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# Large trees in restored tropical rainforest

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## ABSTRACT

Restoration interventions aim to accelerate forest recovery by skipping the early stages of succession where short-lived early-successional tree species dominate. Large trees (≥ 30 cm of Diameter at Breast Height [DBH]) provide ecosystem functions, such as carbon storage and acting as stepping stones for the movement of animals through the landscape. Here, we evaluated two mixtures of planted and, unplanted areas to figure out which restoration treatment was more successful in skipping the early stages of succession. For this, we measured forest structure of large trees in restoration settings after 10 years in Los Tuxtlas, Veracruz, Mexico. In 2006, cattle grazing was excluded from 24 plots (30 × 30 m). Eight of those plots were planted with 12 wind-dispersed tree species, eight plots were planted with 12 animal-dispersed species (a total of 2,304 planted trees), and eight plots were left to undergo natural succession without plantings. Planted and naturally recruited trees have been assessed periodically since 2007. A total of 835 planted and naturally recruited trees of 45 species reached large size. Including all trees (planted and recruited), the richness and abundance of late-successional trees was higher in plantings than under natural succession while richness of large recruits of late-successional species was higher in plantings of wind-dispersed species and in natural succession. Also, including all trees, plantings of animal-dispersed species have higher richness and abundance of trees dispersed by bats and both birds and bats; while species and trees dispersed by birds were present equally at all treatments. Richness and abundance of bat-dispersed recruits were similar in plantings and natural succession while plantings of wind-dispersed species had higher bird-dispersed recruits. Composition heterogeneity, driven by natural recruitment, was largest for early-successional trees in natural succession. After 10 years, the first stages of succession (20-30 years) were skipped in plantings: plantings have higher abundance of large seeded late-successional species. For an overall increase in composition heterogeneity in permanent agricultural landscapes, we suggest establishing areas to undergo natural succession along with plantings that include a higher percentage of late-successional species with large seeds.

*Keywords*: assisted succession, frugivory, restoration plantings, Los Tuxtlas, natural succession, unassisted forest regeneration

## 1. Introduction

In the "Decade for Ecosystem Restoration" (2021-2030; UN, 2020), the main goal is to reverse current forest loss. In the Neotropics, after tropical man-made pastures are abandoned, succession back to forest may take > 100 years (Saldarriaga et al., 1988; Uhl et al., 1988; Finegan, 1996; Bechara *et al.*, 2016); although trajectories vary widely given random effects (Norden *et al.*, 2015; Estrada-Villegas *et al.*, 2020). Three mechanisms for forest succession have been suggested (Connell and Slatyer, 1977; Chazdon *et al.*, 2007): (*i*) the *facilitation model* states that successive waves of colonization of different tree species occur, beginning with early-successionals that modify the environment so late-successionals may establish; (*ii*) the *tolerance model* state that all colonists arrive early in succession and late-successionals are expected to dominate after the mortality of early-successionals (ca. 20 to 30 years; Finegan 1996) and; (*iii*) the *inhibition model* state that early-successionals will suppress incoming species, arresting succession (Connell and Slatyer, 1977). Given that seed banks are usually depleted due to agricultural use (Wijdeven and Kuzee, 2000), succession depends exclusively on the arrival of seeds by dispersal events. Early-successionals have smaller seeds with lower dispersal limitation (failure of seeds to reach a site) than late-successionals (de la Peña-Domene and Martínez-Garza, 2018). Species dispersed by wind may move longer distances in open areas (Nathan, 2006) than those dispersed by animals, that will arrive to open areas if their dispersal agents are attracted (Wunderle, 1997; Laborde *et al.*, 2008). Once seeds arrive and germinate, the conditions under which they must grow are highly adverse, so most species have high establishment limitation (failure of seedlings to survive and grow) in pastures (Nepstad *et al.*, 1996; Hooper *et al.*, 2005; Martínez-Ramos *et al.,* 2016, de la Peña-Domene and Martínez-Garza, 2018). The fastest changes in tree richness and density during succession have been registered in the first 10 years, driven by fast growing early-successionals but recovery of composition may take centuries (Bechara *et al.*, 2016; Rozendaal *et al.*, 2019). For these reasons, human intervention is needed to release or accelerate succession back to forest.

Forest restoration aims to accelerates succession back to forest. This can be achieved by establishing plantings of native species or by favoring natural forest regrowth (Lamb *et al.*, 2005; Gann *et al.*, 2019). Meta-analyses have shown that below-ground biomass (Bonner *et al.*, 2013) or tree height (Crouzeilles *et al.*, 2016) may recover faster under natural forest regrowth, while forest composition (Shoo *et al.*, 2016) or canopy cover (Brancalion *et al.*, 2016) may recover faster using restoration plantings. The effect of planting composition in the resulting forest structure has been less explored (see for example, Guariguata *et al.*, 1995). Tree composition in plantings varies depending on restoration objectives:  fast-growing early-successionals are planted to rapidly recover a canopy and out-compete invasive species (Douterlungne *et al.*, 2013), because they provide benefits for people (Montagnini *et al.*, 1995) or because it is assumed that they are needed for late-successionals to establish (i.e., *facilitation model*). However, plantings of only early-successionals may be a “quick fix” (*sensu* King and Hobbs, 2006), resulting in synchronic early mortality (van Breugel *et al.*, 2006) or in arrested succession (i.e., *inhibition model*). Another strategy to restore biodiversity is to establish a combination of early and late-successional trees (Rodrigues *et al.*, 2009; Ratanapongsai, 2020) that may perform equally well (see Martínez-Garza and Howe, 2003; Osorio-Salomón *et al.*, 2021), supporting the *tolerance model*.

Small trees in restored forest show the potential for future structure; as they get larger, the ecosystem functions and services they provide are also recovered, for example, as carbon sinks (Pan *et al.*, 2011; Sist *et al.*, 2014). Large trees in restored areas also provide microhabitats and refuge for the animals moving through fragmented landscapes (Thompson *et al.*, 2014; Lindenmayer *et al.*, 2017; de Almeida and Viani, 2021). Given that they are more likely to be reproductive (Pennington and Sarukhán, 2005), large trees with fleshy fruits attract frugivores and therefore, under their canopy, a higher seed fall of animal-dispersed seeds and its further recruitment will occur (Howe and Miriti, 2004; Sansevero *et al.*, 2011; Camargo *et al.*, 2020). Therefore, the long-term success of restoration plantings relies on the identity and performance of planted species getting large. At this stage, dispersal vector of large trees will influence animal maintenance in fragmented landscapes and future processes of plant recruitment.

In 2006, we established two planting mixtures including four early and eight late-successional species: (1) 12 species dispersed by wind and, (2) 12 species dispersed by animals (Martínez-Garza *et al.*, 2013b); we also established areas without plantings. Here, we evaluate trees that reached large sizes (Diameter at Breast Height [DBH] ≥ 30 cm and up to 97 cm DBH) after a decade, and that were either planted or recruited naturally early in the experiment (Fig.1a). We aim to elucidated whether planted late-successionals thrive as well as early-successionals, as the *tolerance model* suggest, leading us to expect higher richness and abundance of late-successionals in plantings than in natural succession, when plantings and recruits are included; in this scenario, composition is expected to be unique in each treatment; also, composition heterogeneity would be expected to be higher for early-successionals in unplanted areas given more space for natural recruitment. Alternatively, if only early-successionals thrive, as the *facilitation model* suggests, we expect a converged structure and composition dominated by early-successionals and high composition heterogeneity at all restoration treatments. For recruits, we expect a similar richness and abundance of early-successionals everywhere given their lower dispersal limitation compared to late-successionals; also, higher recruitment in unplanted areas given that there is more space available. Alternatively, harsh environmental conditions in unplanted areas (e.g., higher competition with grasses) may result in lower recruitment compared to plantings. Regarding dispersal vectors, the *tolerance model* predicts that, given thriving plantings, trees dispersed by wind or animals will be dominant where planted. The *facilitation model* predicts dominance of early-successional wind-dispersed species at all treatments due to their lower dispersal limitation (e.g., Nathan, 2006). For recruits, similar richness and abundance of trees with low dispersal limitation in open areas (i.e., wind and bat dispersed species) are expected at all treatments while lower recruitment of bird-dispersed species is likely given the lack of perches. By revealing which restoration treatment increase dominance of large late-successional trees, we can suggest planting compositions that successfully skip early stages of succession to speeds forest recovery the most.

