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Research

Proximity and abundance of mother trees affects recruitment patterns in a long-term tropical forest restoration study

Rakan A. Zahawi, Leland K. Werden, Miriam San-José, Juan Abel Rosales, Jeffry Flores and Karen D. Holl

R. A. Zahawi (<https://orcid.org/0000-0002-5678-2967>) ✉ (rakan.zahawi@gmail.com), L. K. Werden (<https://orcid.org/0000-0002-3579-4352>) and M. San-José (<https://orcid.org/0000-0003-4601-9148>), Lyon Arboretum, Univ. of Hawai'i at Mānoa, Honolulu, HI, USA. RAZ and LKW also at: School of Life Sciences, Univ. of Hawai'i at Mānoa, Honolulu, HI, USA. – RAZ and K. D. Holl (<https://orcid.org/0000-0003-2893-6161>), Environmental Studies Dept, Univ. of California, Santa Cruz, CA, USA. RAZ and MS-J also at: Charles Darwin Foundation, Puerto Ayora, Galapagos, Ecuador. LKW, Dept of Environmental Systems Science, ETH Zürich, Zürich, Switzerland. – J. A. Rosales and J. Flores, Las Cruces Biological Station, Organization for Tropical Studies, San Vito de Coto Brus, Costa Rica.

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Remnant trees and forest fragments in agricultural landscapes can be important sources of propagules to facilitate forest recovery. However, many studies simply quantify forest cover in the surrounding landscape as a percentage, with little attention given to species composition, and subsequently fail to detect an effect on recruitment patterns. We assessed the relative importance of the spatial distribution and life-history traits of 77 tree species on recruitment patterns at a landscape scale in a well-replicated long-term restoration study in southern Costa Rica. We censused and mapped potential mother trees in a 100-m buffer surrounding eight replicate restoration plots and quantified respective tree recruits within each plot. We assessed how mother tree abundance, species life-history characteristics (seed size, dispersal mode), tree size (DBH, height) and distance to restoration plot affected recruitment at coarse (plot: 50 × 50 m) and fine (quadrat: 3 × 3 m) spatial scales. The presence of a mother tree within 100 m of a restoration plot resulted in a 10-fold increase in potential mean recruitment. Mother tree abundance was also an important driver of recruit density, and particularly so for large-seeded (≥ 5 mm) zoochorous species with a fivefold increase in recruit density across the observed mother tree abundance range. An interaction between mother tree abundance and proximity demonstrated that the effect of mother tree abundance on recruit density was important but waned with increasing distance from restoration plots. At the fine spatial scale, proximity was uniformly important; height and DBH of the closest potential mother tree also affected recruit abundance but responses differed by seed size. Results highlight the importance of remnant vegetation composition to the recovery of adjacent degraded habitats, underscoring the outsized role nearby remnant forest and isolated trees can play for the persistence of localized biodiversity.

Keywords: Costa Rica, dispersal limitation, fruiting trees, recruit, remnant forest, seed dispersal, seed source, spatial scale, tropics, zoochory



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Introduction

Most tropical forests in the world have been heavily fragmented with the resulting landscape a patchwork mosaic of interconnected habitats that are less able to support remaining biodiversity (Haddad et al. 2015, de Lima et al. 2020). Restoration has emerged as a key global strategy to counteract the loss of biodiversity and ecosystem services that forests provide with a myriad of synchronous initiatives launched – among them the Bonn Challenge (<www.bonnchallenge.org/>) to bring 350M ha of degraded land into restoration by 2030, and the Initiative 20x20 (<[https://initiative20x20.org/](http://initiative20x20.org/)>) to restore 20M ha in Latin America and the Caribbean. However, scaling-up restoration efforts to meet these goals across highly heterogeneous landscapes is a daunting undertaking, and a thorough understanding of the dynamics that drive forest recovery is critical to prioritize where such efforts are likely to succeed.

Seed dispersal is a key process that affects the rate of forest recovery and the long-term outcomes of restoration initiatives. Although many key tree genera are wind-dispersed (e.g. *Cedrela*, *Ceiba*), seed dispersal in wet tropical forests is overwhelmingly driven by animals (Gentry 1982). Animal movement patterns are impacted by forest fragmentation and loss, which can either increase or decrease their range depending on the species and study system in question (Nield et al. 2020, Ramos et al. 2020). Movement is also driven both by landscape configuration and connectivity (Lehouck et al. 2009a, Kormann et al. 2016, Cadavid-Florez et al. 2019), as well as by resource availability such as the provision of fleshy fruit (Lehouck et al. 2009b, Camargo et al. 2020). Even though landscape-scale research has repeatedly shown that a minimum forest threshold is essential to maintaining a habitat's functional integrity and diversity (Banks-Leite et al. 2014, Arroyo-Rodríguez et al. 2020), and many note that remnant forest patches and trees interspersed in agricultural landscapes are an essential source of tree propagules for recovering habitats (Laborde et al. 2005, Cadavid-Florez et al. 2019), localized site-specific studies often fail to note a direct effect of surrounding forest cover on patterns of recovery (Howe et al. 2010, Zahawi et al. 2013).

This apparent contradiction stems from the fact that most studies evaluate the effect of surrounding forest cover as a simplified quantitative metric, such as percent cover in the landscape, and how that influences recovery of a particular site or the movement patterns of frugivores (Letcher and Chazdon 2009, Zahawi et al. 2013). Whereas the range of forest cover can be shown to influence frugivore behavior in tropical habitats (Florian et al. 2008), the binary categorization of landscapes into simple forest presence/absence, at the expense of identifying the actual species that make up that forest or that are present in the matrix, can obfuscate underlying patterns to the point of not yielding a signal (Reid et al. 2014). This is especially the case for seed dispersal and recruitment (Rocha et al. 2016, Holl et al. 2017).

Clearly, for seeds of a given species to be dispersed to a particular site, there must be a source (i.e. mother tree) in the surrounding landscape. The few studies that have examined dispersal into newly recovering habitats at the species level,

have shown a direct link between the presence of potential mother trees in the surrounding landscape, and the successful recruitment of seedlings in restoration plots (de la Peña-Domene et al. 2016). While dispersal is more nuanced, and recruitment patterns can be strongly affected by the particular location of a given mother tree in the landscape (Aldrich and Hamrick 1998) as well as the many life-history traits of a given species (Muscarella et al. 2013, Werden et al. 2020), the distance of a potential mother tree to a site, in addition to the size of its seeds, are key drivers that modulate dispersal into a particular habitat.

