Title: Persistent effects of landscape connectivity on recruitment dynamics in secondary forests

Running title: Recruitment dynamics in secondary forests

Authors: Michiel van Breugel[1, 2,*], Jefferson S. Hall[2], Mario Bailon[2], Dylan Craven[3,4]

[1] *Department of Geography, National University of Singapore, Singapore*

[2] *Smithsonian Tropical Research Institute, Panamá, Panamá*

[3] *GEMA Center for Genomics, Ecology & Environment, Universidad Mayor, Camino La Pirámide 5750, Huechuraba, Santiago, Chile*

[4] *Data Observatory Foundation, ANID Technology Center No. DO210001, Eliodoro Yáñez 2990, 7510277, Providencia, Santiago, Chile*

[*] *Corresponding author: mvbreugel@gmail.com*

Contents

Abstract

Large scale reforestation is promoted as an important strategy to mitigate climate change and biodiversity loss. A persistent challenge for efforts to restore ecosystems at scale is how to accelerate ecological processes, particularly natural regeneration. Yet, despite being recognized as an important barrier to the recovery of diverse plant communities in agricultural landscapes, the impacts of dispersal limitation on natural regeneration in secondary forests – and especially how this changes as these forests grow older – is still poorly studied at local and landscape scales. Here, we evaluate the multi-scale impacts of proximity to a connected network of forest fragments on recruitment in 1–40-year-old secondary forest. We used eight years of annual census data from 45 sites with paired plots, one directly adjoining a streamside forest fragment and the other further uphill, and a null model approach to test the effects of basal area and proximity to streamside forest fragments. In general, we found that proximity to streamside forest fragments enhanced multiple aspects of recruitment across spatial scales, including species diversity and the proportion of rarer and less-widely distributed species among the recruits. Unexpectedly, this effect did not weaken over time, despite a fast increase in stand basal area, canopy complexity and diversity. This suggests that successional changes in forest structure may not be sufficient to attract the animals that disperse rarer tree species. Our results provide empirical evidence to guide restoration initiatives in agricultural landscapes in tropical regions, principally prioritizing the restoration of forest corridor networks along streams, while also highlighting the knowledge gap about restoring animal dispersers in secondary forests.

Keywords: ecological succession, secondary forest, forest fragments, recruitment dynamics, seed limitation, dispersal corridors, natural regeneration, forest restoration

1. Introduction

Most tropical landscapes that were once covered with forests are now at least partly deforested and dominated by agricultural land uses (Carter et al., 2017; Harvey et al., 2008; Pendrill et al., 2022), which has led to alarming rates of biodiversity loss (Almond et al., 2022; Alroy, 2017; Barlow et al., 2016; Decaëns et al., 2018) and a decline in ecosystem services provided by forests (Estoque et al., 2018; Hall et al., 2015; Lima et al., 2014; Portela & Rademacher, 2001). The last decade has seen a large number of ambitious forest restoration initiatives that aim at slowing or even reversing these losses. The Bonn Challenge, for example, currently includes 70 pledges from more than 60 countries to restore 210 million hectares of degraded and deforested lands within the coming decade (Dave et al., 2019; www.bonnchallenge.org). In addition, buttressed by a handful of international agreements and the UN Decade on Ecosystem Restoration, large scale reforestation is promoted as an important strategy to mitigate climate change and consequently, official and voluntary carbon credit markets provide a growing source of funding for forest restoration projects (Brancalion et al., 2017; Busch et al., 2019). These developments exert growing pressure to accelerate efforts to scale-up reforestation (Edwards et al., 2021; Vincent et al., 2021). Given the ability of secondary forests to rapidly sequester carbon and restore species diversity and ecosystem services (Hall et al., 2022; Poorter et al., 2021), and the challenges and costs associated with active reforestation on infertile soils (Coleman et al., 2021; Sinacore et al., 2023), arguably one of the most effective approaches to restore forest ecosystems is natural regeneration (Cook-Patton et al., 2020; Crouzeilles et al., 2020; but see Lippke et al., 2021).

Key to the successful application of natural regeneration as part of a forest landscape restoration strategy is the presence of seed sources and connectivity (Crouzeilles et al., 2016; Harvey et al., 2008; McConkey et al., 2012; Zahawi et al., 2021). In the highly fragmented landscapes in which tropical secondary forests generally are embedded, the abundance and diversity of local seed sources is more limited (Gardner et al., 2009; Harvey et al., 2008; Ngo Bieng et al., 2022), as open crop fields and pastures impose strong barriers to seed dispersal (e.g., Aide & Cavelier, 1994; Charles et al., 2017; Holl, 1999; Laborde et al., 2008; Wijdeven & Kuzee, 2000;

Wunderle, 1997; Zimmerman et al., 2000). This is especially true when a large proportion of the tree species are animal dispersed, as is the case in many tropical regions (Corlett, 2016; Estrada-Villegas et al., 2022; Howe & Smallwood, 1982; Rogers et al., 2021; Seidler & Plotkin, 2006), with many forest-dependent dispersers rarely or never venturing far outside closed-canopy forests (Bello et al., 2024; Harvey et al., 2008; Mendenhall et al., 2016; Moore et al., 2008). In such landscapes, networks of connected forest fragments are thought to mitigate these constraints by providing seed sources and the habitat that enables animal dispersers to persist in and move through the landscape (Anzures-Dadda & Manson, 2007; Bennett, 2003; Caughlin et al., 2016; Mitchell et al., 2018; San-José et al., 2022; Zahawi et al., 2021). However, we still lack long-term studies that test the effects of forest fragments and corridors on species recruitment across secondary forests in human-modified tropical landscapes at multiple spatial scales (e.g., local and landscape), and changes therein during succession (Arroyo-Rodríguez et al., 2017; Chazdon et al., 2009; Palma et al., 2021).

