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Recruitment limitation in three large-seeded plant species in a tropical moist forest

Carol X. Garzon-Lopez[1,2] [ID] | Eduardo Medina Barcenas[3] | Alejandro Ordoñez[4,5] | Patrick A. Jansen[1,6,7] | Stephanie A. Bohlman[6,8] | Han Olff[1]

[1]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands

[2]Ecology and plant physiology group (Ecofiv), Universidad de los Andes, Bogota, Colombia

[3]School of Environment, Earth & Ecosystem Sciences, The Open University, Milton Keynes, UK

[4]Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus C, Denmark

[5]Department of Bioscience, Centre for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University, Aarhus C, Denmark

[6]Smithsonian Tropical Research Institute, Ancon, Panama

[7]Department of Environmental Sciences, Wageningen University, Wageningen, The Netherlands

[8]School of Forest, Fisheries and Geomatics Sciences, University of Florida, Gainesville, Florida, USA

Correspondence
Carol Garzon-Lopez, Knowledge Infrastructures, Campus Fryslân, University of Groningen, Leeuwarden, The Netherlands.
Email: c.x.garzon@gmail.com

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Abstract

Recruitment limitation—the failure of a species to establish recruits at an available site—is a potential determinant of plant communities' structure, causing local communities to be a limited subset of the regional species pool. Recruitment limitation results from three mechanisms: (i) lack of seed sources (i.e., source limitation), (ii) failure of available seeds to reach recruitment sites (i.e., dispersal limitation), and (iii) failure of arrived seeds to establish at a location (i.e., establishment limitation). Here, we evaluated the relative importance of these mechanisms in three co-occurring tree species (*Dipteryx oleifera*, *Attalea butyracea*, and *Astrocaryum standleyanum*) that share seed dispersers/predators. The study was set up on Barro Colorado Island (Panama) at 62 one-ha sites with varying tree densities. Source limitation was estimated as the proportion of sites that would be reached by seeds if seeds were distributed uniformly. Dispersal limitation was estimated from the number of sites with seeds in the soil bank. Establishment limitation was evaluated by measuring germination and 1-year survival in seed addition experiments. The effect of conspecific and heterospecific densities on the mechanisms was evaluated at three spatial scales (1, 5, and 9 ha). For all species, seed predation was the most important recruitment component (~80% decrease in seed survival). Establishment varied among species and was affected by conspecific and heterospecific species densities across spatial scales. Given that species identity, distribution, and seed dispersal/predation affect recruitment at multiple scales, multiscale studies are required to understand how recruitment limitation determines community structure in tropical forests.

Abstract in Spanish is available with online material.

KEYWORDS
Astrocaryum standleyanum, *Attalea butyracea*, *Dipteryx oleifera*, establishment limitation, Panama, recruitment limitation, seed limitation, tropical forests

1 | INTRODUCTION

How do stochastic processes interact with deterministic processes to structure tropical forest communities? Identifying the strength of stochastic and deterministic processes causing and maintaining the dynamics in tropical forests has been at the core of more than four decades of ecological studies. Such studies have been primarily focused on two perspectives: (i) how deterministic factors, such as habitat characteristics (e.g., geology, temperature and topography; Bohlman et al., 2008), explain the variation in species composition (Burton & Bazzaz, 1991; Jones et al., 2008; Quero et al., 2011; Svenning, 2001), and (ii) to what extent do stochastic factors, such as seed dispersal and asymmetric resource competition (Hurtt & Pacala, 1995; Wright et al., 2005), dilute the community structure patterns expected under a purely deterministic setting (Alcántara et al., 2018; Wang et al., 2016).

The interplay between stochastic and deterministic processes in shaping species distributions and coexistence is especially prominent at the early stages of plant recruitment. At these stages, stochastic processes, such as seed dispersal, limit the arrival of seeds to suitable locations and affect seedling establishment. Such interplay can arise from biotic factors (e.g., animal dispersal vectors, pre- or post-dispersal seed predation, competition for resources, pathogens, or herbivory), abiotic conditions (e.g., dispersal by wind or water, seedling desiccation), or a combination of both (Beckman & Rogers, 2013; Grace & Wetzel, 1981; Schupp et al., 2010). The resulting failure of particular plant species present in the regional species pool to establish in the local community is known as recruitment limitation (Nathan & Muller-Landau, 2000; Schupp et al., 2002).

Recruitment limitation of tropical forest trees can be decomposed into three potentially limiting steps with different mechanisms involved at each stage. First, there might be not enough seeds available to reach all sites (i.e., source limitation sensu Schupp et al., 2002) due to limited parent tree abundance, lack of pollinators, low seed quantity (Goszka & Snell, 2020; Navarro-Cerrillo et al., 2020), or pre-dispersal seed predation (Clark et al., 1998; Jones & Comita, 2010; Maron & Crone, 2006). Second, the local community may not receive propagules of all species present in the region (i.e., dispersal or dissemination limitation sensu Schupp et al., 2002). One example of this mechanism is the absence of suitable biotic (zoochorous birds, mammals, bats) or abiotic (wind, water) dispersal vectors (Dalling et al., 2002; Forget, 1993; Garcia et al., 2005). Third, when viable seeds reach a site, the local biotic and abiotic conditions may not be suitable for the species to successfully transition from seed to established sapling (i.e., establishment limitation sensu Schupp et al., 2002). Such unsuccessful transitions could be due to post-dispersal seed predation (Galvez et al., 2009), resource availability and competition (Paine et al., 2008; Tilman, 1982), herbivory (DeMattia et al., 2004, 2006; Muller-Landau et al., 2008), or pathogens (Hersh et al., 2012; Mangan et al., 2010).