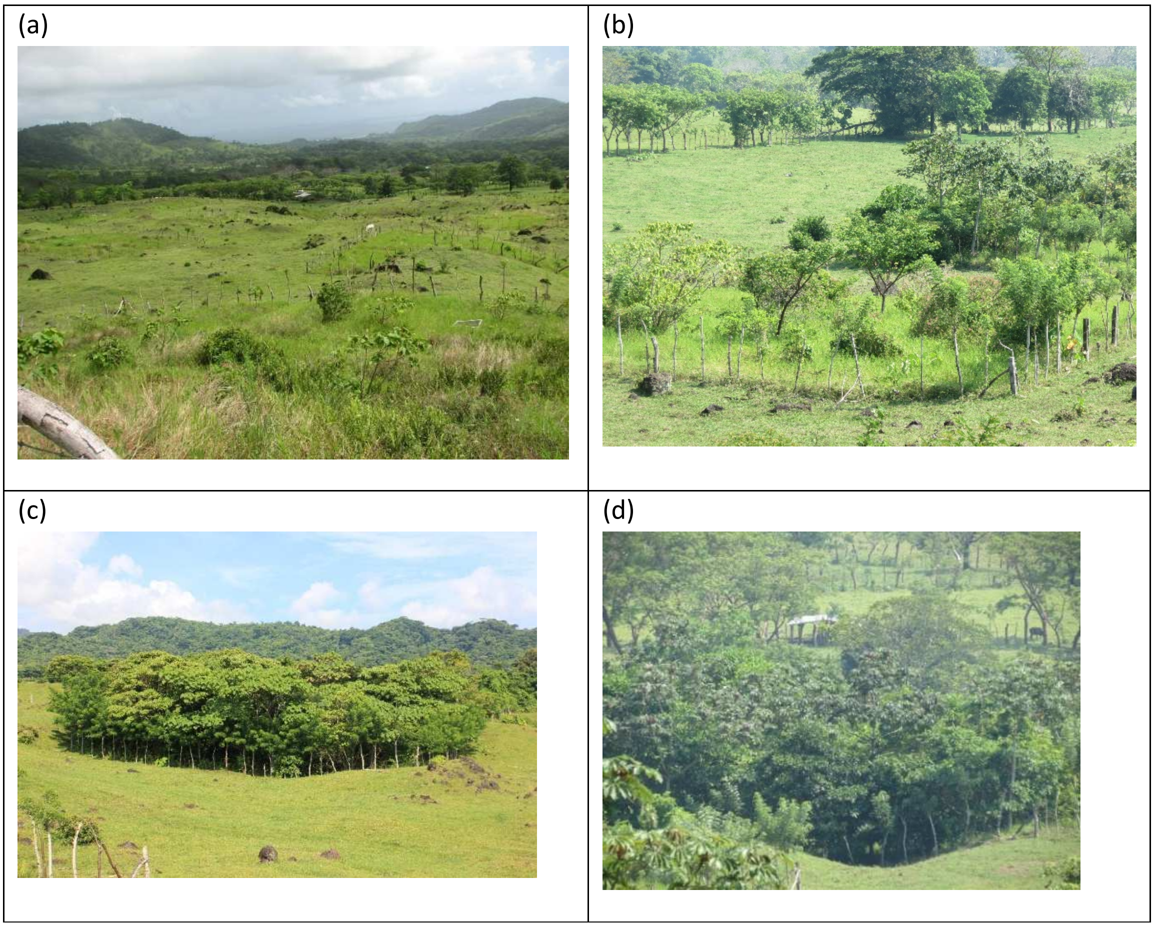


**Fig. 1**. (a) Fenced restoration plots established in 2006; (b) Natural succession, (c) Plantings of wind-dispersed species and (d) Plantings of animal-dispersed species in 2013 in Los Tuxtlas, Veracruz, Mexico. Photos by Marinés de la Peña Domene.

## 2. Materials and methods

### *2.1. Study site*

This study was conducted in Los Tuxtlas, Veracruz, Mexico, a biosphere reserve ranging in elevation from 200 to 1,700 m above sea level (Dirzo *et al.*, 1997). This volcanic region is characterized by acidic soils (pH 4.9) with a large clay component (48.5% clay), having formed from basaltic and andesitic rock mixed with volcanic ash (see Guevara *et al.*, 2004). The mean annual precipitation from 1997 to 2006 was 4,825 mm per year, considering a rainy season from June to February and a dry season from March to May (González-Soriano *et al.*, 1997). The mean annual temperature in the region is 25.8 °C; in altitudes below 200 m, temperature ranges between 24°C to 26 °C (Soto and Gama, 1997). The formerly forested land in which our plots were established had been under intensive cattle ranching for 50 years on ground planted with native and exotic grasses (Howe *et al.*, 2010). Conserved tropical rainforest holds 300 native tree species (Ibarra-Manriquez and Sinaca, 1995, 1996a, b) and more than 150 fruit-eating bird and mammal species, with wide-ranging fruit-eating bats and birds among the most likely dispersal agents of seeds arriving to restoration settings (González-Soriano *et al.*, 1997).

### *2.2. Experimental design*

The study was carried out in active cattle pastures near the village of Adolfo Ruiz Cortines (latitude: 18.595607, longitude: -95.101773). In 2006, we established 24 30 × 30 m plots separated from each other by 35 m in a hillside gradient from 182 to 260 m above sea level (m asl; Martínez-Garza *et al.,* 2013a). Plots are 500–1,200 m from the edge of the conserved rainforest and >90 m from fragments of secondary forest (Howe *et al.*, 2010). All cattle were excluded from these plots with living fences of *Gliricidia sepium* (Fabaceae) and barbed wire (Howe *et al.*, 2010), but outside of the excluded plots, the pasture remained active for grazing. A 2 m wide corridor in the center of plots was marked to allow netting of birds and bats and 1 m corridor close to the fence to walk; those areas were not planted and were not censused for recruits (Howe *et al.,* 2010). Three treatments were established: plantings of two different mixtures of species and one unplanted treatment. The location of the different treatments among plots was assigned systematically to avoid the aggregation of similar treatments by chance. The planting mixtures consisted of eight plots planted with 12 tree species dispersed by wind (hereafter Wind Plantings) and eight plots planted with 12 tree species dispersed by animals (hereafter Animal Plantings). Each planting mixture included four early- and eight late-successional tree species (Martínez-Garza *et al.*, 2013b). A total of 2,304 seedlings were planted at a spacing distance of 2 x 2 m; seedlings were 4–7-month old (96 seedlings of each species); all seedlings were tagged and censused yearly (Table 1S). Within each planting mixture, individuals of all species were planted in mixed stands in a systematic design to maximize the distance among conspecifics and to avoid the aggregation of early-successional trees. Grasses were removed in a radius of 50 cm around the planted trees until they were >1.5 m in height; no fertilizer or water were added to the planted seedlings (Martínez-Garza *et al.*, 2013a,b). In the eight remaining plots, no trees were planted (hereafter Natural Succession). Within the Animal Plantings, four species are known to be dispersed by bats, four species by birds and four species by both birds and bats (Table S2). For one planted species dispersed by birds, *Guarea grandifolia* DC. (Meliaceae), none of the planted individuals reached the size considered for this study (see below; Table 1S). In all plots, we identified, tagged, and measured woody seedlings taller than 10 cm every four months from 12 through 60 months after cattle exclusion and then twice a year for the following years. Initial soil properties at the plots revealed that litter mass was 24.9 ± 3.2 kg $ha^{-1}$ and, Nitrogen and Phosphorous pools in the litter were 37.3 ± 4.8 g N $ha^{-1}$ and 18.4 ± 3.5 g P $ha^{-1}$, respectively. Further, pools of soil nutrients were 18.7 ± 0.7 Mg $ha^{-1}$ for organic carbon, 1.35 ± 0.03 Mg $ha^{-1}$ for total N, C:N proportion was 14 ± 0.3, and 2.87 ± 0.25 kg $ha^{-1}$ for $NH_4^{-3}$ (Tobón *et al.*, 2011). One year after plot establishment, litter mass increased to 54.4 ± 8.2 kg $ha^{-1}$; concentration in the litter of N (1.59 ± 0.08 mg $g^{-1}$), pools of N (86.5 ± 0.07 g $ha^{-1}$) and P (47.5 ± 9.3 g $ha^{-1}$) also increased (Tobón *et al.,* 2011). Further, soils 20 cm from planted legume seedlings showed, after one year, a partial recovery of N cycling, measured as a greater accumulation of N in litter, total N concentrations, soil microbial biomass N concentrations and rates of net N transformations (Roa-Fuentes *et al.,* 2015). Initial planting composition, differential recruitment and improved soil fertility resulted in restoration settings with contrasting physiognomy (de la Peña-Domene *et al.*, 2013; Li *et al.*, 2018). By 2013, plots under natural succession did not have a continuous canopy (Fig.1b); percentage of canopy cover was ca. 20% in natural succession while it was ca. 70% for plantings (Howe and Davlantes, 2017). Plantings of wind-dispersed species had a continuous and homogeneous canopy; in those plantings, 73% of trees were > 3 m in height (Fig.1c). Plantings of animal-dispersed species had a continuous but heterogeneous canopy where 69% of trees were > 3 m in height (Fig. 1d).