If seed limitation (Clark et al., 1998) is a major factor in the assembly of plant communities, we expect proximity to forest fragments to be reflected in spatial recruitment patterns within early successional forests. Specifically, we would expect diversity of newly recruited plants to decline with increasing distance from forest fragments (Cubiña & Aide, 2001; Dosch et al., 2007; Garate-Quispe et al., 2023; González-Castro et al., 2019; but see Lasky & Keitt, 2012; Zahawi et al., 2021). In addition, we would expect newly recruited plants closer to forest fragments to have a higher proportion of rare species and larger-seeded species (González-Castro et al., 2019; Piotto et al., 2019). However, few studies have tracked the effects of proximity to forest fragments on recruitment patterns in secondary forests beyond the first few years of forest succession. This reflects a general paucity of studies on the role of seed source and dispersal limitation in the context of forest restoration through natural regeneration, despite its importance in determining the assembly of plant communities during succession, the rate of forest recovery, and the success of restoration initiatives (Chazdon et al., 2009; Dent & Estrada-Villegas, 2021; Kulikowski et al., 2022; Turnbull et al., 2004) (but see, e.g., Piotto et al., 2019; Verheyen & Hermy, 2001).

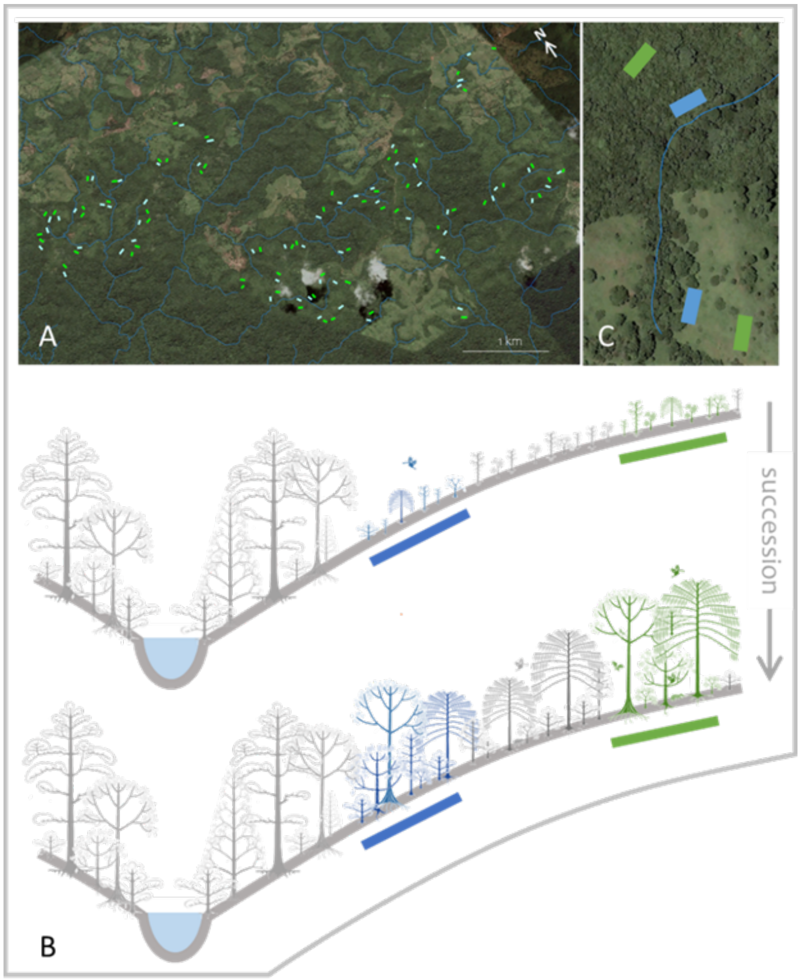

Figure 1. Study design of the Agua Salud Secondary Forest Dynamics study in central Panama. **A**) Distribution of secondary forest plots. A total of 54 sites were selected in 49 0-32 year old forests and 5 >50 year old forests. In each site, one 10x50m plot was established at the lower end of the hill slope, adjacent to the streamside secondary forest fragment (blue) and one plot at the upper section of the hill slope (green). Distance between plots was 23-149m (mean ± sd: 83 ± 25 m). The satellite image is from July 2011, 2 years after the start of the study. The contiguous forest at the bottom of the photo is Soberania National Park. **B, C**) At the onset of succession, the upper slope plot is more isolated, with no direct connectivity to the larger network of forest fragments along streams. In contrast, forest regrowth creates a continuous forest cover along the slope later in succession. C) For illustrative purposes only, rectangles are at scale but do not represent real plot locations.

In the humid lowland tropics, recruitment early in succession is generally dominated by a relatively small group of widely distributed and small-seeded plant species that are dispersed by wind, bats, and birds. As secondary forests grow, decreasing light levels in their understory increasingly limit the establishment of many species of this group, while more seed-limited but shade-tolerant species are more likely to continue recruiting (Craven et al., 2015; Lai et al., 2020, 2021; Lohbeck et al., 2013; Reid et al., 2015; Rüger et al., 2023; van Breugel et al., 2013).

At the same time, the taller and more diverse canopy of older secondary forests provides a more hospitable environment for seed dispersing animals, attracting a higher number and diversity of birds, bats, and non-volant animals (Acevedo-Charry & Aide, 2019; Borges et al., 2021; DeWalt et al., 2003; Hilje et al., 2020; Moran et al., 2004; Muscarella & Fleming, 2007) Succession can thus be described as a process of concurrent feedback loops between a changing environment caused by forest growth and the differential response of plant species in terms of availability and performance (van Breugel et al., 2024). This implies that, as succession proceeds, recruitment patterns within sites are increasingly shaped by local plant communities and less by proximity to adjacent older forest fragments (Chase & Myers, 2011; Huanca Nuñez et al., 2021). Indeed, this is a basic premise of many ecological restoration programs that involve tree planting to accelerate natural regeneration, such as the framework species approach (Elliott et al., 2022) and applied nucleation (Corbin & Holl, 2012; Kulikowski et al., 2022).