These limiting mechanisms in tropical forest recruitment have been extensively studied. Some studies have focused on seed dispersal, predation, competition, and herbivory in determining species recruitment (Augspurger & Kitajima, 1992; Paine & Beck, 2007; Rogers et al., 2019; Terborgh et al., 1993). Other studies have analyzed how species-specific environmental requirements (Ceccon et al., 2003; Huante et al., 1998; Zalamea et al., 2016), or the correlation between plant traits and the environment, control plant establishment (Muñoz et al., 2017). Other studies have focused on the role of negative density-dependent processes in controlling species diversity (Marques & Burslem, 2015; Zhu et al., 2015), mainly inspired by the Janzen–Connell hypothesis (i.e., a disproportional offspring mortality close to parents; Connell, 1978; Janzen, 1970). The outcome of these studies varies in the strength of deterministic and stochastic processes driving species recruitment.

The spatial processes involved in stochastic and deterministic processes (Chase, 2014; Garzon-Lopez et al., 2014) during plant recruitment have been recognized as crucial determinants of community dynamics at multiple scales (Clark et al., 1998; Nathan & Muller-Landau, 2000; Schupp, 1992; Schupp & Fuentes, 1995). However, very few studies have explicitly considered spatial scale in their analyses. Most studies focus on individuals (Garcia et al., 2005; Terborgh, 2020) even though the processes at the individual level might not reflect the patterns at the community scale (Schupp, 1992). Moreover, very few studies (Clark et al., 1998; Schupp, 1992) have attempted to simultaneously evaluate the relative importance of two or more of the main types of recruitment limitation across multiple species with shared predators and dispersers, over a large extent (>50 ha) and at multiple spatial scales.

Additionally, some studies have explored the seed-to-seedling transition, focusing on the effect of conspecific and heterospecific negative density dependence on seed/seedling abundance and diversity (Johnson et al., 2017; Umaña et al., 2016), exploring the importance of pathogens and insect herbivores driving survival (Bagchi et al., 2014; Freckleton & Lewis, 2006; Hersh et al., 2012), or examining the relative importance of dispersal and establishment limitation using long-term seed-fall data and monitoring seedling plots (Norden et al., 2009). While the outcomes of these studies have demonstrated the importance of negative density dependence, species identity, and habitat properties on seed-to-seedling transitions, the research has been performed on data from single plots, which predetermines the spatial scale for which negative density dependence effects across species can be observed. Assuming that all species are affected by deterministic and stochastic factors at the same scale limits our ability to assess the relevance of each component on plant recruitment. Therefore, the question remains about the relative importance of the stochastic and deterministic components of recruitment limitation for tropical forest trees in a multiscale setting and at the community level.

Here, we simultaneously study the relative importance of seed limitation (i.e., source limitation, dispersal limitation, and predation) and establishment limitation (i.e., germination limitation and 1-year survival). For this, we focused on three large-seeded, tropical forest canopy tree species (*Dipteryx oleifera*, *Attalea butyracea*, and *Astrocaryum standleyanum*) that co-occur at Barro Colorado Island (BCI), Panama, and share several mammalian seed dispersers and

predators. To assess the full range of possible adult tree densities, we individually mapped the island-wide distribution for the three focal species using a high-resolution georeferenced mosaic of aerial photographs (Garzon-Lopez et al., 2013). We then selected 62 one-ha sites across the island with varying reproductive adult densities (Figure 1). At each site, seed limitation was estimated as the proportion of sites not receiving seeds. Source limitation was estimated as the proportion of sites seeds would reach if they were dispersed uniformly. We then estimated dispersal limitation using a soil bank survey performed in ten 1-m^2 quadrats at each site where we measured seed density. The effect of seed predation was estimated as the number of intact seeds at each site. Since, from the soil bank samples, we could not determine whether the predation took place at the pre-dispersal (i.e., seed limitation) or post-dispersal (i.e., establishment limitation) stage, it was placed as a separate component of recruitment belonging to both limitation categories. Finally, establishment limitation was studied through a seed addition field experiment at each site, where we measured seed germination and seedling survival. The seed addition field experiment allowed us to estimate the relative importance of this component of recruitment limitation at varying source limitation levels and spatial scales, including analyzing the effect of different habitat properties on the

establishment (Figure 1). We also examined the importance of the initial adult distribution for the realized spatial distribution of saplings, which provides a direct test of the patterns expected from the Janzen–Connell hypothesis at a larger scale than previously studied.