To evaluate structure and composition of the community of large trees for this study, we used a census from 2016 that included all trees that were planted as saplings in

2006 and trees that had recruited naturally since cattle were excluded from the plots. We considered only trees with a DBH ≥ 30 cm, a size at which both early and late-successional trees may be reproductive (Pennington and Sarukhán, 2005; Wright *et al.*, 2005; Howe, 2017). A range from 0 to 76% of the trees planted per species were registered as large ones after a decade (Table 1S). Tree richness an abundance was calculated as the total number of species or trees in each plot.

### *2.3. Statistical analysis*

Generalized linear mixed-effects models (GLMM), were used to determine whether treatment, successional status, or dispersal vector (fixed factors) affect richness and number of large trees. The model formula for the fixed factors were established as a factorial design, while a hierarchical error structure was set in the random factor of the model. Successional status or dispersal vector were nested within treatment and this term in turn was nested in each of eight blocks. Treatment has three levels: Animal Planting, Wind Planting and Natural Succession; successional status has two levels: early- and late-successionals and dispersal vector has four levels: wind, bats, birds and both bats and birds. A Poisson type error was used with a log-link function for richness and number of large trees. The minimal adequate model was selected following Crawley (2013) by eliminating those factors contributing a minimum percentage of variation to the model ($P > 0.05$). Differences in richness and abundance among significant levels of GLMMs were assessed through contrast tests (Crawley, 2013). The generalized linear mixed models were fit by maximum likelihood (Laplace approximation), with the 'lme 4' package in R, v 3.3.2 (R Foundation for Statistical Computing, Vienna, AT). Separated analyzes were ran for all trees (planted and recruited) and for recruited trees only. Means and standard errors of richness and abundance are reported in Results.

To analyze composition of large trees planted and recruited by treatment, we performed non-metric multidimensional scaling analyses (NMDS; Gauch, 1982). The species similarity metric used was Bray–Curtis, and the stress value in the NMDS was used to determine the ordination fitness (McCune *et al.*, 2002). The effect of treatment on the composition of large trees was evaluated for all trees (≥ 30 cm DBH), by successional status and by dispersal vector using Permutational Multivariate Analysis of Variance (PERMANOVA) with a Bray-Curtis dissimilarity matrix (Anderson, 2001). When treatment was significant, pairwise multiple comparisons were conducted. The impacts on false positive error rates from multiple comparisons were controlled by adjusting p-values based on the Benjamini–Hochberg false discovery rate (FDR) procedure (Benjamini and Hochberg, 1995). In the PERMANOVA, the significance of all tests was assessed from p-values calculated after 9,999 permutations. The significance level considered in all tests applied was <0.05. The "adonis" and "metaMDS" functions were implemented for running the PERMANOVA and NMDS analysis, respectively, available in the Vegan library (Oksanen *et al.*, 2018) of R, v 3.3.2 (R Foundation for Statistical Computing, Vienna, AT).

## 3. Results

In the 24 plots, a total of 835 planted or naturally recruited trees with DBH ≥ 30 cm were recorded with an average of 35 ± 4 trees per plot; these large trees were of 45 species (23 species planted, 22 species recruited) from 22 families (Table S2). Twenty were late-successional and 22 were early-successional species. Of the species recorded, 28 species (12 planted, 16 recruited) were in the Wind Plantings, 23 species (11 planted and 12 recruited) in the Animal Plantings, and 22 species in the Natural Succession plots. Of the trees recorded, 74 % were planted (616 trees), 50% in each planting mixture. The highest number of large naturally recruited trees was recorded in the Natural Succession plots (101 trees), followed by Wind Plantings (80 trees), and 38 trees recruited in the Animal Plantings (Table 1). Overall, the bat-and-bird-dispersed tree *Cecropia obtusifolia* Bertol. (Urticaceae) was the most abundant species with 94 trees, 81% of which had been planted (76 trees; Table S1). The bird-dispersed tree *Bursera simaruba* (L.) Sarg. (Burseraceae) was the most abundant naturally recruited species, with 54 trees (Table S2). Overall, composition of trees was different among treatments (Fig. S1; Tables S3a&b): Animal Plantings (purple circles) had the lowest composition heterogeneity (size of ellipse in Fig. S1) with eight species dispersed by animals clustered with those plots (Table S4). Twelve species dispersed by wind were associated with Wind Plantings (orange circles) while the highest composition heterogeneity was recorded in Natural Succession plots (blue circles) with zero species clustered with those plots.

**Table 1**. Total number of planted and recruited species and trees by successional status (Succ S) and dispersal Vector (Dispersal V) registered as large trees (> 30 cm DBH) in restoration settings in Los Tuxtlas, Veracruz, Mexico after 10 years.

| **Dispersal V** | **Succ S** | **Planted** | | **Recruited*** | |
|---|---|---|---|---|---|
| | | Species | Trees | Species | Trees |
| Bats | Late | 3 | 65 | 0 | 0 |
| | Early | 0 | 0 | 1 | 2 |
| Both Bats and birds | Late | 2 | 17 | 3 | 14 |
| | Early | 3 | 155 | 4 | 36 |
| Birds | Late | 2 | 56 | 4 | 70 |
| | Early | 1 | 17 | 4 | 26 |
| Wind | Late | 8 | 158 | 1 | 12 |
| | Early | 4 | 148 | 5 | 59 |

*species planted that were also recruited are not considered.

### *3.1. Successional status*

Average richness of large trees planted and recruited was twice higher in Wind Plantings (6.6 ± 0.52 species) compared with Natural Succession (3.1 ± 0.35 species); Animal Plantings had intermediate values (5.0 ± 0.40 species). Richness of large trees differed by treatment ($\chi 2 = 18.0$, $P \leq 0.001$) and there was an interaction between treatment and successional status ($\chi 2 = 18.1$, $P \leq 0.001$). Richness of early-successionals was similar among treatments (Fig. 2a). Richness of late-successionals was higher in Wind (7.3 ± 0.7 species) and Animal Plantings (5.0 ± 0.7 species) compared with Natural Succession (2.0 ± 0.6 species; Fig. 2a). The number of large trees was four times higher in Wind (24.2 ± 2.7 trees) and Animal Plantings (21.8 ± 1.9 trees) than under Natural Succession (6.3 ± 1.2 trees; Fig. 2b). The number of large trees differed among treatments (χ2 = 29.5, P ≤ 0.001) and there was an interaction between treatment and successional status (χ2 = 31.8, P ≤0.001).

Richness of large recruited trees differed by treatment (χ2 = 7.9, P ≤ 0.02) and there was an interaction between treatment and successional status (χ2 =7.6, P ≤ 0.001). Richness of early-successional recruits was higher in Natural Succession (3.8 ± 0.5 species) and Wind Plantings (3.0 ± 0.7 species) compared with Animal Plantings (1.8 ± 0.5 species) (Fig. 2c). Richness of late-successional recruits was higher in Natural Succession (2.1 ± 0.4 species) and Wind Plantings (2.0 ± 0.5 species) compared with Animal Plantings (0.9 ± 0.4 species; Fig. 2c). The number of large recruited trees did not differ among treatments (χ2 = 5.7, P > 0.05), successional status (χ2 = 1.1, P > 0.7), and there was not an interaction between treatment and successional status (χ2 = 6.3, P > 0.09; Fig 2d).