Here, we use an eight-year study on secondary forest dynamics to test the hypothesis that proximity to a connected network of forest fragments moderates recruitment dynamics in secondary forests. The study includes 45 0-30y old secondary forest sites, each with one plot in close proximity to and another plot further from narrow strips of older secondary forests along the streams that border the study sites (SFF; Fig. 1). We further hypothesize that feedback dynamics between the regrowing vegetation and dispersers (an environment–species-availability-feedback loop, sec. van Breugel et al., 2024) leads to a weakening of an initially strong effect of proximity to the SFFs on recruitment as succession proceeds. Based on these hypotheses, we predict that, within a secondary forest, the diversity of tree recruitment is higher, with more rare and large-seeded species, in plots adjacent to SFF than in plots further from SFFs. We further expect the composition of recruitment closer to SFFs to be more similar to the composition of the extant trees in adjacent forest fragments than recruitment further from SFFs. Across the landscape, we expect that recruitment closer to SFFs will be more influenced by variation in rarer, more dispersal limited species in the local species pools, and recruitment further from SFFs to be more dominated by species that are widespread. This would lead to higher species turnover among plots closer to SFFs and, consequently, a higher landscape-scale diversity. We therefore predict that the effect of proximity to SFFs on recruitment dynamics weakens over the course of succession at both local and landscape scales.

2. Methods

2.1 Site description

Our study was conducted as part of the Agua Salud Project that seeks to explain how different land-uses and forest restoration approaches impact ecosystem services in rural tropical landscapes. The study area is located in a 15 km^2 area in the central Panama Canal watershed (9°13' N, 79°47’ W, 330 m amsl), adjacent to the 19,545 ha Soberania National Park (SNP), which consists of a mosaic of ≥ 80 year old secondary and old-growth forests and which is part of a much larger buffer zone that runs from the Atlantic to the Pacific coast along the Panama Canal. Annual precipitation averages 2700 mm per year, with a dry season from mid-December to early May (Ogden et al., 2013). The area is characterized by an undulating topography, with short, steep slopes intersected by a dense network of narrow streams (Hassler et al., 2011)(Fig. 1a). Soils are classified predominantly as Inceptisols, and are strongly weathered, infertile, and well drained. Topsoil texture (silty clays to clays) and soil nutrient concentrations vary little across the landscape (Neumann-Cosel et al., 2011; van Breugel et al., 2019). On a local scale, soil fertility and dry season soil water tend to be slightly higher at downslope locations than at locations towards the top of the hill slopes, even though this varies strongly from site to site (Fig. S1). The landscape is dominated by active and abandoned cattle pastures and secondary forest of different ages (van Breugel et al., 2013). Over at least the last 40 years (age of oldest plot in this study at the end of the study), farmers have typically preserved narrow strips of secondary forest fragments alongside streams that cross or border their active pastures. These fragments cover on average 14.3% (± 6.6 sd) of the pasture areas (Suppl. Information SI1) and presumably act as corridors that connect many parts of the landscape to the SNP (Estrada-Villegas et al., 2022).

2.2 Field data

In 2009, 54 sites were randomly selected within the study area and information on land-use history and time since abandonment was acquired from interviews with former landowners and local residents and corroborated with aerial photos. Sites were defined as a single slope within a secondary forest on an abandoned pasture. Two plots of 20 m x 50 m were established in each site; one plot near the bottom of the slope adjacent to the streamside CFF (LS plots) and another near the top of the slope (US plots; Fig. 1). The age of streamside fragments was unknown but was always at least a decade older than the secondary forest on the hill slope (and thus the study plots). Distance between plots within a site ranged between 23 m and 149 m (mean ± sd: 83 ± 25 m). The age of the five oldest sites was not known (but > 50 years) and in four sites the upper and lower slope plots turned out to be of different ages. These nine sites were excluded from analyses that compare slope positions within sites, but not from the landscape-scale analyses. Time since abandonment of the other sites at the onset of this study varied from one to 32 years (Fig. 1).

In each plot, all stems of trees, shrubs, and palms with a diameter-at-breast-height (DBH) equal to- or more than five cm and all stems of woody climbing plants with a diameter of one cm or more were tagged, identified and their DBH was measured. In one-half of each plot, stems of trees, shrubs, and palms with a DBH of 1 to 4.99 cm DBH were also included (van Breugel et al., 2013). From 2009 until 2017, the growth and mortality of established plants and the recruitment of new plants, i.e., individuals that surpassed the size threshold since the previous inventory, was monitored annually, with the exception of 2013 (Lai et al., 2017, 2018).

Data on the floristic composition of streamside CFFs adjoining the study sites was collected in 2010. An inventory of trees ≥ 20cm DBH was performed in two-meter wide transects perpendicular to the stream, from the waterside to the border of streamside vegetation at 5 m intervals over a total distance of 150m, at alternating sides of the stream. The average length of these transects – and thus mean width of the SFF – was 11.8m (± 0.19 SE) and the mean combined sample area of the transects in the SFFs was 737m^2 (± 26 SE) (Suppl. Info. SI3).

Seed dry mass data (g) was collected for 88 common species in the Agua Salud study area. For another 140 species, seed mass data was collected from trees in forest plots across the Panama Canal Watershed (Wright et al., 2010). Seeds were collected from 3 to 6 trees per species. Per species, seed mass data was calculated from 2 to 6 fruit replicates, with each replicate consisting of between one and >20 seeds, depending on seed size. Seed dry mass was measured without testa, unless seeds were too small to separate the testa from the seed. We acquired seed dry mass data for an additional 51 species from published databases (Daws et al., 2004; Moles et al., 2007). In the case of multiple data sources, priority of seed dry mass was given to measurements taken locally, followed by data collected in the region, to data collected at other sites. Seed mass data covered on average 80.7% (± 6.4 SD) of the species and 89.6% (± 7.1 SD) of individuals in the study plots.

2.3 Explanatory variables

The main variables of interest in our study were plot basal area (m^2ha^{-1}) and landscape context. Landscape context was defined as either lower slope plots adjacent to or upper slope plots further from the streamside strip of older secondary forest (LS and US, respectively). We used basal area and not forest age because, while both are strongly correlated (Fig. 1a), basal area is a better predictor of temporal and spatial variation in local site conditions (e.g., understory light levels; Suppl. Info. SI1)(Lebrija-Trejos et al., 2011; van Breugel et al., 2007, 2013). To model within-site differences in recruitment variables as a function of within-site variability in local site conditions, we calculated the mean of the basal areas of the upper and lower-slope plots ($BA_m = (BA_{LS} + BA_{US}) /2$) and the within-site differences in their basal areas ($BA_{dif} = BA_{LS} - BA_{us}$). Recruitment differences between upper and lower slope plots may also reflect spatial heterogeneity in soil resources within a site. To account for this, we included data on between-plot differences in dry-season soil water content (SWC_{dif}, %) and in soil fertility (SF_{dif})(van Breugel et al., 2019) as predictor variables in our analyses (Suppl. Info. SI2).