2 | METHODS

2.1 | Study site and species

Barro Colorado Island (hereafter BCI), located in Panama (9°9′N, 79°51′W), is a 1560-ha tropical moist forest island. The island was isolated from the surrounding mainland between 1910 and 1914 when the Chagres River was dammed to form the central part of the Panama Canal (Leigh, 1999). The island has a dry season starting in December and ending in April or early May. BCI lies at the midpoint of a gradient between the deciduous dry forests of the Pacific shore, with an annual rainfall of 1800 mm, and the Caribbean side's rain forests with an annual rainfall of 3000 mm (Leigh, 1999). The forest on the northeast half of the BCI is secondary forest that has regrown after widespread cutting and clearing late in the nineteenth century. The other half of the island has received little or no
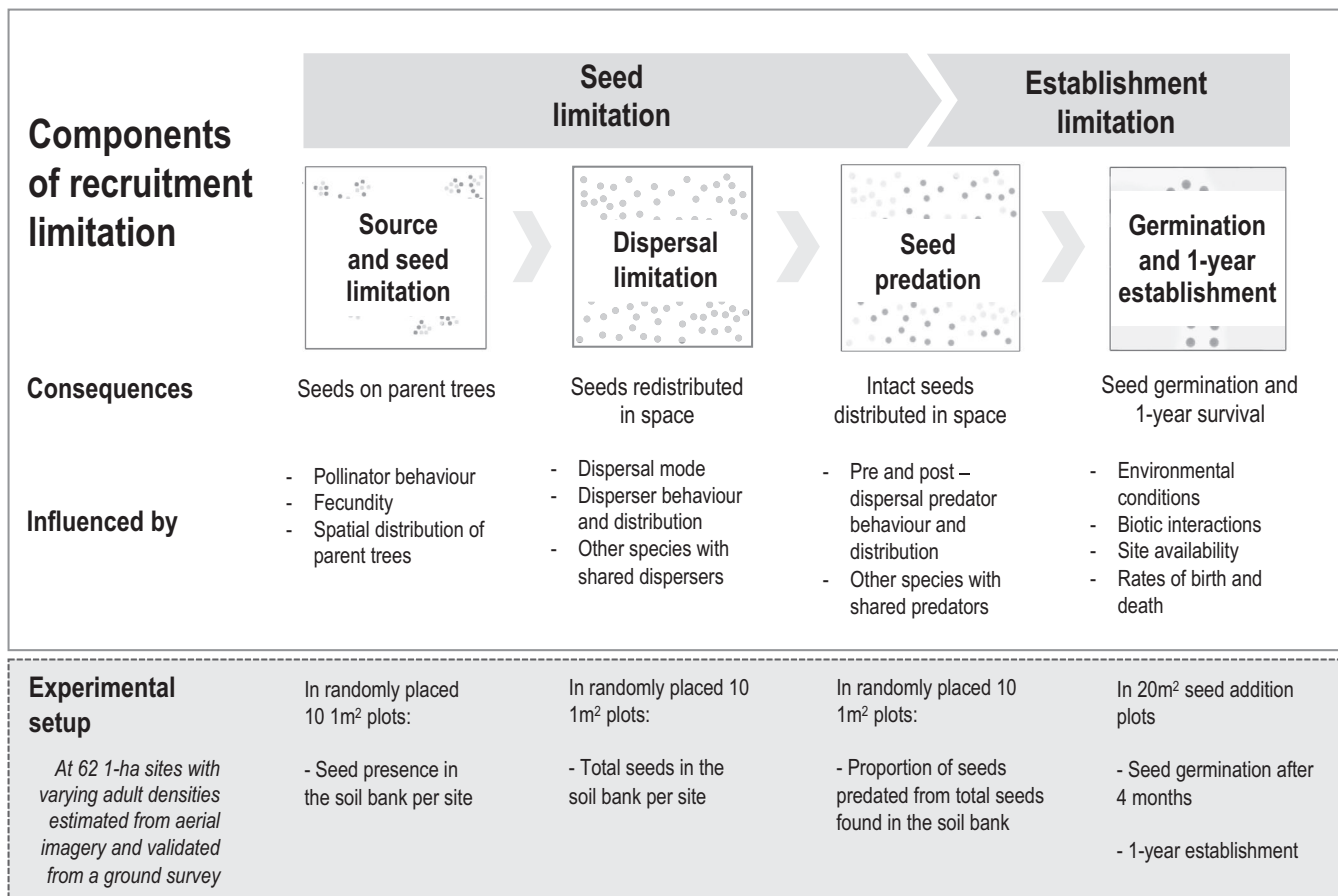
FIGURE 1 Diagram of the components of recruitment limitation evaluated in this study and the experimental approach used to evaluate each component. Since we cannot distinguish pre-dispersal (seed limitation) from post-dispersal (establishment limitation) seed predation events, seed predation was placed as a component shared by seed and establishment limitation

disturbance. The island was declared a reserve in 1923 and has been administered by the Smithsonian Institution since 1946. The island consists of two main geologic formations dating from the Oligocene, known as Bohio and Caimito. The top of the island consists of a non-sedimentary Andesite lava (Baillie et al., 2007).

We selected three species (*Dipteryx oleifera*, *Attalea butyra-cea*, and *Astrocaryum standleyanum*) that produce large seeds that are dispersed and depredated by rodents. Island-wide distribution maps of these species were made in a previous study (Garzon-Lopez et al., 2013) by digitizing the location of canopy-statured individuals on georeferenced high-resolution aerial photographs. This digitization captures the reproductive individuals (Jansen et al., 2008). We validated generated maps using ground data from the 50-ha forest dynamic plot (Garzon-Lopez et al., 2013). The fruits of the selected species constitute a critical component in the diet of many generalist mammals and a key element in the life cycle of four specialist beetle species (Forget et al., 1994; Johnson et al., 1995; Smythe, 1989). The three study species share dispersers and predators which affects their seed survival (Garzon-Lopez et al., 2015).

Dipteryx oleifera (hereafter *Dipteryx*) is an emergent tree that grows slowly, reaching 40–50 m in height and a diameter between 1 and 1.6 m (Fournier, 2002). This species produces approximately 5-cm fruits (Caillaud et al., 2010) that reach maturation between January and April. The fruit is fleshy and has one single seed covered with a stony endocarp. It is dispersed initially by frugivorous bats and monkeys and secondarily by scatter-hoarding rodents (Forget & Milleron, 1991). Known seed predators include peccaries, rodents, squirrels, and the great green macaw (Flores, 1992).

The arborescent palm *Attalea butyracea* (hereafter *Attalea*) reaches 30 m in height and 30–60 cm diameter. It produces one to three infructescences per year between May and July (Forget et al., 1994). The seeds are dispersed by scatter-hoarding rodents and monkeys and predated by rodents and peccaries. The fleshy fruit contains one or two seeds protected by a stony exocarp (Forget et al., 1994). The specialized beetles *Speciomerus giganteus* and *Pachymerus cardo* depend on the inflorescence and the seed to complete their life cycle. These beetles' larvae drill a hole in the exocarp to develop inside while feeding on the endosperm until larval development is completed. Then, the larvae drill an exit hole, leaving a conspicuous exit mark on the exocarp (Bradford & Smith, 1977).

