; Figure 2 left panel), especially in the high-intensity disturbance. This tended to increase slightly over time in both plot disturbance areas (Figure 2 left panel). Species horizontal segregation was less common (Figure 1), but was always above the theoretical expectation (8%–12% vs. 5% expected by chance; Figure 2 left panel). Species

three-dimensional aggregations were the least frequent type of associations (only 2.5%–3.8% vs. 5% expected by chance; Figure 2 left panel) and showed no strong variation between disturbance areas or over time.

Species differed in the degree to which they were involved in different types of associations and therefore they differed in their potential to interact or compete with other species. More abundant species (e.g., *P. acuminata*) and species that accumulated more basal area (e.g., *D. excelsa*), were clearly engaged in more associations involving horizontal or vertical segregation from other species. This was reflected by the total number of species horizontal/vertical segregations (Figure 3a,b) and the mean |SES| of all the associations in which the species was involved (Figure 3c,d). Some species such as *P. acuminata* and *G. guidonia* were involved in many associations of

horizontal segregation (Figure 2 right panel), but, for the most part, common species avoided other species more frequently in the vertical dimension than horizontally. Three-dimensional aggregation was infrequent and accounted for the minority of species–species associations; <5% of them, for most of the species (Figure 2 right panel).

DISCUSSION

Based on 71,000–390,000 non-zero pairwise crown overlaps at the individual level, we describe patterns of species co-occurrences and how these associations vary through time and disturbance levels in the LFDP (Puerto Rico). The spatial organization of the forest is clearly not random. Spatial organization increased through time as the forest recovered from