2.4 Recruitment variables

We defined recruitment as plants that grew into the ≥ 1cm DBH diameter class during the eight-year study period (2009-2017), irrespective of whether they survived until the last census. Therefore, we used only data from the half of the plot with the 1-cm DBH limit to calculate eight *plot-level* recruitment variables (Table 1). We calculated for each recruitment variable the pairwise differences between the lower and upper slope plots ($RV_{dif} = RV_{LS} - RV_{US}$).

Table 1. Recruitment variables (RV). See Suppl. Info. SI4 for details.

RV	Description
1	Counts of the total number of recruits
2	Species richness of recruits
3	Hill-Shannon diversity of recruits, calculated using Hill number of order 1 (exponential of the Shannon-Wiener index, Jost, 2006)
4	Number of recruited species that were new to the plot
5	Species dissimilarity between the extant trees (≥ 20cm DBH) of the streamside forest fragments and tree recruits within the same site, using Ružička dissimilarity (abundance-weighted analogue of the Jaccard index, Ružička, 1958).
6	The proportion of recruited tree species that were among the species (trees ≥ 20cm DBH) in the streamside older forest fragments
7	Occupancy, i.e. how common the average recruit was across the secondary forests of the Agua Salud study area. For this, we calculated the proportion of all 108 study plots in which the species occurred (henceforth, occupancy). Because site locations were randomly selected, we assume that this represents an unbiased estimation of their prevalence across the secondary forests in the study area (van Breugel et al., 2013). We then calculated for each plot the community-weighted mean (CWM) of the occupancy of recruits, weighted by species' relative abundances.
8	Community-weighted mean of seed dry mass (g) of the recruits

2.5 Statistical analyses

We used generalized linear mixed-effects models to examine successional trends in recruitment variables, how these varied between lower and upper slope plots, and their interaction with plots within site as the random intercept. We fit nested models with subsets of explanatory variables using the 'MuMIn' package (Bartoń, 2020). Prior to analyses, we standardized basal area to a mean of zero and standard deviation of 1. Recruitment variables 1-4 and 8 are count variables and were modelled with the negative binomial family and logit link using the 'lme4' package (Bates et al., 2015). Recruitment variables 5-7 are proportions and were modelled with the beta distribution and logit link using the 'glmmTMB' package (Brooks et al., 2017).We subsequently ranked all models using the Akaike information criterion with a correction for small sample sizes (AICc) and performed model averaging using all models within the top 2 AICc to predict and plot recruitment variables as a functions of landscape context and basal area (Burnham & Anderson, 2004). We used the full-averaging approach because full-averaging minimizes model selection biases and is advocated when the study objective is to produce a predictive model (Symonds & Moussalli, 2011).

To test if recruitment variables 2-8 differed between topographic positions as predicted, we first fitted the linear regression model: $RV_{dif} \sim BA_{m} \times (BA_{dif} + SF_{dif} + SWC_{dif})$ and all nested models. We averaged the coefficients of the selected models as described above, predicted values of the recruitment variables for a range of BA_{m} from 0-30 $m^{2}ha^{-1}$ and with BA_{dif}, SF_{dif} and SWC_{dif} set at zero. Next, we repeated this procedure with three sets of permuted data, each representing a different null model. For the first null model, we permuted the landscape context (LS / US) among the recruits within sites × census, while for the second null model we permuted the landscape context within sites, and for the third null model, we resampled landscape context within sites with replacement. The first null model retains for each plot the observed number of species among the recruits, for each site the observed number of recruits per species, and the observed temporal variation in both. The second null model removes the among-census variability in recruitment and the third null model randomizes, in addition, among-site differences in the number of recruits. For each null model, we permuted the data 1000 times and computed 95% percentile confidence intervals for all predicted values. In other words, we examined successional change in RV_{dif} for a hypothetical site in which the LS and US plots do not differ in soil or stand variables. Because results were similar, we only present the results of the first null model.

To examine the effects of landscape context on landscape-scale diversity of recruits and how this effect changes over the course of succession, we calculated gamma and beta diversity for each landscape context (LS/US) and basal area class. Basal area was calculated at the site level as the mean of both plots within the site and across all censuses. Next, basal area class boundaries were set at 12.2, 16.5 and 20.2 m^2ha^{-1} to obtain four intervals with approximately equal numbers (11 or 12) of plots. We then resampled plots without replacement to obtain an estimated mean number of recruited species per 10 plots for each basal area class. We computed beta diversity for each landscape context as the average pairwise Růžička dissimilarity using the R package 'vegan' (Oksanen et al., 2020). We performed type III ANOVAs using the R package 'car' (Fox & Weisberg, 2019) to test for differences between landscape context, basal area classes, and the interaction between both. We compared observed differences in gamma and beta diversity with expected values using the same null model as discussed above (Suppl. Info., SI8-9).

See Appendices S3-9 for annotated R scripts for data preparation, analyses and visualization and test statistics. The R package 'tidyverse' (Wickham et al., 2019) was a major part of our workflow and all analyses were performed using R Statistical Software v4.0.3 (R Core Team, 2020).

3. Results

The expected number of recruits over an 8-year period dropped sharply over the first decades of succession, from 421 to 60 new saplings per 1000m^2, in forests with initial ages of one and 28 years, respectively. These numbers did not differ between the upper and lower slope plots (Fig. 2a). In contrast, species richness and diversity of the recruits and the number of newly recruited species were, on average, significantly higher in the lower slope plots than in the upper slope plots during the first four decades of succession (Fig. 2b-e). The number of species among the recruits remained constant, with an average of 53 recruited species over 8 years in the lower slope plots and 45 species in the upper slope plot (Fig. 2b). At the same time, the Hill-Shannon diversity of recruits increased over time (Fig. 2c). As species richness of the plant community increased over the course of succession (van Breugel et al., 2013) – meaning that the species in a plot represented an increasing proportion of the local species pool – a decreasing number of recruited species were new to the plot (Fig. 2e).