Astrocaryum standleyanum (hereafter *Astrocaryum*) is a slow-growing palm characterized by long black spines covering the trunk, reaching over 20 m high and 30 cm diameter (Pedersen, 1994). It produces three to six infructescences with 300–800 fruits (per infructescence) that reach maturation between March and June when they are dispersed by scatter-hoarding rodents, monkeys, and some birds (Smythe, 1989). The fleshy fruit contains a large seed covered by a hard exocarp. The sweet pulp is eaten by a wide variety of mammals (Smythe, 1989) including scatter-hoarding rodents that disperse the seeds. Only a few mammals, such as peccaries (*Tayassu* sp.), predate the seed by cracking open the endocarp. Beetles of the species *Pachymerus bactris* and *Coccotrypes* sp. depend on the seed to complete their life cycle; larvae of these beetles drill a hole into

the endocarp and feed from the endosperm until larval development is completed (Johnson et al., 1995).

2.2 | Sampling design

We estimated recruitment limitation (*sensu* Schupp et al., 2002) across 62 sites in BCI with varying adult tree densities. Site selection was based on a range of tree densities from 0 to the maximum density found in a 1-ha site per species. Since recruitment is affected by the scale at which the sampling is performed (Muller-Landau et al., 2002), spatial scale for the estimation of each of the components of recruitment limitation was established based on the scale of the processes. That is, to assess adult densities we selected three spatial scales (1 ha, 5 ha, and 9 ha) to ensure capturing the scale at which this variable affects recruitment. In the case of seed density and dispersal, ten 1-m^2 plots randomly placed across the 1-ha sites were selected because this scale captures sampling heterogeneity in seed rain (Muller-Landau et al., 2002). Finally, seed germination and 1-year survival were estimated from a 20-m^2 seed addition plot placed in the center of the 1-ha site. The spatial scale for the seed addition plots was selected to ensure at least 1-meter distance among seedlings. At each site, we measured reproductive adult tree density, seed density, seed predation rates, seed germination, and seedling predation as follows (Figure 1):

a. *Tree density*: Tree density was initially estimated from distribution maps of the tree species obtained from high-resolution aerial photographs (Garzon-Lopez et al., 2013). High and low tree density areas for each species were determined by placing a 1-ha grid over the island and estimating the number of individuals per grid cell. We selected grid cells within the lower 25% (low density) and upper 75% (high density) tree density percentiles.

For each species, a total of twenty 1-ha sites at each density range were selected. When possible, the same site was used for various species (22 sites of 2 species and 15 sites of 3 species) so that a total of 62 sites across the entire island were surveyed. The experiments were performed between March and June of 2009 to 2011. Adult density was measured as parent tree density, which was determined using aerial photographs and validated using ground surveys that recorded all adults' GPS positions (i.e., reproductive individuals with current or old infructescences) of the tree species studied.

b. *Seed density and predation level*: Seed density and predation level were measured by collecting endocarps at 10 points selected randomly within each 1-ha site. At each point, we placed a 1-m^2 quadrat and searched for all endocarps in the soil up to 5 cm depth. All endocarps were examined to determine predation events, recording predation status (i.e., predated or intact; Garzon-Lopez et al., 2015; Silvius, 2002). Endocarps of the study species can remain in the soil up to 2 years after dispersal; therefore, the sample obtained summarizes predation that may have happened over approximately two years (methods described in Wright & Duber, 2001). Older endocarps start degrading after

TABLE 1 Environmental variables and levels within each variable

Variable	Levels	Description	Source
Soil type	Ferrasol	FAO soil types	Barthold et al. (2008)
	Cambisol		
	Planosol		
Forest age	Young forest	Regenerated after 1880	Enders (1935)
	Old growth	Regenerated before 1880	
Topography	Shore	<150 m to shore	Johnson and Stallard (1989)
	Flat	>150 m to shore; <5° slope; <63 m elevation	
	Ridge	>150 m to shore; <5° slope; >63 m elevation	
	Shallow	>150 m to shore; 5–10° slope	
	Steep	>150 m to shore; >10° slope	

two years, and identification is more difficult; therefore, only easily identifiable endocarps were included in the analyses. The seeds from the 10 one-m^2 quadrats were added to obtain one measurement per 1-ha site.

c. *Seedling emergence*: Seed germination and seedling survival were assessed by setting up a seed addition experiment at the center of each 1-ha site. To do so, we established 1 addition plot of 20 m^2 within each 1-ha site in which 25 seeds were buried (1 cm depth), each one protected with an iron mesh (50 × 50 cm, 13 mm square aperture) secured to the ground using 15-cm long iron staples to prevent seed predation. Given the limitation of a mesh size that would stop predators while allowing germination, we could only exclude predators bigger than 1 cm^2. Twenty-five seeds were buried at approximately 1 m distance from each other per 20-m^2 plot. Germination and predation were recorded 4 and 12 months after seed addition.

2.3 | Data analysis

Seed, source, dispersal, and establishment limitation were calculated for three groups of sites—high density, low density, and all sites—using the equations in Muller-Landau et al. (2002). Muller-Landau et al. (2002) consider both the arrival/survival of individuals at each stage of limitation and the proportion of seeds/seedlings at each site. Seed limitation was calculated from Equation (1) and is defined as the number of sites (i.e., each site consists of 10 one-m^2 quadrats) not receiving seeds (a) from the total number of sites (*n*).

$$\text{Seed limitation} = 1 - \frac{a}{n} \qquad (1)$$

Source limitation was calculated from Equation (2) following the stochastic approach of Muller-Landau et al. (2002), which uses a Poisson seed rain with random distribution:

$$\text{Source limitation} = \exp\left(-\frac{s}{n}\right) \qquad (2)$$

where *s* is the total number of seeds found at all the sites and *n* is the total number of sites surveyed (i.e., with and without seeds). Dispersal limitation was quantified by comparing the number of sites receiving seeds with the total number of sites (equation 3):

$$\text{Dispersal limitation} = 1 \left(\frac{\frac{a}{n}}{1 - \text{seed limitation}} \right) \qquad (3)$$

where *a* represents the number of sites that received seeds and *n* represents the total number of sites. The effect of seed predation on the number of viable seeds at each site was calculated in a manner similar to how dispersal limitation was calculated, but instead of calculating the number of sites receiving seeds, we calculated the number of sites with intact seeds.