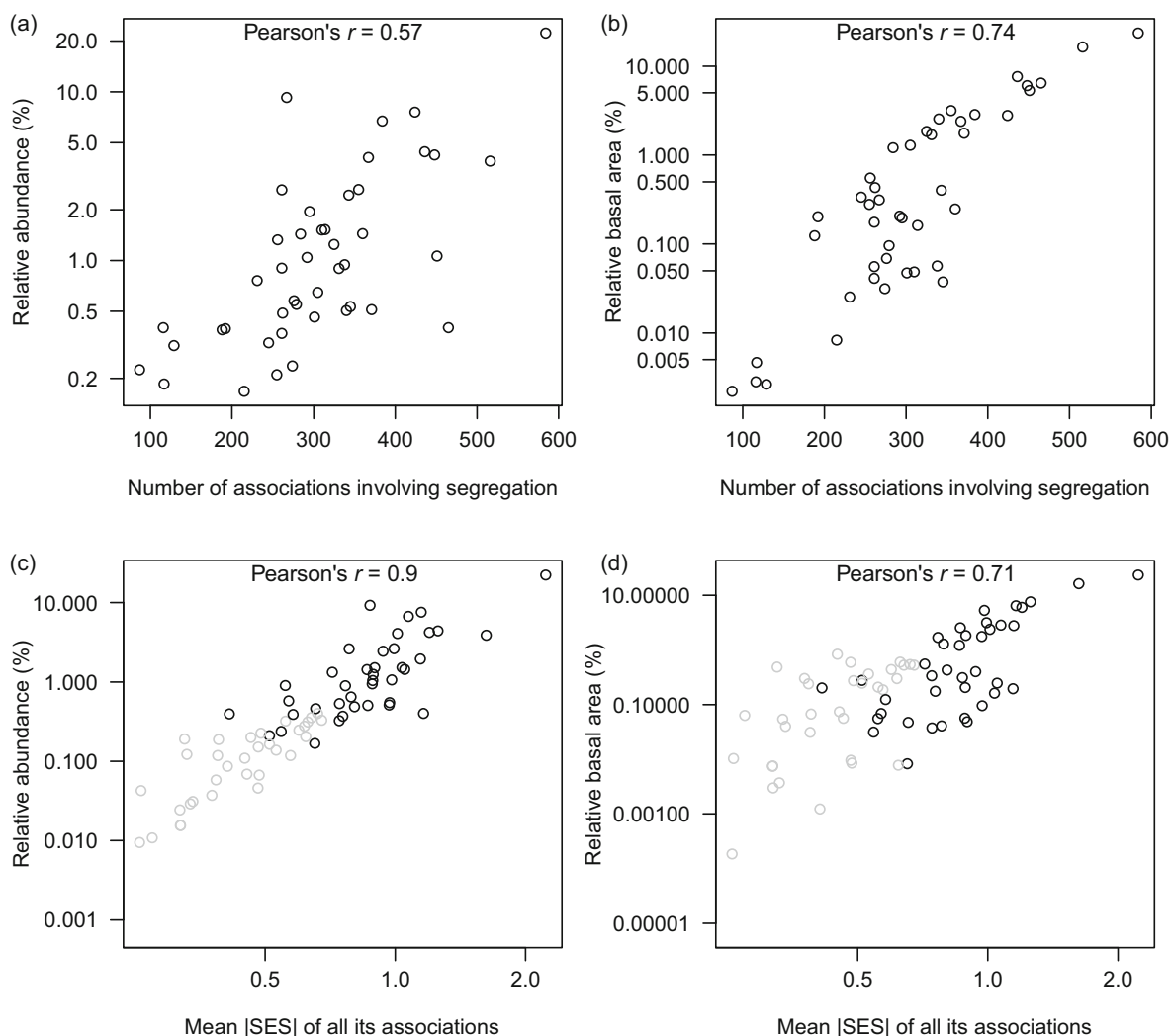


FIGURE 3 Relationship between overall relative abundance (%) and relative basal area (%) of each species and the total number (a, b) and the mean |SES| of associations (c, d) involving horizontal or vertical segregations in which each species was involved. Greater mean |SES| implies fewer random associations on average, further from that expected by chance. Rare species (gray dots) have been included in panels (c) and (d). SES, standardized effect sizes

land-use legacy effects and hurricane disturbances. Overall, species three-dimensional aggregation (a proxy for direct competition between similar species) is absent from Luquillo. Species that show more spatial segregation are generally more abundant and have greater basal area. Our results provide overwhelming evidence for species segregation in space, supporting the idea that co-occurrence of species in tropical forests is promoted by species-specific realized niches.

Horizontal segregation: A phenomenon at very small local scales

Many pairs of species segregated horizontally in the LFDP. This pattern can result from species–habitat associations along environmental gradients or fine-scale processes that result in spatial segregation at the few-meters scale. Horizontal segregation between species is inevitable when species show strong habitat preferences. Forests recovering after a disturbance are composed of distinct size/age cohorts, of variable heights, resulting in a patchy forest depicting gap versus non-gap habitats (Corlett, 1995). This results in a patchy distribution with species associated with different horizontal locations (e.g., habitat preference), and distinct age classes including pre-existing adult individuals and new recruits. Strong habitat preferences have been frequently reported at the 25- to 50-ha scale in tropical forests (Abiem et al., 2020; Harms et al., 2001; John et al., 2007; Lee et al., 2002; Lieberman et al., 1995; Russo et al., 2005). In the LFDP, however, species–habitat associations at these scales are not very apparent. The most obvious specialization in the Luquillo forest is between pioneers and non-pioneer species in young (previous land use and more hurricane damage) versus older portions of the forest (limited human disturbance and less hurricane damage) (Letcher et al., 2015). Buckley et al. (2016) found that the basal area of four common species (*C. arborea*, *C. schreberiana*, *D. excelsa*, *P. acuminata*) varied with the topography at the LFDP. However, Scalley et al. (2009) found no relationship between the distribution of the species and distance from streams in the LFDP. Our results, added to a limited body of unclear results related to species–habitat associations in Luquillo, suggest that in this forest the horizontal segregation of species happens predominantly at the fine, few-meters scale. This could result from at least three non-exclusive mechanisms:

1. Individuals segregate in space, regardless of their species identity. If all individuals were far from each other in non-random ways in the horizontal plane, such as in a regular tree plantation, then all species would also avoid each other. This seems to be the case of *P. acuminata*, the most abundant species at the

LFDP. This species is distributed with high abundance across the plot (Thompson et al., 2002) and yet it is systematically horizontally separated from several species including *D. excelsa* and *C. schreberiana*. *P. acuminata* germinates and establishes well in shade, while being able to grow fast at high light levels (Comita et al., 2009; Zimmerman & Covich, 2007). Recruitment into the ≥ 1 cm dbh class preferentially when there is high light (absence of other trees nearby) could explain the observed ability of *P. acuminata* to segregate horizontally from many other species.

2. Heterospecific negative density dependence: species “avoid” each other, forcing segregation at fine scales. This would require some biotic interaction similar to the interactions hypothesized to underlie conspecific density dependence. Dispersal limitation often results in a clumped distribution of younger individuals, whereas a segregation in space is expected for older plants as the result of density-dependence juvenile mortality (Condit et al., 2020) due to an increase in the attack by herbivores or natural enemies such as pest and pathogens (Connell, 1971; Janzen, 1970). Therefore, if two species share natural enemies, it is less likely that they will occupy the same horizontal locations, regardless of the habitat conditions surrounding them. Some studies conducted in other tropical forests have tested whether phylogenetically or chemically similar species share natural enemies (Paine et al., 2012; Shuai et al., 2014; Umaña et al., 2016), but whether this is related or not to horizontal segregation among species probably varies among forests and species and requires further investigation.
3. Species use different cryptic micro-habitats at the few-meters scale. In the absence of biotic interactions between species, abiotic filtering would be the driving force for spatial segregation. This seems to be the case with pioneer species that opportunistically occupy canopy gaps caused by fallen branches or the death of individual trees (Brokaw, 1985; Clark & Clark, 1992). More permanent micro-habitats (such as concavities with deeper soils, etc.) are possible, and certain species are often found in just such specific locations within the LFDP, such as *S. berteriana*, which is known to prefer wet and concave locations in Luquillo (Heartsill Scalley et al., 2010). In any case, it is clear from our results that two species can be abundant in the same general locations (e.g., the same hectare) while being horizontally segregated and not competing for horizontal resources directly.

Regardless of the mechanisms involved, by using a fine-scale tool (crown-to-crown overlap) we have

confirmed the existence of clear horizontal segregation between species in the LFDP. We hypothesize that many species in tropical forests will show similar small-scale organization that cannot be detected by analyses that focus on spatial organization at a larger scale (landscape, habitat, or hectares).

Although horizontal segregation is a clear pattern in the Luquillo forest, our results indicate that even more species were close to each other in a horizontal plane. This does not mean that species occurring close together in the same horizontal location must compete with each other. In fact, in the LFDP almost all species that co-occur in the horizontal plane avoid interacting in the vertical dimension.

Vertical segregation: The most common non-random association at the LFDP

For the first time, we have studied horizontal and vertical organization simultaneously in a tropical forest. We found that tree species in the LFDP tended to occupy the same horizontal locations but consistently avoided each other vertically. This was the most common form of non-random association between species and accounted for more than one-third of all possible associations among species. Our results highlight the role of vertical niche partitioning promoting the sympatric co-occurrence of species in tropical forests (Chazdon, 1988; Kitajima et al., 2005; Matsuo et al., 2021; Sterck & Bongers, 2001; Terborgh, 1985; Vázquez & Givnish, 1998) and contributes to the maintenance of local tree diversity across the tropics (Marselis et al., 2020).