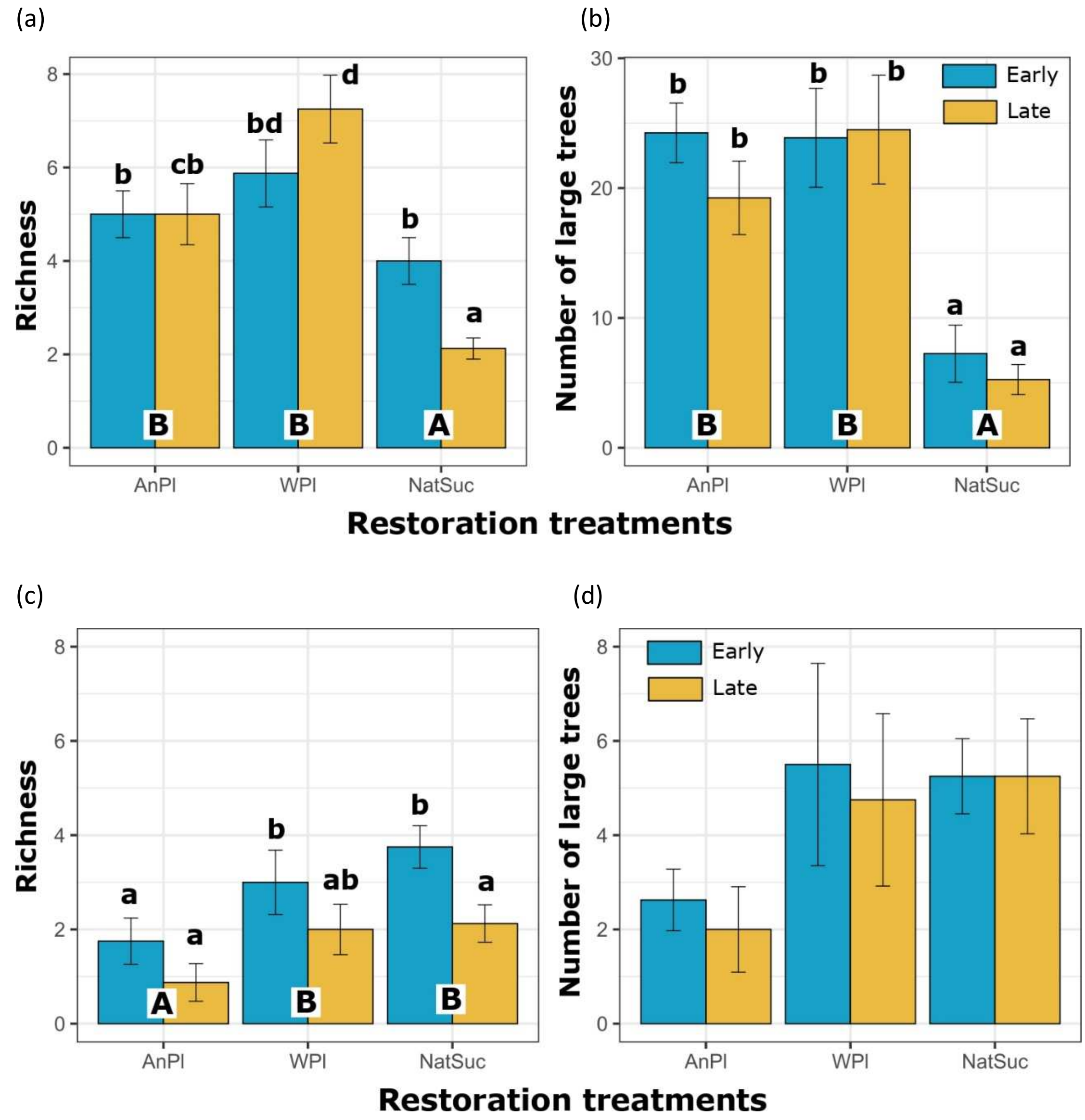


**Fig. 2**. Mean (± standard error) of richness and number of large trees by successional status (early and late-successional species) of planted and recruited trees ( a and b) and only recruits (c and d) in three restoration treatments in Los Tuxtlas, Veracruz, Mexico: Animal Plantings (AnPl), Wind Plantings (WPl) and Natural Succession (NatSuc). Different capital letters indicate differences among treatments while lower case letters indicate differences between successional status within treatments, tested with pairwise contrast comparisons ($p < 0.05$).

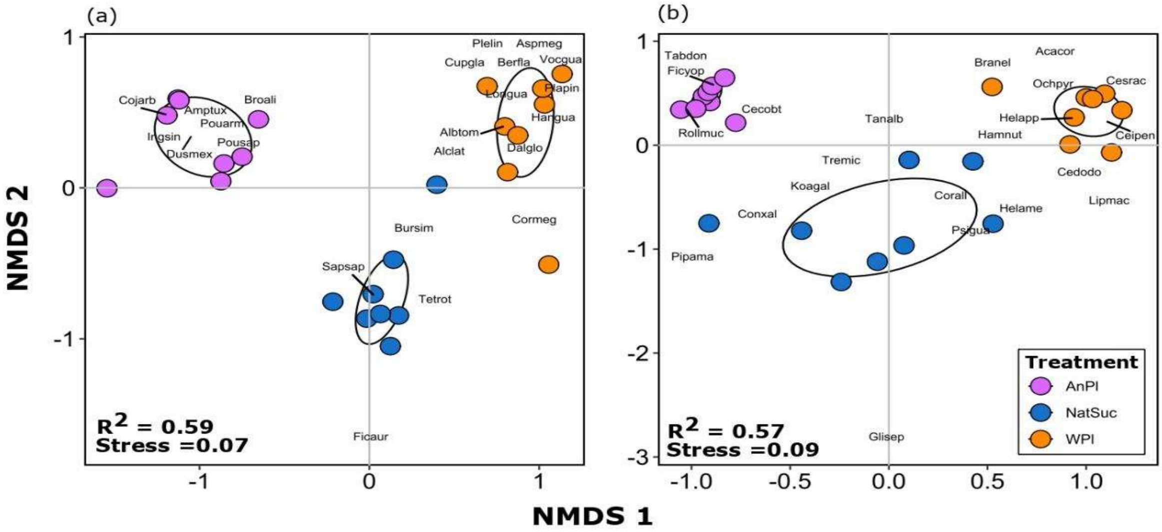


**Fig. 3**. Non-Metric Multidimensional Scaling analysis (NMDS) to discriminate composition of (a) late- and (b) early-successional large planted and recruited trees in 24 30 X 30 m plots in three restoration treatments in Los Tuxtlas, Veracruz, Mexico: Animal Plantings (AnPl, purple, N=8 plots), Wind Plantings (WPl, orange, N=8 plots) and Natural Succession (NatSuc, blue, N=8 plots). $R^2$ from PERMANOVA and stress values from NMDS analysis are shown (Table S5a). Ellipses were drawn at the 95% confidence level (Table S5b). Codes of species are in Table S6.

The composition of late- and early-successional trees (Fig. 3) was different among treatments (Tables S5a&b). For late-successional species, Natural Succession (blue circles Fig.3a) showed the lowest composition heterogeneity; zero species were associated with those plots (Table S6). Eight late-successional species dispersed by wind were associated with Wind Plantings (Table S6). Four late-successional species dispersed by animals were associated with Animal Plantings (purple circles in Fig. 3a; Table S6). For early-successional species, the opposite pattern was observed (Fig. 3b); Natural Succession showed the highest composition heterogeneity with zero species clustered with those plots (Table S6), Animal Plantings showed the smallest composition heterogeneity (Fig. 3b) with four species dispersed by animals associated with those plots (Table S6), and four species dispersed by wind were associated with Wind Plantings (Table S6).