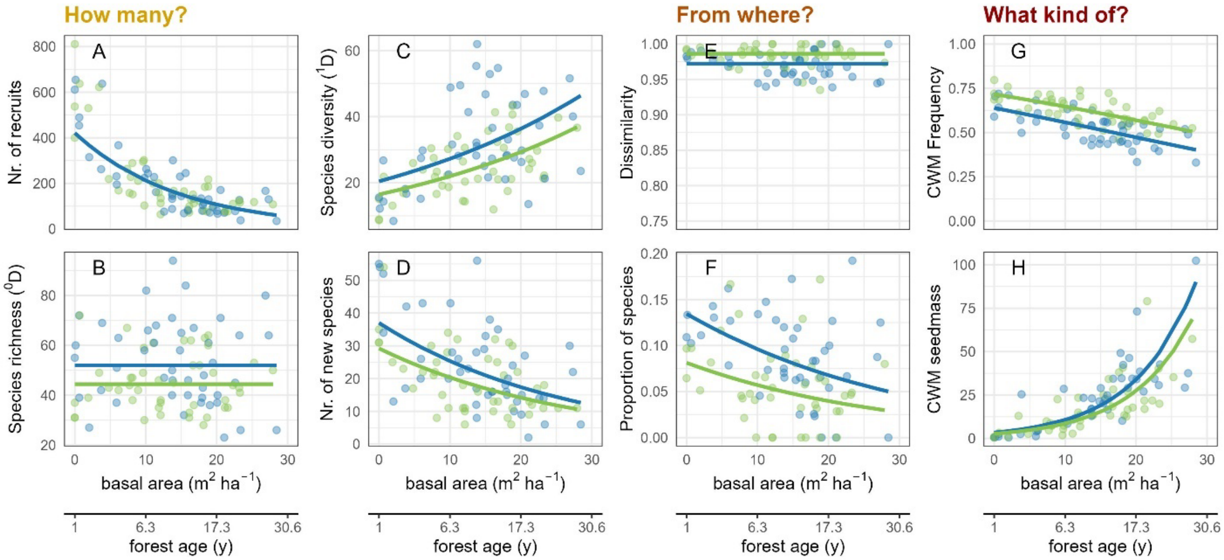

Figure 2. Spatial-temporal variation in recruitment along a successional gradient. Lines plot components of recruitment (recruitment variables; RV) as a function of forest basal area and proximity to streamside forest fragments. The second x-axis gives the predicted forest age for the basal areas on the first x-axis (Suppl. Info., Suppl. Info. SI10). Blue dots and lines represent plots adjacent to older secondary forest fragments along streams that border secondary forest sites and green dots and lines represent the plots located further away from those forest fragments (mean distance: 83 ± 25 m; range: 23-149m). A) RV1: Number of recruited individuals. B) RV2: Number of recruited species. C) RV3: Diversity of recruitment (Hill number of order 1). D) RV4: Number of recruited species that were new to the plot, i.e., not present at the first census. E) RV5: Ružička dissimilarity between extant trees ≥ 20cm DBH in the CFF and the tree recruits in the study plot. F) RV6: The proportion of recruited tree species that were among the species (trees ≥ 20cm DBH) in the CFF. G) RV7: The community weighted mean occupancy of the recruits. Occupancy was quantified as the proportion of 108 sample locations in 54 secondary forest sites in which a species was encountered. H) RV8: community-weighted mean seed mass (g) of the recruits. The eight recruitment variables are numbered as in Table 1.

Compositional similarity and species overlap between recruits in the study plots and extant trees in the strips of older secondary forest along the stream were significantly higher for lower slope plots than for upper slope plots (Fig. 2e,f). Yet, in all sites the species composition of the recruits differed strongly from that of the adjacent streamside forests and the proportion of recruits also found in the streamside forest decreased over the course of succession from an average of 13% to 5% in lower slope plots and from 8% to 2.8% in upper slope plots.

Recruitment in the younger sites was dominated by species that were widespread across secondary forests in the landscape (Fig. 2g), but the dominance of these species among recruits decreased over the course of succession. Community-weighted seed mass of recruits increased rapidly with forest age (Fig. 2h), mostly because of a rapid decline in the recruitment of small-seeded species (Rodriguez Ronderos *et al.*, unpublished data). The steep decline in overall recruitment during succession thus seems to have been driven by a decline in the widely distributed and well-dispersed species, combined with a continuous recruitment of less common and more dispersal-limited species. The community-weighted mean landscape occupancy of recruits was on average 10% higher in upper slope plots than in lower plots (Fig. 2g). In contrast, the community-weighted mean seed mass differed little between lower and upper slope plots (Fig. 2h).