It is well known that most seeds fall directly beneath mother trees (Janzen 1970, Marchand et al. 2020), and progressively fewer seeds are dispersed over greater distances (Holbrook and Smith 2000). Further, while small-seeded species can be dispersed by a breadth of frugivores, large-seeded species are necessarily dispersed by a smaller subset of species (Scott and Martin 1984, Muñoz et al. 2017) due to physical limitations such as gape width (Wheelwright 1985). There is also the well-known tradeoff in seed size, whereby small-seeded species can produce an order of magnitude more seeds than their larger-seeded counterparts (Greene and Johnson 1994, Moles and Westoby 2006, Muller-Landau et al. 2008). Thus, species with larger seeds tend to have both less frequent dispersal events (Freitas et al. 2013, Werden et al. 2021) and are typically dispersed shorter distances from the parent tree (Muller-Landau et al. 2008), but see Holbrook and Smith (2000). If they are dispersed, however, larger-seeded species are more likely to germinate and survive to the seedling stage (Doust et al. 2006, Tunjai and Elliott 2012, Werden et al. 2020). Finally, greater tree height may increase seed dispersal distance (Muller-Landau et al. 2008), and larger trees (i.e. > DBH) typically have greater seed production (Chapman et al. 1992, Greene and Johnson 1994).

We assessed the relative importance of spatial distribution and life-history traits of mother tree species on recruitment patterns in adjacent actively restored forests at the landscape scale. To do so we mapped 77 mother tree species in the immediate area surrounding restoration plots and censused and mapped respective tree recruits in each restoration plot in a well-replicated long-term study in southern Costa Rica. We evaluate how mother tree abundance, species life-history characteristics (seed size, dispersal mode), tree size (DBH, height) and distance to restoration plot affected recruitment at coarse (plot level: 50 × 50 m) and fine (quadrat level: 3 × 3 m) spatial scales. We predicted that mother tree presence and proximity to a restoration plot would have a strong positive effect on recruit abundance, as would the abundance of mother trees. Finally, we hypothesized that tree size would have a positive but weaker effect on recruitment.

Methods

Site description

This study was conducted at eight replicate restoration sites located between the Las Cruces Biological Station (8°47'7"N,

82°57'32"W) and the town of Agua Buena (8°44'52"N, 82°56'39"W) in southern Costa Rica (Fig. 1). All sites are at least 1 km apart and surrounded by a mosaic of mixed land use including pasture, agriculture and remnant forest fragments with approximately 28% forest cover remaining (Zahawi et al. 2015). The forest in this region is classified as Tropical Premontane Wet Forest (Holdridge et al. 1971), and forest cover within a 100-m radius of restoration plots ranged from ~8 to 99% at the time of the survey (J. Amar unpubl.). Mean annual precipitation ranges between 3500 and 4000 mm and mean annual temperature is ~21°C.

Experimental design of restoration study

All study sites had been cleared and used for agriculture for at least two decades before the restoration project was initiated. Vegetation was primarily composed of forage grasses or a combination of grasses, forbs and the fern *Pteridium arachnoideum* (Kaulf.) Maxon. The experiment was established between 2004 and 2006 by uniformly planting seedlings of four widely used agroforestry species plantation-style at 2.8-m spacing throughout each 50 × 50 m restoration plot: two native species *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae), and two naturalized softwoods,

Erythrina poeppigiana (Walp.) Skeels and *Inga edulis* Mart. (both Fabaceae). Structural metrics from a 2019 drone fly-over yielded a mean canopy height of 15.3 m ± 1 SE, and a mean percent canopy cover 97.6 ± 1.4 SE (Zahawi and Werden unpubl.). The study forms part of a larger experiment that compares different active and passive restoration treatments over time (Zahawi et al. 2013); additional details on planting layout and initial maintenance during the establishment phase of the study are detailed in Holl et al. (2011).

Mother tree and recruit census

We surveyed a total of 77 species (Supporting information), which represented a broad range of life-history traits (e.g. successional stage, seed size, dispersal mode), and the majority of species that have recruited in plots over the duration of the restoration experiment. We did not include common early-successional species that are not dispersal-limited as they are ubiquitous in the landscape and in restoration plots. For each species surveyed, all potential mother trees (i.e. potentially reproductive at ≥ 10-cm DBH) within a 100-m buffer around the outer edge of each restoration plot were surveyed between September 2017 and June 2018. For all individuals censused we recorded DBH,