### *3.2. Dispersal Vector*

Richness of large planted and recruited trees differed among treatments ($\chi2 = 7.8$, $P < 0.001$), by dispersal vector ($\chi2 = 125.0$, $P < 0.001$) and there was an interaction between treatment and dispersal vector ($\chi2 = 37.3$, $P < 0.001$). Richness of large recruited trees differed among treatments ($\chi2 = 9.3$, $P < 0.01$), by dispersal vector ($\chi2 = 19.7$, $P < 0.02$) and there was an interaction between treatment and dispersal vector ($\chi2 = 18.7$, $P < 0.002$). The number of large planted and recruited trees differed among treatments ($\chi2 = 18$, $P \leq 0.001$), by dispersal vector ($\chi2 = 152.9$, $P < 0.001$) and there was an interaction between treatment and dispersal vector ($\chi2 = 36.7$, $P < 0.001$). The number of large recruited trees differed among treatments ($\chi2 = 8.4$, $P < 0.02$), by dispersal vector ($\chi2 = 30.4$, $P < 0.0001$) and there was an interaction between treatment and dispersal vector ($\chi2 = 19.7$, $P < 0.001$).

Bats.- Average richness (2.00 ± 0.32 species) and number (8.00 ± 1.30 trees) of large planted and recruited trees dispersed by bats were higher in Animal Plantings compared with Natural Succession (0.12 ± 0.12 species and 0.13 ± 0.13 trees; Fig. 4); Wind Plantings showed averages of zero for both variables (Fig. 4). Richness and number of large recruits dispersed by bats were similar among treatments (Fig. 5). Composition of large planted and recruited trees dispersed by bats was similar among all treatments (Fig. 6, Tables

S7a&b, S8). Two planted species, *Inga sinacae* and *Amphitecna tuxtlensis* clustered with the Animal Plantings (Table S8).

*Both (Bats and Birds).-* Average richness of large planted and recruited trees dispersed by both bats and birds was higher in Animal Plantings (4.25 ± 0.45 species) than under Natural Succession (2.25 ± 0.41 species) and Wind Plantings (1.00 ± 0.33 species; Fig. 4a). Average number of large planted and recruited trees dispersed by both bats and birds was higher in Animal Plantings (22.63 ± 2.13 trees) compared to Natural Succession (3.25 ± 0.96 trees) and Wind Plantings (1.88 ± 0.95 trees), these last two were statistically similar (Fig. 4). Average richness of large recruits dispersed by both bats and birds was higher in Natural Succession (2.25 ± 1.28 species) than in Animal Plantings (0.75 ± 1.39 species), Wind Plantings had intermediate values (1.0 ± 1.06 species; Fig. 5). Average number of large recruits dispersed by both bats and birds was lower in Animal Plantings (1.13 ± 1.64 trees) compared with Natural Succession (3.25 ± 2.82 trees) and Wind Plantings (1.88 ± 3.0 trees), these last two were statistically similar (Fig. 5). Composition of large planted and recruited trees dispersed by both bats and birds was unique in Animal Plantings while Wind Plantings and Natural succession showed similar composition (Fig. 6, Tables S7a&b). Two planted species, *Ficus yoponensis* and *Poulsenia armata* were associated with Animal Plantings (Table S8).

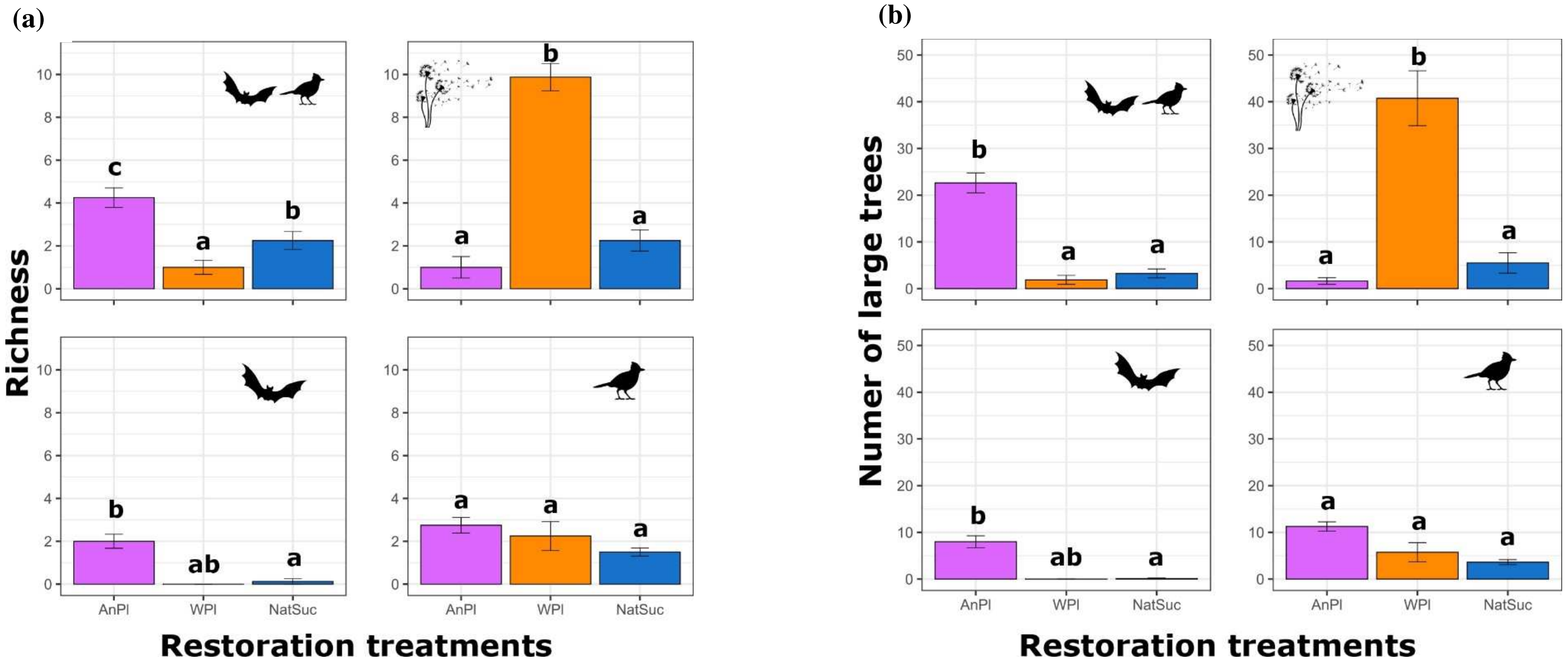
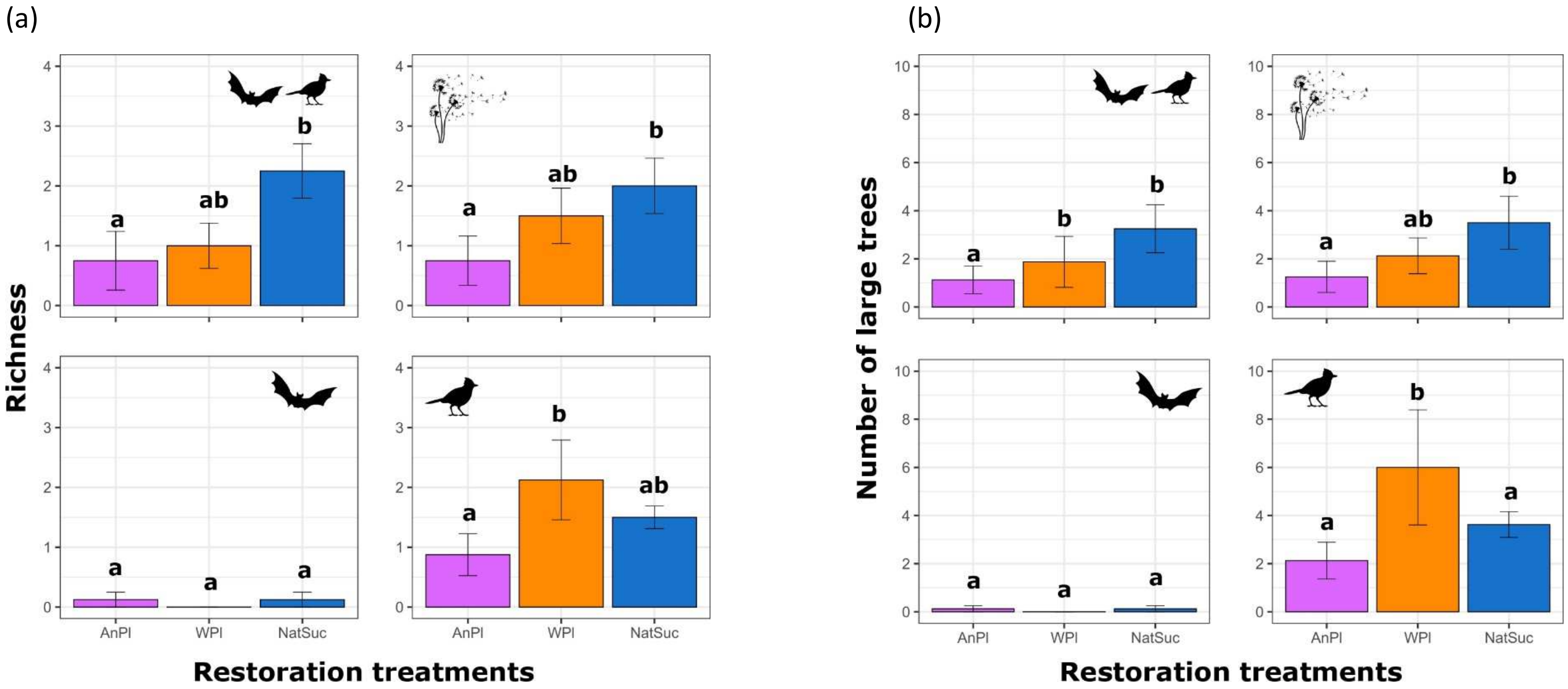