Finally, our assessment of germination and 1-year establishment limitation was independent from our estimation of seed or dispersal limitation, as seeds were added and their survival followed. Germination and establishment limitation were measured as germination 4 months after seed addition (germination limitation) and survival 1 year after seed addition (1-year survival) and was calculated as the proportion of sites (i.e., each site consists of the 20-m^2 grid within each 1-ha site) where a seedling emerged (*r*) to the total of sites with seeds added (*n*) (equation 4):

$$\text{Germination limitation} = 1 - \left(\frac{r}{n}\right) \qquad (4)$$

As site characteristics can affect each stage of recruitment limitation, we evaluated how local environmental properties affected seed dispersal, seed predation, seed germination, and 1-year survival. Evaluated environmental properties included: (i) forest age (old or secondary forest) (Svenning et al., 2004), (ii) soil type (i.e., Ferrasol, Cambisol, and Planosol) derived from a soil map of Barro Colorado Island (Barthold et al., 2008), and (iii) topography, defined as the combination of slope, elevation, and distance to shore (i.e., shore, flat, ridge, shallow, and steep; Table 1, Figure S1). Additionally, since previous studies have shown an indirect effect of heterospecific

FIGURE 2 Scatterplot of variation for each component of limitation (dispersed seeds, seedlings, 1-year saplings) in sites with increasing tree density. The y-axis shows the proportion of seeds for each of the species per stage. Points correspond to each site. Solid lines represent the fitted logistic regression models. The shaded area around the solid line corresponds to the 95% standard error
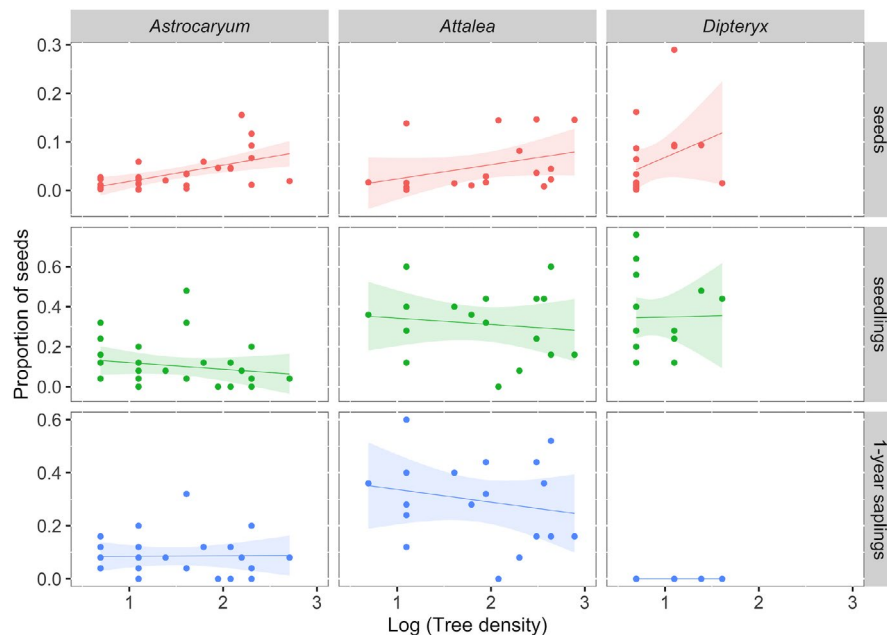
adults/seeds on seed survival via shared predators' preferences (Garzon-Lopez et al., 2015; Umaña et al., 2016), we included in the analysis the effect of conspecific and heterospecific tree densities on focal species recruitment. Since we do not know the spatial scale at which tree density interacts with seedling survival, we quantified conspecific and heterospecific tree densities at three spatial scales (1 ha, 5 ha, and 9 ha). Heterospecific tree density was determined only from the three species used in this study and was defined as the two non-focal species compared with the focal species (e.g., conspecific) in each model.

Finally, we quantified spatial autocorrelation calculating Moran's I-test (Cliff & Ord, 1981), which demonstrated a high correlation among sites and thus the need to apply a statistical method that accounts for such spatial association. Therefore, we fitted a residual autocovariate model (Crase et al., 2012) which includes an autocovariate term representing the residuals' spatial autocorrelation. This autocovariate term was implemented as a spatial weight matrix, representing the spatial relationship between observations, which quantified patterns in the response variable related to the values in the neighboring sites (cf. Crase et al., 2012; Dormann et al., 2007).

Statistical analyses were performed using a model averaging approach. We fitted a global model (i.e., conspecific seed density + conspecific adult density at 1 ha + conspecific adult density at 5 ha + conspecific adult density at 9 ha + heterospecific seed density + heterospecific adult density at 1 ha + heterospecific adult density at 5 ha + heterospecific adult density at 9 ha + soil type + forest age + topography + spatial) taking each of the recruitment stages as the response variable (i.e., seed dispersal, seed predation, seed germination, and 1-year seed survival) and calculated the Akaike weight (AICwv) across all fitted models for each variable v (Burnham & Anderson, 2002). An AICwv value can be interpreted as a normalized relative likelihood representing the fit of the model, facilitating model comparison and model averaging. Thus, to estimate relative

importance of each explanatory variable, we summed the AICwv across all models in which the variable occurred. Higher AICwv values indicate a higher the importance of that variable relative to the other variables. Such "model averaging" allows assessments to be based on multiple models, avoiding problems with colinearity among predictors, as observed in the case of 5 and 9 ha tree densities, as well as bias in parameter estimation that may occur selecting a single best model (Burnham & Anderson, 2002, Figure S2). The set of models with a gamma value higher than four was selected for each analysis to approximate the true model (Burnham & Anderson, 2002). Environmental variables were estimated as presented in Table 1. All the analyses were performed in R software (R Core Team, 2020) using packages sf (Pebesma, 2018) for data preparation; ggplot2 (Wickham, 2016) for the figures; and MuMIn (Bartoń, 2020), arm (Gelman & Su, 2020), and spdep (Bivand et al., 2013) for model averaging.