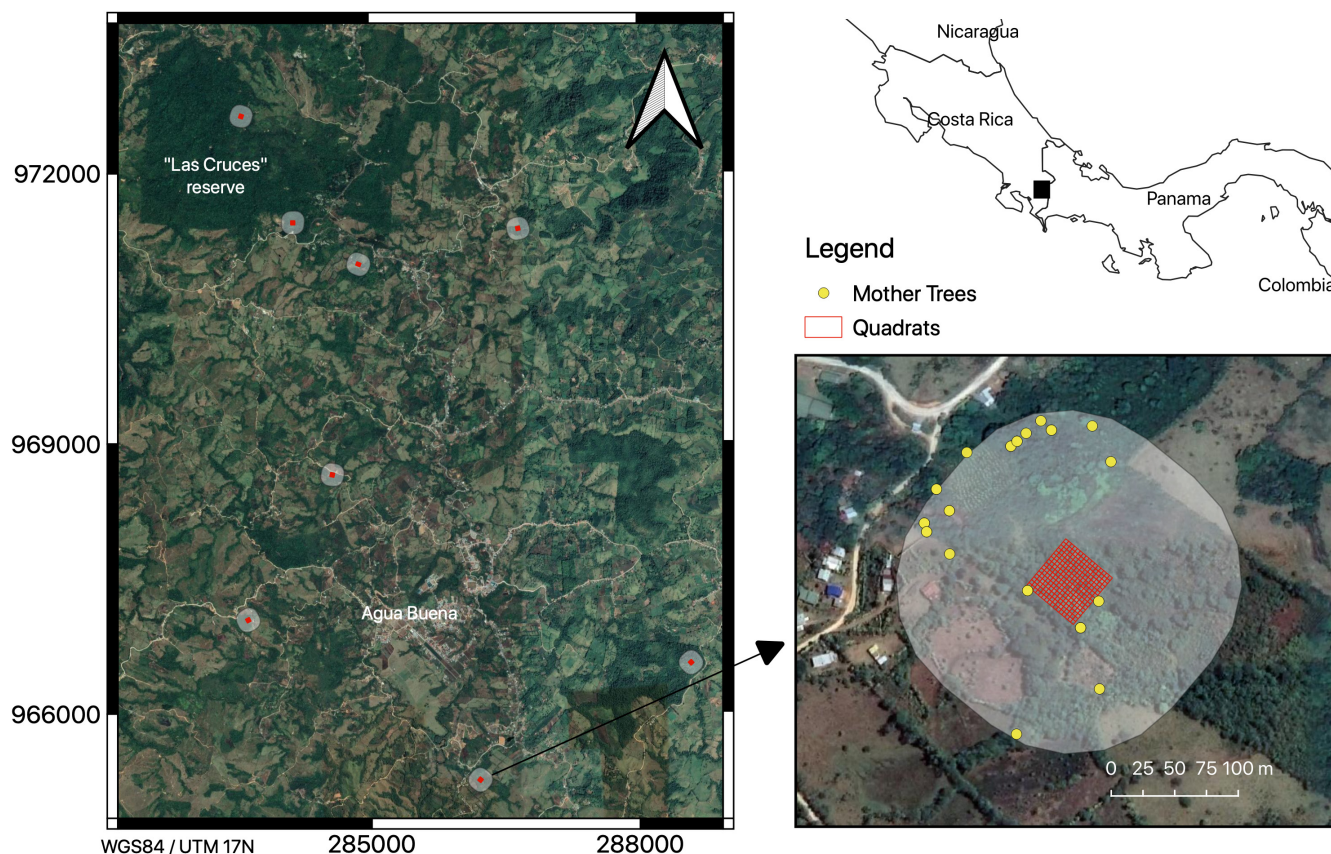


Figure 1. Study location in southern Costa Rica, regional map highlighting the eight study sites (left) and an example of one plot (inset lower right). Inset shows distribution of a sampling of mother trees (yellow) in the surveyed 100-m buffer (shaded area) surrounding a 50 × 50 m plantation forest restoration plot where all recruits were surveyed and mapped.

height (using a Leica Disto D2 laser rangefinder) and GPS location to within ± 5 m (Garmin 64s). All tree recruits ≥ 10 -cm height were mapped in each restoration plot between February and April 2017 and identified to species level. Three recruit species may have had reproductive individuals within plots (i.e. ≥ 10 -cm DBH; *Croton draco*, *Koanophyllum pittieri* and *Verbesina tapantiana*), however, all had larger conspecific individuals censused as mother trees at their respective sites and analyses excluding these species did not change overall results. To map recruit spatial distribution, we gridded each 50×50 -m plot into 3×3 -m quadrats excluding a 1 m outer buffer edge for each plot ($n = 256$ quadrats/plot). Dispersal mode and seed size for all species were determined using literature reviews, local knowledge and seed measurements. We grouped species into zoochorous and non-zoochorous categories. The latter includes wind-, gravity- and explosively-dispersed species and made up a small percentage of mother trees ($\sim 4.4\%$) and recruits (0.4%) overall. Seeds were binned into two size classes, small < 5 mm and large ≥ 5 mm in length, as dispersal of larger-seeded animal-dispersed species is limited by frugivore gape width (Wheelwright 1985).

Spatial analyses

We used the 'distance to nearest hub' tool to determine the distance of each recruit to the nearest potential mother tree and to the edge of the nearest plantation plot. We used 'distance matrix analysis' to calculate the distance between each recruit and all potential mother trees associated with a given plot, and from each quadrat cell (whether a recruit was present or not) to all potential mother trees at a given site. We used 'kernel density estimation' to generate recruit abundance maps for a subset of species. All GIS spatial analyses were done in QGIS 3.4.13 Madeira.

Assessing presence/absence patterns of mother trees and recruits

Across all replicate sites, there were instances where we observed only mother trees ($n = 63$), only recruits ($n = 76$) and both mother trees and recruits ($n = 190$) for each individual species. To determine if the composition of species within each of these three mother tree/recruit presence groups differed by seed size we calculated the 'proportion of large-seeded species' observed in each category at the site-level: (total no. large-seeded species recruiting)/(total no. of all recruiting species). We tested for differences in the proportion of large-seeded species recruiting among the mother tree/recruit presence categories with a likelihood-ratio test performed on a mixed-effects zero-inflated beta regression, with site as a random effect:

$$\text{Prop. large-seeded species}_{ij} = \beta_0 + \beta_1 \text{ mother tree/recruit presence category}_{ij} + b_{1,ij} + \epsilon_{ij} \quad (1)$$

where i indexes observations, j indexes sites, b_1 are the normally distributed random intercepts for sites and ϵ are the beta distributed subject residuals with a logit distribution for zero outcomes. For this and all following models, we used a likelihood-ratio χ^2 test to assess for significant terms and determined differences between groups with Tukey's HSD (*emmeans* package). All statistical analyses were performed in R v.3.6.2. (<www.r-project.org>) and all generalized linear models were fit with the *glmmTMB* package (Brooks et al. 2017).

Effect of mother trees on recruitment

We determined whether the mother trees surrounding a restoration plot and their life-history characteristics predicted the abundance of recruits observed within a restoration plot. The amount of surrounding forest cover within a 100 m radius was strongly correlated with the abundance of mother trees (Pearson's correlation $r = 0.82$, $p = 0.01$); as such forest cover was not included in models. We initially assessed the effect of zoochorous and non-zoochorous mother trees on recruitment separately. Since there were insufficient non-zoochorous mother trees and recruits across sites to make robust inferences, they were assessed only as part of 'all species' analyses.

Plot-level recruitment patterns (Coarse scale: 50×50 m)

Our first goal was to evaluate the relationship between recruitment and the presence or absence of a mother tree within 100 m of restoration plots. To do so, we determined the effect of mother tree presence/absence on the abundance of recruits at the coarse scale with a likelihood-ratio test performed on a mixed-effects zero-inflated Poisson regression. We included random effects for site and species:

$$\text{Number of recruits}_{ijk} = \beta_0 + \beta_1 \text{ mother tree presence/absence} + b_{1,ij} + b_{2,ik} + \epsilon_{ijk} \quad (2)$$

For this and the following models (Eq. 3 and 4), i indexes observations, j indexes species and k indexes sites; b_1 are b_2 are the normally distributed random intercepts for species and sites, respectively; ϵ is the Poisson distributed subject residuals to model the count process, and a logit distribution to model zero outcomes.