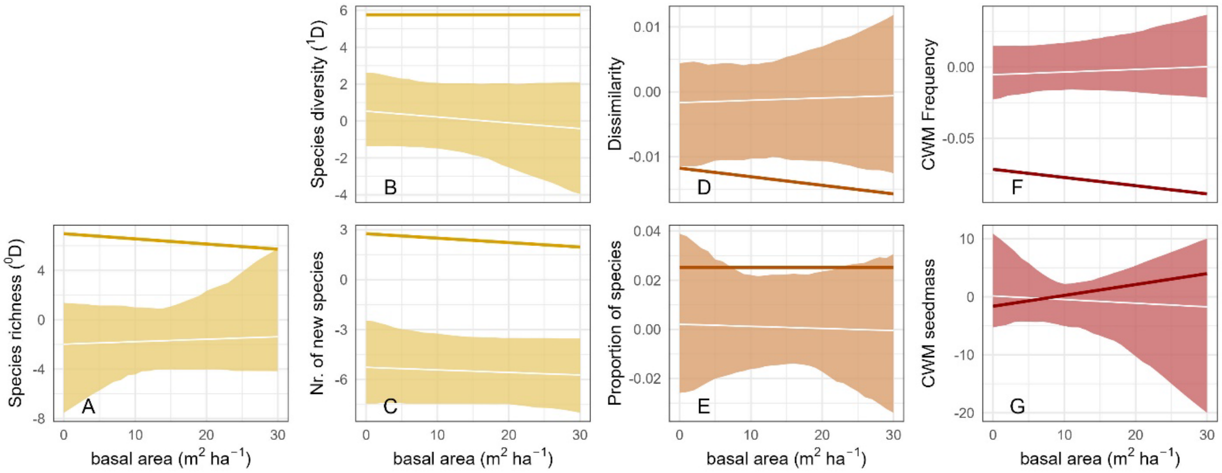

Figure 3. Within-site differences in recruitment ($RV_{LS} - RV_{US}$). Darker lines plot predicted within-site differences in recruitment variables (LS-US plots) and white lines with shaded area plot predictions with 95% percentile confidence intervals from a null model. In both cases, within-site differences in soil fertility, soil water content and forest basal area set at zero (Suppl. Info. SI7). Lines falling outside of the 95% confidence intervals indicate that the observed within-site differences are significantly different from expected differences under the null model. A) Number of recruited species. B) Diversity of recruitment (Hill number of order 1). C) Number of recruited species that were new to the plot, i.e., not present at the first census. D) Ružička dissimilarity between extant trees ≥ 20cm DBH in the CFF and the tree recruits in the study plot. E) The proportion of recruited tree species that were among the species (trees ≥ 20cm DBH) in the CFF. F) The community weighted mean occupancy of the recruits. Occupancy was quantified as the proportion of 108 sample locations in 54 secondary forest sites in which a species was encountered. G) community-weighted mean seed mass (g) of the recruits.

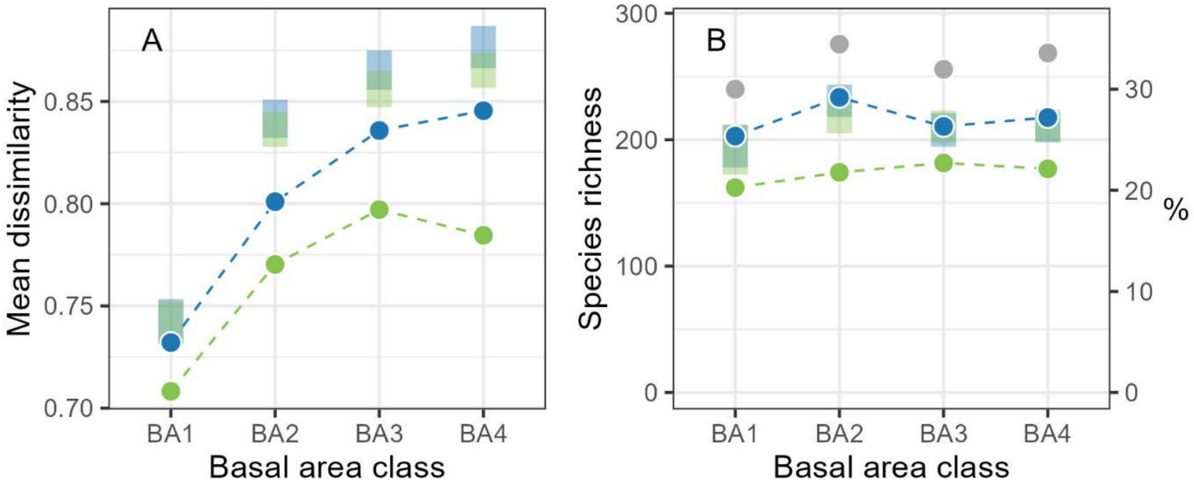

Figure 4. Landscape-scale diversity of woody plant recruitment across 45 secondary forests sites in relationship with forest stature and proximity to streamside forest fragments. Blue series: plots adjacent to the stream-side forest fragments. Green series: further from the forest fragment (mean distance: 83 ± 25 m; range: 23-149m). Grey series: both proximity categories combined. Dots give observed values and shaded bars give the 95% confidence interval of the expected values under a null model of equal probabilities for species to recruit in lower and upper slope plots. Dashed lines are added to illustrate trends. a) Beta diversity, calculated as the mean of the Jaccard dissimilarities among all combinations of plots within forest basal area intervals (see Suppl. Info. SI8 for details). b) Total number of recruited species across 10 plots within each forest basal area intervals. The right-hand axis converts this number into percentage of the estimated total species pool of the total study area. a-b) Basal area classes (BA1-4): 3-12 m^2ha^{-1}, 12-16.5 m^2ha^{-1}, 16.5-20.5 m^2ha^{-1} and 20.5-29 m^2ha^{-1}. See Suppl. Info, SI8 and SI9 for details.

Model predictions for the differences in recruitment between lower and upper slope plots mostly confirmed the patterns discussed above (Fig. 3): Recruitment in lower slope plots was more diverse than in upper slope plots (Fig. 3b-d); their composition was more similar to that of extant tree species in adjacent streamside forest fragments (Fig. 3e,f); and their recruitment was dominated by species that were less widely distributed across the landscape (Fig. 3g). For these six components of recruitment, predictions generally changed little over the course of succession (Fig. 3, dark lines) and for the most part diverged significantly from expectations under the null model (white line with shaded confidence interval). CWM seed mass was the only component of recruitment whose predicted differences between upper and lower slopes did not differ from those expected under the null model (Fig. 3h). Together, these results indicate that components of recruitment of upper and lower slope plots failed to converge over the course of the first four decades of succession.

Of the 426 plant species that recruited in all study plots over the 8-year study period, representing 53% of the 811 species that were found and identified to species-level in the Agua Salud area (Suppl. Info. SI1), 89% recruited in the lower slope plots and 73% in the upper slope plots. The number of recruited species was consistently lower across upper slope plots (Fig. 4b). Moreover, in all basal area classes, overall species richness of recruitment in lower slope plots combined was within the 95% confidence intervals of expected values under the null model. In contrast, gamma diversity of recruitment in upper slope plots was much lower than expected under the null model (Fig. 4b). Beta diversity increased from basal area class 1 to 4 (Fig. 4a). There was little difference between the two slope positions in the youngest forests, but beta diversity diverged quickly as forests grew older, with higher beta diversity among locations adjacent to streamside forest fragments and lower beta diversity among upper slope forests. In all basal area classes and in both slope positions, observed values of beta diversity were significantly lower than expected under the null model.