3 | RESULTS

A total of 769 adults of the study species were ground-censused, with densities ranging between 0 to a maximum of 56 individual adult trees/ha of *Astrocaryum*, 39 trees/ha of *Attalea*, and 8 trees/ha of *Dipteryx*. A total of 5790 endocarps of the three species were collected across all sites. Densities ranged between 0 to 139 endocarps/10 m^2 of *Astrocaryum*, 196 endocarps/10 m^2 of *Attalea*, and 219 endocarps/10 m^2 of *Dipteryx*. Of the 25 seeds per species per 20 m^2 added to each site, 10% (SE = 2.1) of *Astrocaryum*, 28% (SE = 4.1) of *Attalea*, and 34.7% (SE = 4.1) of *Dipteryx* germinated (Figure 2).

Source limitation was zero across all sites ranging from high and low tree densities, but there was some variation among species. At least one seed was found at 77%, 82%, and 96.6% of the sites for *Attalea*, *Dipteryx*, and *Astrocaryum*, respectively. Dispersal

TABLE 2 Source, seed and dispersal limitation, seed predation, and establishment limitation estimation (based on Equations 1–4) with percentages and total counts for all species grouped in all sites, high tree density sites, and low tree density sites

	Source limitation		Seed limitation	Dispersal limitation		Seed predation		Germination and establishment limitation			
Tree species		Total number of trees (1-ha site)	Seed limitation	Total number of seeds found (10 m²)	Dispersal limitation	% seeds escaped predation	Dispersal limitation after predation	% seeds germinated (4 months)	Germination limitation (4 months)	% seedling 1-year established	Establishment limitation (1 year)
All sites	Astrocaryum	3.2 (0.6)	0.033	26.9 (5.2)	0.021	3.9 (1.5)	0.583	10.5 (2.1)	0.167	8.5 (1.6)	0.167
	Attalea	8.3 (2.1)	0.230	48.5 (11.3)	0.176	9.1 (2.3)	0.412	28.6 (4.1)	0.059	26.8 (3.9)	0.059
	Dipteryx	0.4 (0.2)	0.181	41.6 (13.1)	0.194	2.1 (0.7)	0.516	34.7 (4.1)	0	0	1
Low tree density sites	Astrocaryum	1.9 (0.4)	0.042	18.2 (2.9)	0.042	4.4 (1.9)	0.667	11.5 (2.6)	0.208	8.9 (1.9)	0.208
	Attalea	2.5 (0.6)	0.353	35.1 (15.3)	0.353	10.3 (3.7)	0.588	32.4 (4.8)	0.059	31.2 (4.8)	0.059
	Dipteryx	0	0.133	24.1 (9.7)	0.133	1.2 (0.7)	0.733	36 (5.2)	0	0	1
High tree density sites	Astrocaryum	8.7 (0.9)	0	60 (17.8)	0	1.6 (1.0)	0.500	6.7 (2.8)	0.167	7.3 (2.8)	0.167
	Attalea	15.4 (3.2)	0	64.9 (16.1)	0	7.6 (2.6)	0.222	24 (7.0)	0.111	21.3 (6.1)	0.111
	Dipteryx	1.6 (0.4)	0.285	87.2 (34.4)	0.286	4.5 (1.6)	0.286	31.2 (6.6)	0	0	1

limitationvwas higher at low tree density sites than at high tree density sites for *Attalea* and *Astrocaryum*. In the case of *Dipteryx*, dispersal limitation did not vary with tree density (Table 2). Seed predation reduced the number of available seeds for further stages of establishment by 96.7% (SE = 1.55) for *Astrocaryum*, 92.5% (SE = 2.31) for *Attalea*, and 97.7% (SE = 0.72) for *Dipteryx*. Germination limitation was low (<0.25) for all species, and the differences between high and low tree density were not significant. After 1 year, seedling limitation remained almost unchanged for *Attalea* and *Astrocayrum*, but for *Dipteryx*, all the seedlings had been killed (Table 2).

3.1 | Environmental and neighborhood correlates of recruitment limitation

Models including environmental properties explained little of the variation in seed density for all the species. Interestingly, models including heterospecific densities at varying spatial scales better explained seedling survival than models that did not include heterospecific densities. At the 1-ha tree density scale, *Attalea* seed density was negatively correlated with heterospecific densities, while at the 5-ha scale, *Astrocaryum* and *Dipteryx* seed densities were positively correlated with heterospecific adult densities. No conspecific adult densities at any scale had an effect on seed densities (Figure 3).

Models including environmental factors explained variation in seed predation, especially for *Astrocaryum*, where seed predation and topography (i.e., ridge, steep, and flat areas) showed a negative correlation. Conversely, in the case of *Attalea*, both conspecific and heterospecific seed densities positively affected seed predation.

In the case of seed germination and 1-year survival, a model including environmental properties explained little of the variation in *Attalea* and *Dipteryx* establishment. For *Astrocaryum*, seed germination and 1-year survival had a significant negative correlation with forest age. The spatial component (*spatial*) had high relative importance only for *Attalea*. Interestingly, models including heterospecific adult densities at varying spatial scales better explained seedling survival than models that did not include heterospecific densities. At the 5-ha tree density scale, *Astrocaryum* germination was positively correlated with heterospecific densities, while the correlation was negative for *Dipteryx*. Heterospecific seed densities were negatively correlated with *Attalea* germination and 1-year survival (Figure 3).