Next, we determined the influence of mother trees in the immediate vicinity of plots on recruitment. As such, we excluded instances where recruits but no mother trees of a certain species were observed at a site. To investigate how the abundance of mother trees at a site, their mean distance to the plot edge, and their interaction influenced the abundance of recruits in restoration plots, we fit a generalized linear mixed-effects model with a zero-inflated Poisson error distribution (Eq. 3) with counts of recruits for each species observed in a plot as the response (253 total species $\times$ site combinations). We included the abundance of mother trees of each species surrounding a plot (MTabundance) and the

species-level mean distance of mother trees to the edge of a plot (MTdistance) as fixed-effects predictors. Species and sites were included as random effects:

$$\begin{aligned} \text{Number of recruits}_{ijk} = & \beta_0 + \beta_1 \text{MTabundance}_{ijk} + \beta_2 \\ & \text{MTdistance}_{ijk} + \beta_3 \text{MTabundance}_{ijk} \\ & \times \text{MTdistance}_{ijk} + b_{1,ij} + b_{2,ik} + \epsilon_{ijk} \end{aligned} \quad (3)$$

To determine how seed size influenced overall recruitment patterns for zoochorous tree species only, we fit the same model as Eq. 3 with the addition of species' seed size as a fixed-effect, including interactions between seed size and all predictors. To account for potential effects of negative density dependence (NDD; Wright et al. 2005), we also included quadratic terms for the mean distance of the mother trees to a plot edge and its interaction with seed size, which substantially improved model fit (Eq. 4). We omitted the quadratic term from Eq. 3 as it decreased model performance:

$$\begin{aligned} \text{Number of recruits}_{ijk} = & \beta_0 + \beta_1 \text{MTabundance}_{ijk} + \beta_2 \text{seed size}_{ijk} \\ & + \beta_3 \text{MTdistance}_{ijk} + \beta_4 \text{MTdistance}_{ijk}^2 \\ & + \beta_5 \text{MTabundance}_{ijk} \times \text{seed size}_{ijk} \\ & + \beta_6 \text{MTdistance}_{ijk} \times \text{seed size}_{ijk} \\ & + \beta_7 \text{MTdistance}_{ijk}^2 \times \text{seed size}_{ijk} \\ & + b_{1,ij} + b_{2,ik} + \epsilon_{ijk} \end{aligned} \quad (4)$$

Quadrat-level recruitment patterns (Fine scale: 3 × 3 m)

To evaluate the effect of mother tree characteristics on recruitment we fitted generalized linear mixed models with the same approach as plot-level analyses (i.e. a zero-inflated Poisson error distribution). We included three mother tree characteristic predictors (fixed effects) in the model: distance to the closest mother tree, and height and DBH of the closest mother tree. Again, we included a quadratic term for the distance to the closest mother tree to account for potential effects of NDD, which substantially improved model fit. Random effects included species, site and quadrat, with quadrat nested within site. Response variables were the abundance of all recruits and zoochorous species grouped by seed size. To determine the proportion of the variance explained by each random effect we calculated intraclass correlation coefficients using the *performance* package.

Results

A total of 1485 mother trees and 9018 recruits, collectively representing 77 species, were censused (Supporting information; n = 72 mother tree species, n = 68 recruit species). The majority of mother tree individuals were zoochorous (n = 1302); 955 were large- (≥ 5 mm) and 347 were small-seeded (< 5 mm). There was a total of 183 non-zoochorous mother tree

individuals. Instances where a specific species of non-zoochorous mother tree was observed at a site was low (n = 31) compared to zoochorous species (n = 222; Supporting information). Of the species surveyed, there were overwhelmingly more zoochorous (n = 8541) than non-zoochorous (n = 477) recruits. Large-seeded zoochorous recruits (n = 6410) were also more prevalent than small-seeded recruits (n = 2578), which is not surprising given that we excluded several common early-successional, small-seeded species from the survey. The vast majority of recruits were seedlings (> 10 cm and < 1 m tall; n = 7977), followed by saplings (≥ 1 m tall and < 5 cm DBH; n = 1002), small (≥ 5 but < 10 cm DBH; n = 24) and large (≥ 10 cm DBH; n = 15) trees.

Effects of mother tree presence, abundance, distance and seed size on recruitment at the coarse scale (plot-level)

The presence of a mother tree within 100 m of a restoration plot resulted in a > 10-fold increase in recruitment on average (Eq. 2: $\chi^2_{df=1} = 2090.60$; $p < 0.001$; Fig. 2A). Moreover, we found interactions between the abundance of mother trees, distance to plot and seed size that influenced recruitment, both for all species (Eq. 3: $R^2_m = 0.05$; $R^2_c = 0.67$; Supporting information) and for zoochorous species alone (Eq. 4: $R^2_m = 0.12$; $R^2_c = 0.72$ Supporting information). In both cases, a majority of the variation in plot-level recruit abundance was explained by species- and site-level random effects. The abundance of all species recruits in a plot was strongly influenced by the abundance of mother trees surrounding a plot ($p < 0.001$), the mean distance of mother trees to a plot edge ($p < 0.001$) and the interaction between the two ($p < 0.001$). The influence of the abundance of surrounding mother trees on recruitment decreased drastically as the average distance of mother trees to plots increased (Fig. 3; Supporting information). There was only a ~20% increase in expected average recruit abundance over the range of observed mother tree abundances when mother trees were on the outer edge of the sampling area (75 m from plots), versus a 53-fold average increase when mother trees were close to plots (within 25 m).

For zoochorous species, the abundance of mother trees ($p < 0.001$) and large-seeded species ($p = 0.03$) were positively related to recruit abundance, and there was a strong interaction between mother tree abundance and seed size ($p < 0.001$; Fig. 4A; Supporting information). Over the observed range of small- (range: 1–31) and large-seeded (range: 1–88) mother tree densities, the average abundance of recruits expected within a plot increased > 5-fold for large-seeded species but was negligible for small-seeded species (Fig. 4A). The mean distance of mother trees to the edge of a plot had a negative relationship with recruitment ($p < 0.001$), and this relationship had a strong interaction with seed size ($p < 0.001$; Fig. 4B; Supporting information). Recruitment was over fourfold greater for large-seeded species, and almost threefold higher for small-seeded mother trees directly adjacent to plots (≤ 5 m), compared to when mother trees were at the outer edge of the sampling area