**Figure 4**. Average and standard errors of (a) Richness and (b) number of large planted and recruited trees by dispersal vector in Animal Plantings (AnPl), Wind Plantings (WPl) and Natural Succession (NatSuc) in Los Tuxtlas, Veracruz, Mexico. Different letters indicate differences among treatments within each dispersal vector tested with pairwise contrast comparisons (Table S9).



**5Figure 5**. Average and standard errors of (a) Richness and (b) number of large recruited trees by dispersal vector in Animal Plantings (AnPl), Wind Plantings (WPl) and Natural Succession (NatSuc) in Los Tuxtlas, Veracruz, Mexico. Different letters indicate differences among treatments within each dispersal vector tested with pairwise contrast comparisons (Table S9).

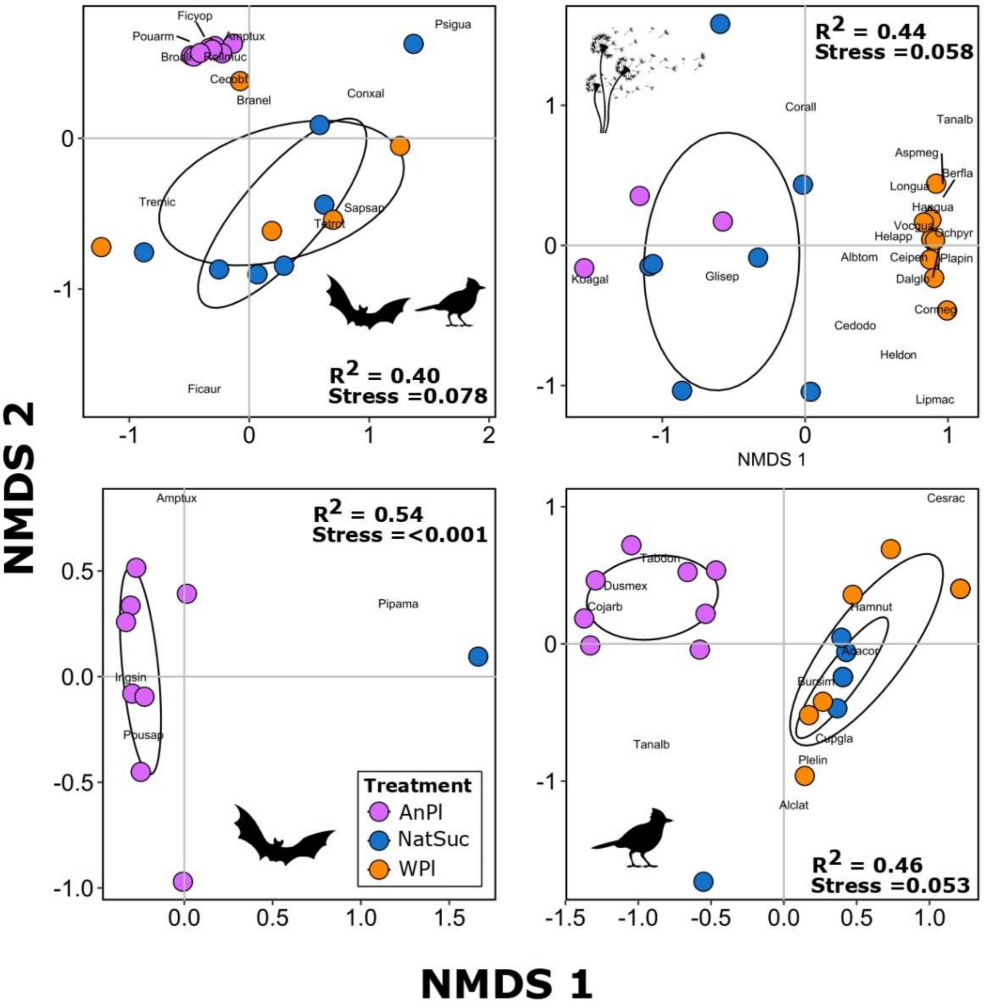


**Fig. 6**. Non-Metric Multidimensional Scaling analysis (NMDS) to discriminate composition of large planted and recruited trees by dispersal vector in 24 30 X 30 m plots under three restoration treatments: Animal Plantings (AnPl, purple; N=8 plots), Wind Plantings (WPl, orange; N=8 plots) and Natural Succession (NatSuc, blue; N=8 plots) in Los Tuxtlas, Veracruz, Mexico. $R^2$ from PERMANOVA and stress values from NMDS analysis are shown (Table S7a). Ellipses were drawn at the 95% confidence level (Table S7b); ellipses could not be drawn for wind-dispersed trees in AnPl and bat-dispersed trees in NatSuc and WPl due to n<4. Codes of species are in Table S8.

*Birds*.- Richness and number of large planted and recruited trees dispersed by birds were similar among treatments (Fig. 4). Average richness of large recruits dispersed by birds was higher in Wind Plantings (2.4 ± 0.8 species) than in Animal Plantings (0.9 ± 0.4 species); Natural Succession had intermediate values (1.5 ± 0.2 species; Fig. 5). Average number of large recruits dispersed by birds was higher in Wind Plantings (6.3 ± 2.5 trees) than in Animal Plantings (2.1 ± 0.8) and Natural Succession (3.6 ± 0.5 trees), these last two were statistically similar (Fig 5). Composition of large planted and recruited trees dispersed by birds was unique in Animal Plantings, while Wind Plantings and Natural Succession showed similar composition (Fig. 6, Tables S7a&b). One planted species, *Cojoba arborea*, was associated with Animal Plantings (Table S8).

*Wind.*- Average richness (9.88 ± 0.64 species) and number (40.75 ± 5.87 trees) of large planted and recruited trees dispersed by wind were higher in Wind Plantings compared with Animal Plantings (1.00 ± 0.50 species, 1.63 ± 0.71 trees) and Natural Succession (2.25 ± 0.49 species, 5.50 ± 2.19 trees; Fig. 4). Average richness of large recruits dispersed by wind was higher in Natural Succession (2.0 ± 0.5 species) than in Animal Plantings (0.8 ± 0.4 species); Wind Plantings had intermediate values (1.4 ± 0.4 species; Fig. 5). Average number of large recruits dispersed by wind was lower in Animal Plantings (1.3 ± 0.6 trees) compared with Natural Succession (3.5 ± 1.1 trees) and Wind Plantings (1.9 ± 0.6 trees), these last two were statistically similar (Fig. 5). Composition of large planted and recruited trees dispersed by wind was unique in Wind Plantings, while Animal Plantings and Natural Succession showed similar composition (Fig. 6, Tables S7a&b). Seven planted and one recruited species dispersed by wind were associated with Wind Plantings (Table S8).