4 | DISCUSSION

Using a combination of field experiments and aerial observations that allow for the direct and independent quantification of each of the recruitment stages at the landscape scale, we find evidence that all three stages of recruitment of *Dipteryx*, *Astrocaryum*, and *Attalea* are primarily affected by conspecific and heterospecific tree and seed densities. However, the magnitude and direction of this effect depend on the recruitment component and the combination of spatial scale and species identity. Specifically, we found that
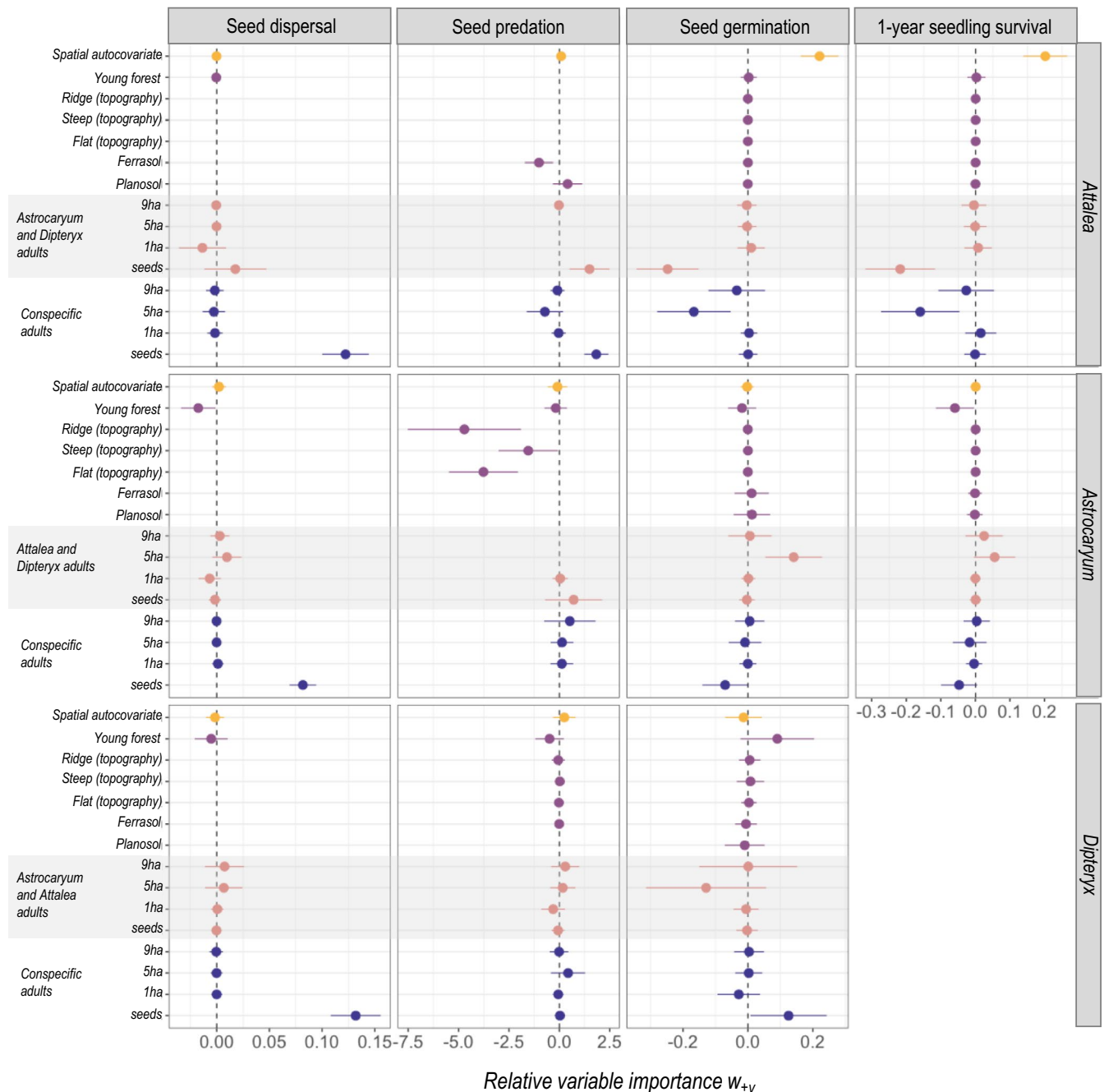
FIGURE 3 Model-averaged effect sizes of the density of conspecific and heterospecific seeds and trees quantified at three spatial scales, environmental properties (topography, soil type, and forest age) and the spatial autocovariate variables modeled against seed density, seed predation, seed germination after 4 months, and 1-year seedling survival for three large-seeded tree species. The coefficients correspond to the relative variable importance (i.e., w_{+v}), and the bars correspond to the 95% confidence intervals. The model means are represented by the dashed vertical line. The variables missing in the figure were not included due to their low correlation with the response variable. See Table S1 for model description

models including conspecific and heterospecific adult and seed densities explained all stages of plant recruitment better than models based on conspecific densities alone. Moreover, we found that the effect of both conspecific and heterospecific tree densities on all plant recruitment stages depends on spatial scale. Finally, we found that environmental properties such as topography and soil type did not play a relevant role in the germination or 1-year survival stages

as expected. However, topography and forest age affected seed predation.

In our study, plant recruitment was not limited by seeds failing to reach available sites, as seeds of all species were present in the seed bank of 80% of the sites. Yet, only 40% of sites had adult trees of all the species (85% had *Astrocaryum*, 40% *Dipteryx*, and 67% *Attalea*). Thus, the spatial distribution of seeds could have been controlled by

dispersal (e.g., we found seeds in areas with no adult trees), which can be a critical factor allowing seeds to reach areas of low adult densities. This outcome is in concordance with previous studies showing the importance of dispersal in allowing seeds to arrive at new sites (Beckman & Rogers, 2013; Clark et al., 2007; Nathan & Muller-Landau, 2000; Terborgh et al., 2014, 2019), thereby shaping community structure.