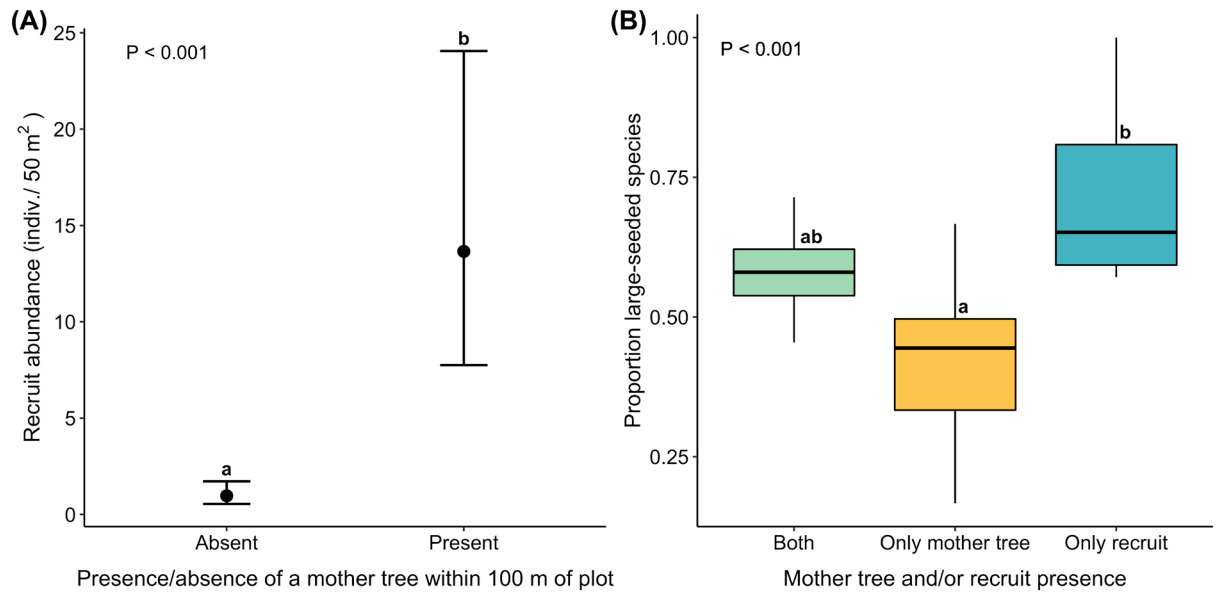


Figure 2. (A) Effect of the presence or absence of a mother tree within 100 m of a restoration plot on recruit count (abundance). Points are predicted means and error bars are 95% confidence intervals. (B) The proportion of large-seeded species in three site-level mother tree/ recruit presence categories: both mother trees and recruits, only mother trees and only recruits. The centerline is the median and the top and bottom of boxes are the upper and lower quartiles, respectively. For both panels, letters indicate significant differences ($\alpha=0.05$) between category means (pairwise Tukey's HSD tests on mixed-models; Eq. 1 and 2).

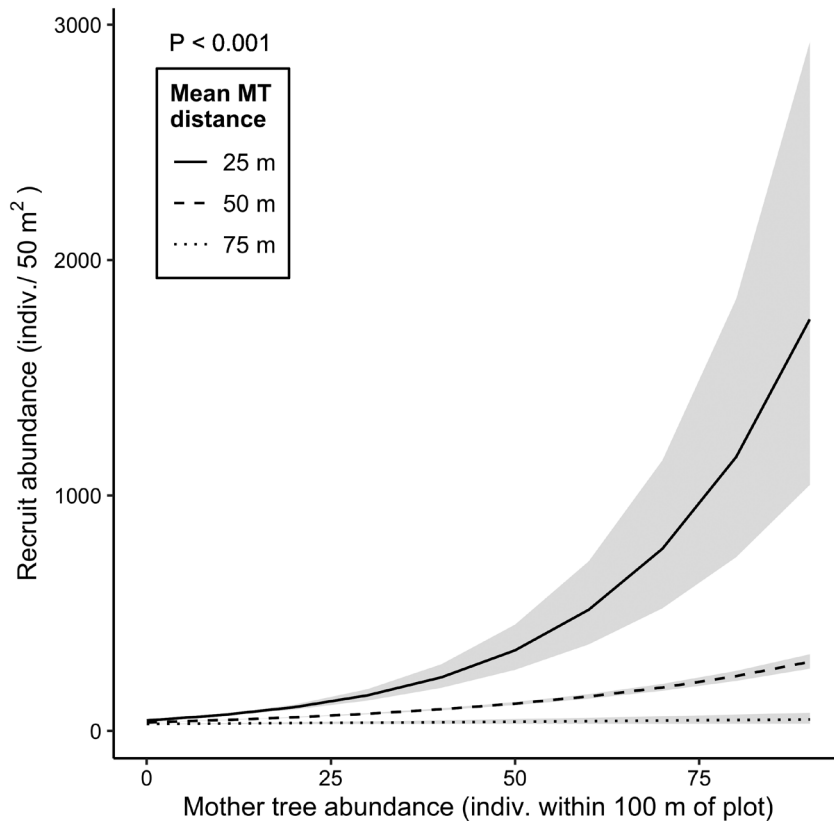


Figure 3. The relationship of recruit count (abundance), count of mother trees surrounding a restoration plot and the mean distance of mother trees to a plot edge. Plotted lines are predictions from a generalized linear mixed-effects model (Eq. 3) and shaded bands are 95% confidence intervals.

(~100 m to plot edge). Interestingly, recruit abundance peaked when mother trees were at intermediate distances to plot edges (between 20 and 30 m) for large-seeded species, but small-seeded species did not show this hump-shaped pattern (Fig. 4B; $p < 0.001$ for $MTdistance^2 \times seed\ size$ term; Supporting information).

Effects of mother tree characteristics on recruitment at the fine scale (quadrat-level)

Increasing the distance of the closest mother tree to a quadrat consistently had a strong negative effect on the abundance of recruits (Fig. 5). However, recruitment appeared to peak at intermediate distances ($Distance^2$), indicating that NDD influenced recruit dynamics. DBH and height of the closest mother tree were also important but opposite effects were noted depending on the zoochorous seed size category. The DBH of the closest mother tree had a positive effect on the abundance of large-seeded recruits but it was negative for small-seeded recruits, whereas for small-seeded species height of the closest mother tree had a significant positive effect but the response was negative for large-seeded species. In all models, a vast majority of the variation (i.e. $> 75\%$) in quadrat-level recruit abundance was explained by species-level random effects (Supporting information); less than 16% was explained by site or quadrat.

Patterns of mother tree and recruit presence/absence across sites

The proportion of large-seeded species observed at a site differed strongly across mother tree and recruit presence

categories (Eq. 1: $\chi^2_{df=2} = 14.36$; $p < 0.001$), and was driven by differences between instances where only mother trees or only recruits of a species were observed (Fig. 2B; $p = 0.001$; Tukey's HSD). In instances where mother tree(s) were present but no recruitment was observed ($n = 9$), species tended to be smaller-seeded (Fig. 6C). By contrast, instances where only recruits of a given species were observed ($n = 5$) skewed toward large-seeded species (Fig. 6A–B), indicating that mother trees for these species were located at distances > 100 m from the plot edge.