4. Discussion

A key question when it comes to the conservation and restoration of plant diversity in human-modified landscapes is how variability in landscape connectivity across spatial scales shapes recruitment dynamics across regrowing forests. In our study, streamside forest fragments (SFFs) generated spatial variability in the diversity and distribution of woody plant species that recruit into and across secondary forest patches, reflecting their importance in mitigating seed source and dispersal limitation in fragmented agricultural landscapes.

4.1 Network of forest fragments drives spatial variability in recruitment

We found that the spatial patterns of multiple aspects of recruitment supported our prediction that proximity to streamside forest fragments (SFFs) has a positive effect on recruitment in secondary forests of all ages. Within sites, recruitment in locations adjacent to SFFs had a higher species diversity than locations further afield and their species composition overlapped more with the species composition of the extant canopy trees in adjacent SFFs. This indicates the impacts of dispersal barriers on recruitment during secondary forest succession and highlights that proximity to streamside forest fragments can mitigate seed limitation of more dispersal-limited plant species. While the effect of distance from forest edges has been documented in early post-agriculture forest succession (e.g., Bennett, 2003; Charles et al., 2017; Piotto et al., 2019; Wijdeven & Kuzee, 2000) and in recently planted reforestation sites (e.g., Kulikowski et al., 2022; Pohlman et al., 2021; Zahawi et al., 2021), here we examined the effect of streamside forest fragments on the spatial and temporal dynamics of recruitment over 36 years of succession, at local and landscape scales.

Being connected to larger, contiguous old-growth forest has been found to be critical for the reassembly of diverse disperser communities (Barlow et al., 2007; Dent & Joseph Wright, 2009; M. E. Jones & Davidson, 2016; Luck & Daily, 2003; Moran & Catterall, 2014), including in our study area (Mayhew et al., 2019) and this, in turn, is thought to affect the dispersal of propagules across the landscape (Bello et al., 2024; Link & Fiore, 2006; Moran et al., 2004; Stevenson, 2011; Wright et al., 2000). The low degree of species overlap between recruitment and potential seed trees in the adjoining 150m long segment of the stream-side forest fragments indicates that many seed sources were from further away along the streamside forest fragment. However, the observed decline in the proportion of recruited species that were new to the site during succession, with no change in the total number of recruited species, indicates that recruited species originated predominantly from limited local species pools (i.e., much smaller than the landscape species pool). From these two observations we infer that the streamside forests fragments, rather than facilitating significant long-distance dispersal across the landscape, mitigate dispersal limitation at local scales (Ismail et al., 2017; San-José et al., 2022), resulting in larger, more diverse local species pools available for the colonization of secondary forests close to forest fragments.

We note two caveats. First, we examined sapling recruitment rather than propagule availability (F. A. Jones & Muller-Landau, 2008). This approach does not distinguish among other factors that affect post-dispersal recruitment success, such as germination, establishment, growth and survival (Dalling et al., 2002; Nathan & Muller-Landau, 2000). Second, recruitment differences between upper and lower slope plots could also reflect a topographical gradient in soil resources. Indeed, in an earlier study we found that within-site dissimilarities in species composition were correlated with differences in soil fertility, with no significant effects of forest age and within-site differences in basal area (van Breugel et al., 2019). However, in the present study we accounted for differences in soil fertility, dry season soil water content and forest structure. We therefore conclude that within-site differences in recruitment likely reflect spatial variation in dispersal limitation to a greater extent than local environmental filters (Kraft et al., 2015).

4.2 The role of dispersal limitation in successional feedback dynamics

In contrast to our predictions, we found that the legacy effect of fragmentation continued to shape local recruitment dynamics decades after forest regrowth started. One model of forest succession is that of a successional environment–species-availability feedback loop in which, as succession proceeds, a more complex and diverse canopy attracts an increasing number, diversity and size range of seed dispersers. This, in turn, increases the diversity and the proportion of dispersal-limited plant species dispersed into secondary forests (Caughlin et al., 2016; Dent & Estrada-Villegas, 2021; van Breugel et al., 2024). This conceptual model predicts that, within sites, recruitment directly adjacent to SFFs is less dispersal limited than in locations further from SFFs at the onset of succession. As forests regrow, recruitment in the latter locations becomes less dispersal limited and, thus, increasingly similar to the recruitment in the former locations. Yet, we found that even after over 30 years of secondary succession, the recruitment dynamics of lower and upper slope plots did not converge (Fig. 3), despite significant changes in canopy structure and composition over the course of succession (See Suppl. Info. S2)(van Breugel et al., 2013). This may indicate that in our study site, changes in forest structure over the first three decades of succession were not sufficient to facilitate the movement of some of the animal dispersers and the plant species they disperse from stream-side forest fragments further uphill into the regrowing secondary forests.

We found that the CWM seed mass of recruits increased as succession proceeded, which could be interpreted as being driven by an environment–species-availability loop. However, recruitment is also shaped by a successional feedback loop between seedling performance and light availability (environment–species-performance feedback loop; van Breugel et al., 2024). During forest succession, tree species that first colonize a site are typically fast-growing and light-demanding species. Decreasing light levels in the understory (Matsuo et al., 2021; van Breugel et al., 2013) subsequently limit the recruitment of these species and favor the recruitment of more shade-tolerant species (Finegan, 1996; Rüger et al., 2023; van Breugel et al., 2007). Life history tradeoffs link the two feedback loops, as both acquisitive traits associated with fast growth under favorable conditions (e.g., photosynthetic rates, SLA) and traits associated with fecundity and dispersal (e.g., seed size) have been found to trade off with the ability to survive in the shade in tropical forests (Lai et al., 2021; Turner, 2008) (but see Clark et al., 2004). That implies that, because we analyzed sapling recruitment rather than seed dispersal, the pattern of increasing CWM seed mass may reflect that larger-seeded species became less dispersal limited, but also that decreasing light levels increasingly limit seedling establishment and survival of smaller-seeded species (Gratzer et al., 2022; Kraft et al., 2015; Rand et al., 2020). An earlier trait-based study in our field site provides support for the latter, showing that maximum photosynthesis was a better predictor of successional changes in species' recruitment and mortality rates than seed mass (Lai et al., 2021). This suggests that successional shifts in community-weighted mean seed mass and landscape occupancy reflect the inability of many widely-distributed, smaller-seeded species to establish and survive in an increasingly light-limited environment (Baraloto et al., 2005; Bruun & Ten Brink, 2008; Metcalfe & Grubb, 1995; Poorter & Rose, 2005; Wendt et al., 2022).