Seed predation is also an important filter in dispersal limitation (Turnbull et al., 2000). Our study confirmed this, as it was the most important filter determining the observed distribution pattern of viable seeds (more than the 80% of seeds in the seed bank were predated and thus would fail to germinate). Seed predation was an important cause of seed mortality, becoming a critical limiting factor shaping the spatial distribution and subsequent establishment rates of viable seeds. Seed predation is a spatial process that depends on granivores' spatial distribution, which in turn depends on the spatial arrangement of their food, shelter, and predators (Brown, 1999; Mayor et al., 2009) and environmental properties, such as topography, influencing these resources. Seed predation appears to be a dynamic determinant of seed distribution and might only be surpassed in importance by dispersal, particularly in cases where seed production is high enough to match seed predation rates (Crawley, 2000; Garzon-Lopez et al., 2015; Orrock et al., 2006).

Once seeds reached their final location, site abiotic and biotic conditions will control the fate of the seed (whether it will germinate, remain in the soil bank for secondary dispersal, or die due to predators or pathogens). In our study, establishment limitation (up to 1 year) was low, as at least one seedling germinated at every site, and was mostly affected by conspecific and heterospecific tree densities at multiple scales. These results concur with a number of seed addition studies which have reported low establishment limitation, where seedling survival is not explained by environmental heterogeneity but rather the availability of seeds for germination (Ehrlén et al., 2006; Paine & Harms, 2009). For example, Paine and Harms (2009) studied resource competition among seedlings by monitoring seedling growth among sites with varying stem densities. They found no significant differences in seedling survival demonstrating that resource competition is not important for recruitment and suggesting that if competition is weak, then recruitment is more dependent on the availability of viable seeds for germination.

Mortality due to pathogen and predator density is hypothesized to be higher close to parent trees (Augspurger, 1984; Connell, 1978; Janzen, 1970), known as negative density dependence (Harms et al., 2000; Wright et al., 2005). We found support for this hypothesis for only two of the three species studied. Interestingly, this effect in *Astrocaryum* was in relation to seed density, while in *Attalea* it was related to tree density and depended on the spatial scale considered. For *Dipteryx*, tree density did not affect seedling survival, but contrary to *Astrocaryum*, seed density positively affected seedling survival. This finding aligns with Schupp (1992) which found negative density dependence effects did not scale from the individual level to larger spatial scales. The satiation effect could explain this outcome at high densities. Up to a point, high local tree density of

species with shared seed predators would enhance seedling mortality by fostering high predator and pathogen densities. However, enhanced seedling mortality will take place only up to a threshold above which patches of high seed density satiate predators, which might decrease mortality on species that are less abundant and that are not eaten (Schupp, 1992).

Especially in *Dipteryx*, the positive effect of seed density on seedling survival might be an example of satiation as establishment limitation due to seedling predation appeared to be high in this species, and survival was positively correlated to seed density. In this case, seedling predation was extreme, and no seedling was found alive six months after the initial survey. This strong seedling predation pattern versus the high seed germination rates was previously reported for BCI by De Steven and Putz (1984) and was credited to the abundance of granivorous mammal populations on the island. A general finding is that each species responded differently to the site conditions, suggesting that the species-specific requirements and density-dependent processes have particular effects that depend on the autoecology of each species.

Although rarely explored, studies examining the effect of heterospecific seed and adult density have found an important effect of heterospecific densities on species recruitment (Johnson et al., 2017; Umaña et al., 2016). As in previous studies, we found an impact of heterospecific seed and adult densities on seedling survival for all the species studied. However, the direction and strength of the effect changed with species identity and scale. This finding aligns with our previous result on the important impact of indirect interactions among species on seed predation performed on the same set of species because they have shared predators (Garzon-Lopez et al., 2015).

Our results highlight the importance of estimating seed predation as a separate component of recruitment limitation and including the effect of heterospecific species, especially in the case of species with shared predators and dispersers. These two mechanisms are important to accurately determine at which stage environmental and neighborhood properties impact the recruitment. Even though a specific variable might appear to positively affect recruitment for a species, its presence in a certain space might not be sufficient to ensure recruitment. That is the case of *Astrocaryum*, where topography interacts with seed predators to reduce seed predation; identifying this connection illustrates that the presence of both environmental heterogeneity (i.e., topography) and seed predators can influence the population dynamics and enhance species coexistence.

4.1 | Caveats and future research

The scope of this study only goes as far as 1-year germination and survival and does not include the effect of seed predation of the added buried seeds to measure establishment. Extending the timeframe would include seeds that would have germinated later, and the effect of local biotic and abiotic conditions in the establishment of the species studied. We collected some of the added seeds of each species and did not find viable seeds. However, we cannot ensure

that this pattern was pervasive across all seeds added. Burial has been observed to exponentially decrease seed predation (Andresen & Levey, 2004; Garcia-Orth & Martínez-Ramos, 2008), but further research would be required to ensure that this is also the case for *Astrocaryum*, *Attalea* and *Dipteryx*.

Future research should investigate the negative density dependence processes across scales and species to understand better its relevance as a driver of diversity maintenance (Bagchi et al., 2014) while including high-resolution environmental factors that match local requirements for seedling establishment. For example, an important next step is to determine whether there is an effect of species characteristics such as body size, cluster size, and densities, as well as predators and pathogens behavior (Forrister et al., 2019), not only on negative density dependence itself (Murphy et al., 2017) but also on the spatial scale at which these processes take place.

5 | CONCLUSIONS

We found that stochastic and deterministic processes interact at multiple spatial scales throughout plant recruitment to determine early establishment and distribution of three co-occurring species. Moreover, we found that the strength of each process at each stage largely depends on three factors: (a) the identity of the species, (b) the local conditions, and (c) the spatial scale observed. Our work demonstrates the importance of combining remote sensing with field experiments to integrate landscape extents and varying resolutions in the study of stochastic and deterministic processes.

AUTHORS CONTRIBUTION
CXG, HO, PJ, and SB conceived the ideas and designed the methodology. CXG and EM collected the data. CXG analyzed the data and led the writing of the manuscript.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.0vt4b8h09 (Garzon-Lopez et al., 2021).

ORCID
Carol X. Garzon-Lopez https://orcid.org/0000-0002-4099-2740

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