Spatial patterns of mother tree and recruit presence varied strongly by species and also by site, and as noted earlier accounted for a substantial portion of variance in analyses at the plot and quadrat level. For example, recruitment for *Calophyllum brasiliense*, a large-seeded late-successional species, was high at the EC site where numerous potential mother trees surrounded the plot (Fig. 6A); recruitment was also high at the OM site, even though only one mother tree was censused within 100 m of the plot. By contrast, both *Garcinia intermedia* (Fig. 6B), another large-seeded species and *Lacistema aggregatum* (Fig. 6C), a small-seeded species, had extremely high recruitment at the SG and BB sites, respectively with only one censused mother tree (directly adjacent to the plot). *L. aggregatum* had considerably lower recruitment at the EC site, despite a number of potential mother trees in the vicinity and is reflective of the overall result found for small-seeded species (Fig. 4A). Finally, recruitment for *Alchornea latifolia* (Fig. 6D) showed interesting discrepancies and was notably high at SG, a site with one mother tree at the limit of the census area, but also comparable to OM where several potential mother trees were censused.

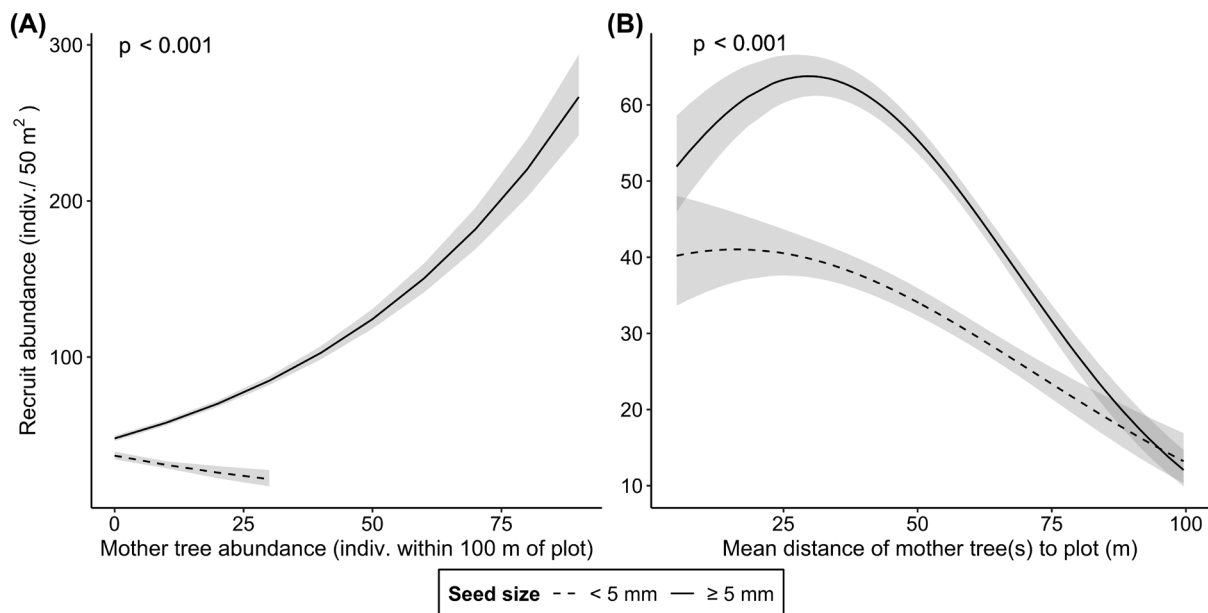


Figure 4. Interactions between (A) seed size and the abundance of zoochorous mother trees surrounding a restoration plot; (B) seed size and the mean distance of zoochorous mother trees to a plot edge, and their relationship with zoochorous tree recruit abundance. Plotted lines are predictions from a generalized linear mixed-effects model (Eq. 4) and shaded bands are 95% confidence intervals.

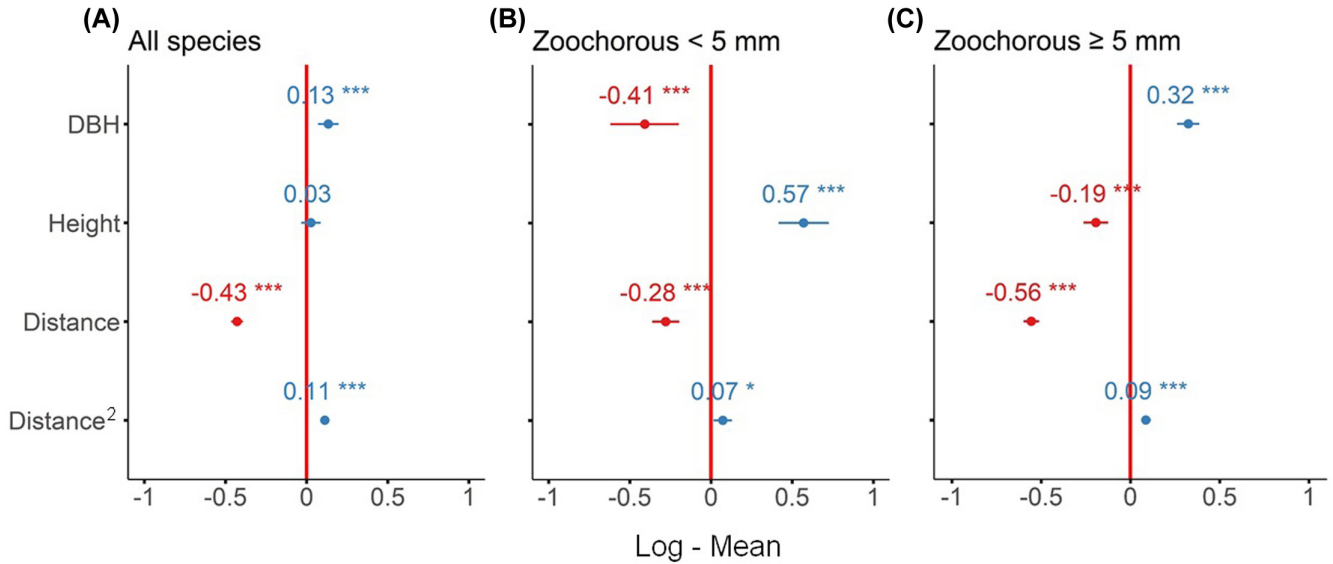


Figure 5. Effects of diameter at breast height (DBH), height and linear and quadratic distance of closest mother tree (i.e. fixed effects) on recruit abundance at the quadrat level. Recruit categories include all species (A) or zoochorous species only grouped into small- (B) and large-seeded (C) species. Standardized coefficients values and standard errors following Gelman (2008) are reported. Significance terms indicated as * $p < 0.05$ and *** $p < 0.0001$.