## 4. Discussion

The forest structure of large trees (≥ 30 cm DBH) in these restoration settings depended on the successional status and dispersal vector of the planted and recruited species. After a decade (1) planted late-successional species dominate, proving that 20-30 years of succession were skipped in plantings; (2) Bird-dispersed species recruited successfully at young plantings of wind-dispersed species.

In these restoration settings, we planted twice as many late-successionals as early-successionals; late-successionals thrived as well as early-successionals, supporting the *tolerance model* of succession. Regarding recruits only, *tolerance model* was also supported given that a similar number of early- and late- successional trees recruited and reached large size at all treatments. This model suggest that all species arrive at the beginning of succession, but they will dominate at different times, depending on their growth rates and mortality (Connell and Slatyer, 1977; Chazdon *et al.*, 2007): late-successionals are expected to dominate after early-successionals die off (20 to 30 years; Finegan 1996). In this study, the 15 planted late-successional species recorded as large trees showed lower initial survival and diameter growth rates than early-successionals, as expected (Martínez-Garza *et al.*, 2013b). Legumes were an exception: some planted $N_2$-fixing late-successional species (e.g., *Cojoba arborea*, *Inga sinacae*) became large trees, with growth rates as high as those of early-successionals (Martínez-Garza *et al.*, 2016). Further, $N_2$-fixing late-successional species *Albizia tomentosa* was planted but also recruited naturally, revealing that seedlings from both origins showed similar growth rates in height (1.59 ± 1.44 and 2.19 ± 2.16 cm/month) and in diameter at the base (0.86 ± 1.60

and 1.19 ± 1.64 mm/month) for the first 5 years, even when transplants showed higher mortality (*transplant shock*; Guzmán-Luna and Martínez-Garza 2016). Connell and Slatyer (1977) stated that to confirm later stages of the *tolerance model*, it was necessary to register that "…*invasion and growth to maturity of later species neither requires conditions produced by earlier species nor are inhibited by them*", this fact has been verified in the present study. Finally, compared with natural succession, plantings have more late-successional species and trees, corroborating that the early stages of succession have been successfully skipped due to thriving planted trees; also, plantings of animal-dispersed species recruited the lowest number of early-successional species, suggesting that natural succession was at more advanced stage there.

Composition of large trees in the restoration treatments is driven by thriving planted species while composition heterogeneity (i.e., size of the ellipse in figures 3 and 5) is driven by successful early recruitment.  The differential survival and growth of the planted late-successionals resulted in distinctive compositions in each planting treatment: in plantings of animal-dispersed species, a range from 0 to 56% of the trees planted per species were registered as large ones after a decade while for plantings of wind-dispersed species the range was from 3 to 49%. Lower composition heterogeneity of late-successionals under natural succession revealed similar composition of these species recruiting among those plots. Further, only three late-successional species that recruited naturally and reached large size were recorded under all treatments while another three late-successional species did not recruit under Natural Succession (Table S2). The mechanisms explaining these results are early dispersal limitation and tree demography, predation and competition. Evaluation of seed rain in the restoration setting for the first years, revealed that the composition of late-successional species arriving at pastures comprised a different group of species compared to those landing in secondary and primary forest (Martínez-Garza *et al.,* 2009). Further, dispersal limitation in the first year was highest for late-successional species dispersed by animals (de la Peña-Domene et al.2018). Further, in pastures excluded from cattle, herbivores may decimate seeds and seedlings of late-successionals, later, exotic grasses may prevent surviving seedlings from thriving, decreasing rates of natural recruitment (Nepstad *et al.*, 1990; Guzmán *et al.*, 2021). In contrast, composition heterogeneity of early-successionals was highest in natural succession and lowest in plantings of animal-dispersed species revealing that five of the planted early-successional species also recruited in natural succession and eight early-successional species that recruited in natural succession, did not recruit in plantings, increasing the composition variability among plots under natural succession. On the other hand, all the plantings of species dispersed by animals welcomed few new early-successional species (Table S1). This agrees with results from restoration plantings in Brazil, where plantation favored less natural recruitment than nucleation and plots under natural succession (Bechara *et al.*, 2021). At natural succession, higher rates of change in community attributes may be registered for years to come but also, in some plots dominated by early-successionals, succession might be arrested (i.e., *inhibition model*), due to a high predation of seeds and seedlings of late-successional species and competition with exotic grasses and ferns.

Part of the long-term success of restoration plantings relies on their influence of large trees in the future recruitment processes given by their dispersal vector. In general, areas with trees bearing fleshy fruits are expected to speed succession in comparison with trees with dry fruits (Wunderle, 1997; Camargo *et al.*, 2020). The *tolerance model* predicts that planted trees dispersed by wind or animals will be dominant where planted while for recruits, potential mobility of dispersal vectors early in succession was predicted to determine presence of large trees after a decade. Our results, when planted and recruited trees were included, support the *tolerance model* for trees dispersed by bats, both (birds and bats) and by wind while for species dispersed by birds another pattern emerged. When recruits were evaluated separately, potential mobility of dispersal vectors only explained presence of trees dispersed by bats.

When including planted and recruited trees, the richness and density of large trees dispersed by bats and, by both bats and birds were higher in the plantings of animal-dispersed species, as expected. Also, as expected, including only recruits, a similar richness and abundance of trees dispersed by bats were registered at all treatments. Bats defecate during flight, so they are expected to frequently disperse seeds into open areas (Fleming, 1988), like the pastures when plantings were newly established (Fig. 1a). Also, small bats disperse many small seeds of few species (Medellin and Gaona, 1999; Galindo-Gonzalez *et al.*, 2000; Fleming and Kress, 2011), increasing the probability of their early recruitment (de la Peña-Domene *et al.*, 2014). In this experiment, counts of bats one year after planting over 192 net hours (two 12 m mist nets set in each plot for one night), yielded only three individuals of *Sturnira lilium* (Howe and Martínez-Garza, 2012). *S. lilium* is a small frugivorous bat (17 gr) that is abundant in agricultural landscapes (Estrada and Coates-Estrada, 2002) and is known to disperse early-successional trees and shrubs of the genera *Solunum*, *Piper*, *Cecropia*, and *Ficus* (Marinhofilho, 1991; Gonzalez-Cerezo *et al.*, 2018). In this study, the only recruited species dispersed by bats was the early successional *Piper amalago*. Large trees belonging to these genera dispersed by *S. lilium* were recorded in the restoration plots yet, they could also be dispersed by birds (see Table S2). Even when there is a small amount of overlap in the diet of bats and birds (Fleming, 1988; Gorchov *et al.*, 1995), the few tree species dispersed by both may reach more habitats than those dispersed by one or the other (Jacomassa and Pizo, 2010). This was supported by our results: the number of recruited species (7) and trees (50) dispersed by both birds and bats was much higher than those dispersed by bats only (1 sp, 2 trees; Table 1 & S2). Further, the richness and number of large recruited trees dispersed by both bats and birds were higher in natural succession than in plantings of animal-dispersed species; more intriguing, richness and number of large trees dispersed by both bats and birds were similar in natural succession and plantings of wind dispersed species despite higher number of seeds of early-successional species falling in plantings of animal dispersed species (132 seeds) than in natural succession (72 seeds) and plantings of wind dispersed species (27 seeds; Martínez-Garza *et al.,* 2009; Urincho-Pantaleon, 2010). These results suggest that plantings composition did have an early effect on establishment of trees; animal plantings seem to offer inferior conditions for recruitment of early-successional tree species.

Of the species likely dispersed by both bats and birds, *Cecropia obtusifolia* (Urticaceae) was the most abundant species in these plots. This species is found in forest fragments embedded in pastures (Guevara *et al.*, 1994; Martínez-Garza and González-Montagut, 1999). *Cecropia* has a tiny seed (0.0007 gr; Ibarra-Manríquez and Oyama, 1992) that is potentially dispersed by 48 animals inhabiting the areas: 33 resident or migratory birds and 13 flying, terrestrial or arboreal mammals (Estrada *et al.*, 1984). Still, four times more *Cecropia* trees were recorded as planted (76 trees) than naturally recruited (18 trees; Table S2); therefore, even the most successful early-successional tree of this landscape may suffer high establishment limitation in pastures.