Our results show an increase in species vertical organization over time, parallel to a decrease in the number of random associations. Although we found substantial variation between species (Zambrano et al., 2021), this trend was observed across both disturbance levels and consistently throughout the four censuses. This suggests that increased three-dimensional organization is one of the processes involved in succession and recovery from disturbance at the decadal scale. Forests recovering after a disturbance are often composed of distinct size/age cohorts, of different heights (Guariguata & Ostertag, 2001; Peña-Claros, 2003; Uhl & Jordan, 1984). The vertical stratification shown by cohorts of different heights may just reflect recruitment pulses (a form of temporal niche partitioning) and is not necessarily deterministic or trait-based.

As forests reach later successional stages and maturity, self-thinning reduces the predominance of some cohorts, gaps disappear as the canopy closes, the generally shorter lived pioneer species reach the end of their life and the gap

area becomes populated by more late-successional species, species recruitment pulses become less frequent, and communities converge toward a single species assemblage (Busing, 1995; Hendrickson, 1988; Roberts & Richardson, 1985; Sprugel, 1984). At this stage, species can occupy the forest strata according to their traits (i.e., *D. excelsa* will occupy the canopy, *P. acuminata* and small trees such as *Faramea occidentalis* or *Casearia sylvestris* the subcanopy, and small shrubs such as *Psychotria brachiata* and *Piper glabrescens* the understory).

An important finding in this study is that species three-dimensional aggregation was uncommon in both halves of the plot and in all censuses. Specifically, we consistently found a negligible amount of three-dimensional aggregation, always lower than 5% and therefore attributable to Type I error rate. Therefore, we conclude that three-dimensional aggregation is absent from the Luquillo forest, at least for the most common species. If three-dimensional aggregation is a proxy for direct competition, we must conclude that spatial sorting reduces the competition of common species in this forest. It is likely that the observed current absence of three-dimensional aggregation is the outcome of prior intense competition at the individual level during the development of the trees. Early life stages (seedlings, juveniles) are known to experience stronger competition than adult trees (Metz et al., 2010), but it is not clear if three-dimensional aggregation between species changes through ontogeny as a result of these competitive dynamics and self-thinning of cohorts of trees of similar size. Overall, our results provide strong support for the limiting similarity theory (MacArthur & Levins, 1967), with very few species showing preferences toward the same three-dimensional locations. In sum, in this forest, species avoid each other in the horizontal and/or the vertical dimensions.

Dominant species more consistently segregate in space than less dominant species

Our results show that species that most often segregate in space have more individuals and greater basal area. This trend cannot be due to statistical reasons, as in our analyses species abundances do not play any role in the assignment of the species association types. In fact, each and every one of our species should be present in 85% of random associations just by chance, regardless of its abundance. The relationship between dominance and the ability to segregate from others accords with previous studies from other forests reporting that abundant species show lower niche overlap than rare species (Mason et al., 2008) and that communities with less niche overlap

contain a greater number of more abundant species (Arellano et al., 2016). Rare species are often associated with transient dynamics, with stochastic colonization determining the occurrence of these species within a community (Holt & Gaines, 1992; Wissel & Zaslack, 1994) that could result in a lack of spatial organization. It is likely that species segregation in three-dimensional space has adaptive implications by allowing different species with a variety of functional traits to maintain successful populations in a forest.

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CONFLICT OF INTEREST

There are no competing interests to declare.

AUTHOR CONTRIBUTIONS

This study was conceived by Jenny Zambrano, William F. Fagan and Nathan G. Swenson. Jenny Zambrano and Gabriel Arellano conducted the analyses and wrote the initial manuscript. Jill Thompson managed forest data collection. William F. Fagan, Nathan G. Swenson, Phillip P. A. Staniczenko and Jill Thompson contributed to revisions.

DATA AVAILABILITY STATEMENT

Data (Zimmerman, 2018) are available from the Environmental Data Initiative at <https://doi.org/10.6073/pasta/6061298660b4ceb806ba49805a950646>. Disturbance-related and time-related changes in the direction of the different types of species associations were assessed visually, with figures (Zambrano et al., 2021) provided in Zenodo at: <https://doi.org/10.5281/zenodo.5148761>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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