Discussion

The central argument that remnant forest habitat is important to the natural recovery of adjacent degraded areas (Crouzeilles et al. 2020) is not disputed in the literature. However, a number of studies have found a minimal effect of the amount of remaining forest in a given area on recovery patterns, including in this experimental study (Cole et al. 2010, Holl et al. 2017), creating a seeming paradox with major potential implications for conservation and restoration efforts. We hypothesized that such results may be an artifact of the coarse resolution at which remnant forest cover is assessed, and predicted that distinct patterns would emerge if recruit dynamics were examined at the species level by mapping the presence of adult trees in remnant forest habitat surrounding targeted restoration plots.

We found a strong effect of the presence of potential mother trees within 100 m of a restoration plot on recruitment, and mother tree proximity to restoration plots resulted in a three- to four-fold difference in average recruitment within the distance range covered. The abundance of potential mother trees, and especially those proximal to restoration plots (within a 25 m buffer), was also a strong predictor for recruitment. This pattern was driven by large-seeded species and supports results from intact tropical forests such as Barro Colorado Island where the abundance of large-seeded recruits was strongly linked to the proximity of conspecific adults (Dalling et al. 1998). Negative density dependence may have influenced recruitment patterns as recruitment appeared to peak when mother trees were at intermediate distances to plot edges for large-seeded species (Fig. 4B), and at intermediate distances in all cases at the quadrat-level (Fig. 5). Interestingly, results contrast with those found by

Lebrija-Trejos et al. (2016) who noted that large-seeded species were typically more tolerant of neighboring conspecific recruits. The abundance of mother trees was also strongly correlated with the percent of forest cover surrounding a restoration plot ($r=0.82$), underscoring the importance of the amount of surrounding forest remaining in predicting recovery patterns, but that its value can only be ascertained when examined at an appropriate scale and at the species level.

Large-seeded species are of focal interest in restoration as they represent the majority of late-successional species in mature tropical forests and typically have greater dispersal limitation and low recruitment in disturbed and recovering habitats (Martínez-Garza and Howe 2003, de Melo et al. 2006, Palma et al. 2021). Indeed, Palma et al. (2021) note extremely low recruitment of large-seeded species even in mature secondary forests (> 20 years) that are older than the restoration plots in this study, suggesting that direct seeding of large-seeded species is likely necessary in recovering habitats where nearby large-seeded conspecific adults are absent (Bonilla-Moheno and Holl 2010, Cole et al. 2011). Patterns for smaller-seeded species, many of which are pioneers, were inconclusive in our study, largely because we excluded the most common and widely recruiting species found in this area from the survey. That said, a number of studies suggest that small-seeded, early-successional species are more recruitment than dispersal-limited (Muscarella et al. 2013, Werden et al. 2020).

At still finer spatial scales (quadrat-level) we found that, in addition to the importance of proximity, the size (i.e. DBH and height) of the closest potential mother tree were also important predictors (Fig. 5). Height was positively correlated with dispersal distance across 44 tree species in Barro Colorado Island (Muller-Landau et al. 2008) and across