The richness and number of planted and recruited large trees dispersed by birds converged among treatments, contrary to our predictions. Also, contrary to predictions, the number of recruited species and trees was higher in plantings of wind-dispersed species. In these same experimental plots, recruitment data for the first 6 years showed 20 bird-dispersed tree species establishing (de la Peña-Domene *et al.*, 2014). Of those, the species recorded as reaching large size have small seeds (range 0.003-0.19 g; (Ibarra-Manríquez and Oyama, 1992), suggesting that they were dispersed by small birds. According to this, a study of birds moving in different habitats of an agricultural landscape in Brazil showed that few birds, mostly small ones (< 40 gr) that consume small seeds, visit active pastures (DaSilva *et al.*, 1996). This was also observed in the early stages of this study: five bird species were recorded in the plots one year after fencing, although many more were seen flying over the pastures (Howe, 2017). The most abundant bird-dispersed species among recruits was *Bursera simaruba* (Burseraceae); this species is common in this landscape due to its use in living fences (Budowski and Russo, 1993; Howe *et al.*, 2010). *Bursera* was not recorded in the seed rain of the first year (Martínez-Garza *et al.*, 2009) but it was recorded establishing soon after fencing in all restoration treatments, suggesting that seeds that recruited early in the experiment were already present in the seed bank (Howe *et al.*, 2010). Further, higher number of species and trees of large recruited trees dispersed by birds in plantings of wind-dispersed species suggests that the planted species with the highest initial height (Martínez-Garza *et al.*, 2013a), *Heliocarpus appendiculatus* (Tiliaceae; 40.3 ± 13.6 cm) and *Ochroma pyramidale* (Bombacaceae; 39.8 ± 19.2) were used as perches by these small birds. Plantings of species dispersed by animals had a unique composition of large trees dispersed by birds given planted species (i.e., *Tabernaemontana donnell-smithii, Cojoba arborea and Dussia mexicana*) that were not recorded in the other treatments. Planted species have large seeds (ranging from 0.065 to 3.40 gr; Martínez-Garza *et al.*, 2013b) and were never recorded in the early seed rain (Martínez-Garza *et al.*, 2009). Other large seeded species have arrived at the restoration settings but have not yet reached ≥30 cm DBH. For example, IUCN listed *Ocotea uxpanapana* (Lauraceae) was recorded in these restoration settings when the recovered canopy favored the movement of larger birds (de la Peña-Domene *et al.*, 2016). Therefore, small birds visited and dispersed small-seeded species to the barren pasture perching in saplings of planted wind-dispersed species, resulting in a higher richness and abundance of bird-dispersed trees at plantings of wind dispersed species. Currently, including planted and recruited trees, they are a similar number of species and trees dispersed by birds which are large and reproductive and will attract and feed birds in all restoration settings, speeding succession.

A higher richness and abundance of large trees dispersed by wind were registered in the plantings of wind-dispersed species, as expected given thriving plantings. For recruits, higher number of wind-dispersed species and trees were registered in natural succession than in planting of species dispersed by animals, contrary to our predictions. This suggests, as show above for other species, stronger establishment limitation in plantings of animal-dispersed species (Wunderle, 1997; Ingle, 2003) despite a general low dispersal limitation in of wind-dispersed species in open areas (Nathan, 2006; San-José *et al.*, 2020). From the 18 wind-dispersed species registered as large trees, five early- and one late-successional species recruited naturally (Table 1). Forests dominated by wind-dispersed species were expected to have a lower recruitment of animal-dispersed species and therefore a lower successional speed (Wunderle, 1997); here, unexpected positive effect of taller saplings of wind-dispersed species on recruitment of bird-dispersed species were shown (see above). Further, the plantings of late-successional wind-dispersed species established here may act as local populations, decreasing the probability of extinction of a meta-population in permanent agricultural landscapes (Vandermeer and Carvajal, 2001), given that their natural recruitment is not expected for a long time, if ever.

## 5. Implications for management

Small recruits in restoration plots represent the future forest structure in areas under intervention, but for these synthetic fragments to serve as metapopulations, trees must reach reproductive size (see van Breugel *et al.*, 2013). The structure provided by large trees act as stepping stones for animals that move seeds through permanent agricultural landscapes.

By elucidating which model of succession fit the forest structure in permanent agricultural landscapes, management actions to further accelerate forest recovery can be suggested. Connell and Slatyer (1977) suggested management actions for each model: when the *facilitation model* is identified, early-successionals should be favored; in the *tolerance model*, late-successional should be favored and early-successional deterred (e.g., Swinfield *et al.*, 2016) and when the *inhibition model* is identified, early-successionals should be removed and late-successional should be planted (e.g., Boyes *et al.*, 2011). In this study, the *tolerance model* was identified in mixed plantings of early- and late-successionals. Areas under natural succession harbored more species (22) and individuals (101) of large, naturally recruited trees than plantings due to higher available space, but more than half of the species (16) and trees (59) were early-successionals (Table S2). Initial analysis of reproductive potential showed that growth rates of recruits in areas under natural succession are higher than growth rates of those trees recruiting in plantings given higher light levels; therefore, recruits in natural succession may reach reproductive size earlier (Caughlin *et al.*, 2019). However, it has been shown that after cattle exclusion, rodent populations in pastures grow exponentially in the first few years, when grasses are abundant and tree cover is sparse (Howe and Davlantes, 2017). Rodents may suppress the establishment of late-successional species, especially those with smaller seed size (Guzmán et al., 2021), that are also the ones with the highest probability of arriving to pastures early in succession (Martínez-Garza et al., 2009). Thus, if areas under natural succession recruit mostly early-successional species, a *pioneer desert* may develop (Martínez-Garza and Howe, 2003), and may not favor the establishment of new species for a long time (*inhibition model*; Connell & Slatyer, 1977). This highlights the importance of planting late-successional tree species with inherently low mobility (i.e., large seeded species) to accelerate succession back to forest.

There has been some debate about whether natural succession or plantings accelerate the restoration of biodiversity or ecosystem function (see for example, Meli *et al.*, 2017; Jones *et al.*, 2018). Our results show that both treatments should be used: increasing heterogeneity improves the matrix for the movement of seeds and animals in agricultural landscapes (Vandermeer and Carvajal, 2001) and favor forest landscape restoration (Stanturf *et al.*, 2017); to this end, planting as many species in as many combinations as possible and including protected areas without plantings for natural succession to occur (Chazdon *et al.*, 2020) will increase the number of microhabitats available for frugivorous animals to disperse seeds and for plants to establish (see (Abeysinghe and Punchi-Manage, 2020). Planting designs such as nucleation (reviewed in (Bechara *et al.*, 2016) should also be incorporated, as this is relevant for the restoration of large areas. Also, planting a mix of early- and late-successional tree species will favor gap dynamics in older areas and thus maintain tree diversity (de Oliveira *et al.*, 2019). Later, cutting some early- successional trees may favor further recruitment and growth of late-successional species (Swinfield *et al.*, 2016). Heterogeneity in restoration settings will allow a differential response of these areas to unpredictable but expected changes in climate conditions (Anderson-Teixeira *et al.*, 2013; Howe and Martínez-Garza, 2014; Uriarte *et al.*, 2016). Ultimately, landscape heterogeneity will trigger more complex interaction networks that will foster recovery of ecosystem functions.

## 6. Conclusions

Our results showed that after a decade of intervention, early stages of natural successional was skipped in the plantings by 20-30 years. Further, areas under natural succession harbor a higher composition heterogeneity of early-successional species given greater natural recruitment. Establishing plantings with different tree composition including species with low mobility (i.e., large seeded species), together with areas protected for natural succession to take place, increases overall richness of large trees to favor forest landscape restoration and to maintain diversity of plants and animals in permanent agricultural landscapes.

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## Authors' contributions

C.M-G, E.R-A and M.dP-D conceived the ideas, designed methodology and collected data. E.R-A and M.M-T analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.

## Data availability statement

All data is included in supplementary tables.

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