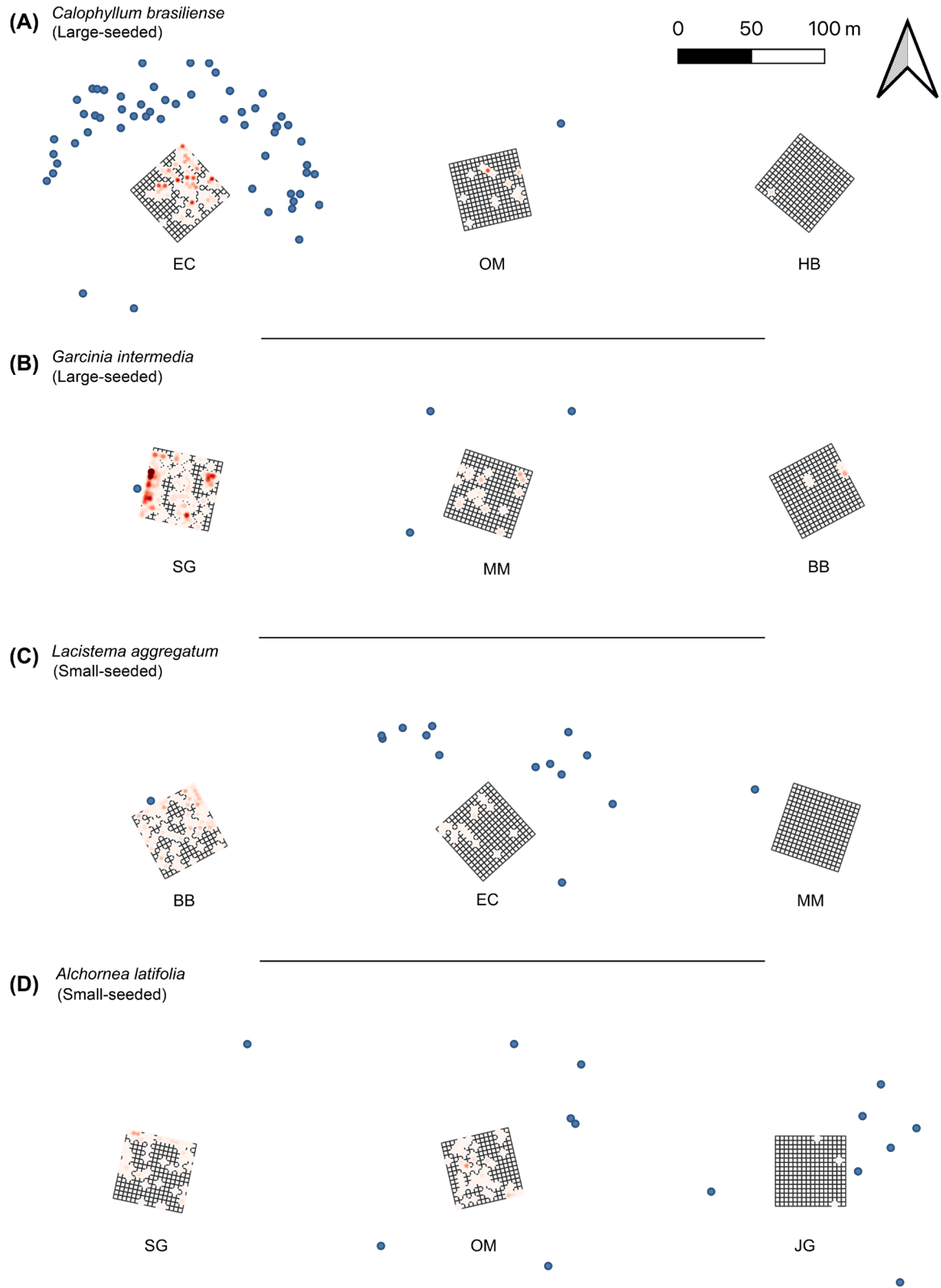


Figure 6. Recruit density for two large-seeded (A, B) and two small-seeded (C, D) zoochorous species, each ordered by decreasing density of recruits in restoration plots (left to right). Potential mother trees for each species are shown as blue circles outside the restoration plots (shown as a grid). The color intensity of recruits in red illustrates density: range 1 to ≥ 9 seedlings (light to dark red, respectively). Maps are reflective of the broad patterns found in analyses but also showcase species- and site-specific mother tree and recruit variability.

growth forms, seed dispersal distance is more strongly correlated with plant height than with seed mass (Thomson et al. 2011). In our study, we found an interesting trade-off in seed size for zoochorous-dispersed species. For small-seeded species, the height of the closest mother tree correlated with increased recruitment, but for large-seeded species it did not. In turn, for large-seeded species, the DBH of the closest mother tree was more strongly linked with increased recruitment, a pattern not found for small-seeded species. As such, effects were more dependent on species-specific characteristics. While greater tree DBH can result in more seed production (Greene and Johnson 1994, Norghauer and Newbery 2015) this variable may be more important for large-seeded species given that they produce fewer seeds overall (Moles and Westoby 2006, Muller-Landau et al. 2008) and smaller-seeded species can produce copious numbers of seeds even when small (Alvarez-Buylla and Martínez-Ramos 1992). It is also important to note that while we used a 10 cm DBH mother tree reproductive size cutoff in our study, different species become reproductively mature at distinct cohort stages (Muller-Landau et al. 2008), which may be partly driving the recruitment patterns found for small- and large-seeded species.

Whereas we found strong effects of mother tree characteristics on recruit patterns, site-level and species-specific patterns were enormously important (see conditional R^2 in Supporting information), with species generally predicting a majority of the variation in responses across all models assessed (Supporting information). There were a few notable and interesting anomalies. For example, there were a few cases where conspecific recruits were censused but no mother tree was found within 100 m. Seed dispersal can clearly exceed that distance (Marchand et al. 2020) and interestingly, longer-distance recruit events skewed toward large-seeded species, likely because they have higher establishment rates than small-seeded species (Muscarella et al. 2013, Werden et al. 2020). As such, only a few seeds may need to be dispersed to result in a successful recruitment event. Secondary dispersal may have also contributed to the movement of large-seeded species beyond the 100 m boundary censused (Baldoni et al. 2017). While in most cases such recruits were few one exception was *Persea caerulea*, a large-seeded species, for which almost all recruits were censused at one site (103 of 104) but no mother trees were found. However, a follow-up field survey located more than a dozen potential mother trees at ~120 m distance (these trees were not included in overall analyses). In other cases, a nearby mother tree may have been removed prior to the field survey as the landscape where our study was conducted is largely agricultural (Zahawi et al. 2015) and the felling of trees, especially isolated ones, is not uncommon. Finally, while our study quantified dispersal events that surpassed 100 m, the majority of seed dispersal and recruitment did occur within the 100 m dispersal kernel – a result that is supported by other studies (Muller-Landau et al. 2008, Lavabre et al. 2014).

There were a few cases where mother trees were present but recruits were absent. Fourteen potential mother trees of

Quararibea aurantiocalyx were censused within the 100 m perimeter of one site with high surrounding forest cover but no recruits were recorded. This result highlights the fact that many other processes affect recruitment including the presence of dispersers (Wotton and Kelly 2011, Boissier et al. 2020), the abundance of seed predators (Fadini et al. 2009), suitable establishment conditions (Augsburger and Kitajima 1992, Harms et al. 2000) and a host of other biotic and abiotic factors (Muscarella et al. 2013, de la Peña-Domene et al. 2017).

Conclusions

By assessing the species composition of remnant forest surrounding restoration plots, our study demonstrated a clear connection between the presence and abundance of nearby mother trees and recruits in plots. As such, remnant habitats that retain a significant portion of their local biodiversity, and that are proximal to targeted sites, are essential to rapid community reassembly. How potential mother trees are distributed spatially (i.e. within riparian corridors, forest patches or as an isolated remnant tree) may also have important implications for seed dispersal dynamics and what ultimately results in successful recruitment (Lavabre et al. 2014, de la Peña-Domene et al. 2016, Mendes et al. 2016, Cadavid-Florez et al. 2019). This may be especially the case for large-seeded species that tend to be more dispersal-limited, as they typically rely on dispersers that need larger remnant forests. In turn, restoration sites that are either surrounded by species-poor habitat or are spatially isolated from the remnant forest may require active strategies such as direct seeding (Doust et al. 2006, Bonilla-Moheno and Holl 2010). By extension, large-scale active restoration efforts that encourage the planting of millions of trees for conservation should maximize the diversity of trees planted (Di Sacco et al. 2021), as the common monoculture planting approach presents a significant risk to the future composition of forests because seed rain will be heavily dominated by these planted species.

Our results underscore the importance of assessing both the composition and spatial distribution of potential mother trees in the landscape in order to prioritize the selection of restoration sites that have greater potential for natural recruitment of native biodiversity. This is becoming increasingly more feasible through remote sensing and high-resolution imagery acquired with drones (Sothe et al. 2019), which will collectively decrease costs and optimize the effectiveness of site selection for habitat recovery.

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Author contributions

Rakan Zahawi: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (equal); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Leland Werden:** Data curation (supporting); Formal analysis (equal); Software (equal); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Miriam San Jose:** Data curation (supporting); Formal analysis (equal); Software (equal); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Juan Abel Rosales:** Conceptualization (supporting); Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Visualization (supporting). **Jeffrey Flores:** Data curation (supporting); Methodology (supporting); Resources (supporting); Validation (supporting). **Karen Holl:** Conceptualization (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.7291/D1SH5T>> (Zahawi et al. 2021).

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