Overall, we found surprisingly little support for the prediction that recruitment further from SFFs becomes more like the recruitment adjacent to the SFFS in terms of the assessed recruitment variables. This, in combination with observations on trait-based recruitment dynamics, suggests that environment–species-performance feedback dynamics, more than environment–species-availability feedback dynamics, is the main driver of shifts in functional species composition over the first few decades of succession in our secondary forests.

4.3 Implications for conservation and restoration

Natural regeneration is proposed as a cost-effective strategy for meeting ambitious forest restoration goals, either by itself or in combination with a range of site preparation and protection and tree planting and management schemes (Chazdon & Guariguata, 2016; Cook-Patton et al., 2020; Martínez-Ramos et al., 2016; Shono et al., 2007; Veryard et al., 2023). In our site, recruitment of woody plant species over the first 40 years of secondary forest regrowth was remarkably diverse at both local and landscape scales, with a total of 426 recruited species – more than half the woody species found across multiple studies in the Agua Salud study area. This indicates that restoration of plant diversity through natural regeneration is a good option in this and similar landscapes (but see Gibson et al., 2011; van Breugel et al., 2013).

It is important to point out that the Agua Salud study area is characterized by various factors that buffer seed source and dispersal limitations and thus support the recruitment of diverse assemblages of woody plant species in regenerating forests: an abundance of secondary forests in various stages of succession and relatively high densities of non-forest trees in most pastures (Laborde et al., 2008; Pignataro et al., 2017; Reid et al., 2015); a dense network of streamside forest fragments (Bennett, 2003; Caughlin et al., 2016; Harvey et al., 2008; Mitchell et al., 2018; Zahawi et al., 2021); and proximity to a large national park (Gilroy et al., 2014; Mayhew et al., 2019). Equally important is the preservation of a diverse disperser community in human-modified landscapes (Ripperger et al., 2015; Stoner et al., 2007; Tucker et al., 2021). In our study area, communities of birds (Mayhew et al., 2019) and frugivorous bat communities (Brändel et al., 2020) have been found to be still abundant and highly diverse. We have no data on other disperser groups, but Mantled Howler monkeys (*Alouatta palliata*) and White-throated Capuchin monkeys (*Cebus capucinus*) are regularly observed in the study area, especially along streams and in the older (older than the secondary forests included in this study) secondary forest fragments. Similar studies in agricultural landscapes with different land-use histories and intensities are likely to produce different results (Caughlin et al., 2016; Jakovac et al., 2021), and are thus needed to develop more comprehensive guidelines for incorporating natural regeneration in forest landscape restoration strategies (Arroyo-Rodríguez et al., 2017; Ashton et al., 2001; Chazdon & Guariguata, 2016). It is also important to emphasize that the feasibility of natural regeneration as restoration strategy depends, from a socio-economic point of view, on the restoration goals of stakeholders and financing options (Martin et al., 2021; Sinacore et al., 2023).

While recruitment was generally diverse in both lower and upper slope portions of the secondary forests, recruitment at lower slope locations was significantly more diverse at both the local and the landscape scale, with a higher proportion of rarer species. From a restoration perspective, this so-called biodiversity spillover effect of forest fragments (Brudvig et al., 2009) emphasizes the importance of preserving or restoring a continuous network of forest fragments along streams. Our results provide further support for the idea that streamside forest fragments preserve local populations of tree species (seed sources) and critical habitat and movement corridors for a range of animal dispersers (Araujo Calçada et al., 2013; Carrasco-Rueda & Loiselle, 2019; Pardini et al., 2005; Sánchez-Montoya et al., 2023), thus facilitating the arrival of more dispersal-limited species in adjoining forests (Brudvig et al., 2009; Tang et al., 2014; Tewksbury et al., 2002).

A key assumption of many forest restoration approaches is that the growth and increasing complexity of a forest canopy will attract an increasing number of animal dispersers, resulting in a greater diversity of species dispersed into the restoration site. However, as discussed in the previous section, we found that it may take longer than 36 years of natural forest regrowth before these secondary forests become sufficiently hospitable for a subset of the local species pool of animal dispersers (Lennox et al., 2018). Our results are relevant not only in the context of passive restoration through natural succession, but also in the context of active restoration that aims at accelerating natural regeneration through tree planting (e.g., Boeschoten et al., 2021; de la Peña-Domene et al., 2013; Elliott et al., 2022; Pohlman et al., 2021; Vieira et al., 2021). A common recommendation in the literature on the ecological restoration of forests is the planting of early successional fruiting trees to attract frugivorous birds and bats and accelerate the dispersal and recruitment of trees into the restoration site (Camargo et al., 2020). We suggest that we need to extend this by investigating how to enhance dispersal in later successional forests as well, including the choice and planting of tree species that may act as dispersal foci later in succession.

In summary, the results of our study support, at least in landscapes similar to that of the current study, a hierarchy of priorities for restoration initiatives that include natural regeneration and aim to restore biodiverse forests in agricultural landscapes (Bennett, 2003; Cook-Patton et al., 2021; Harvey et al., 2008; Tarabon et al., 2021): (1) conserve and, where necessary, restore networks of forest corridors along streams; (2) prioritize areas directly along these corridors for restoration; and (3) when active restoration measures are feasible, investigate how dispersal into regrowing forests can be accelerated.

Acknowledgements

The Agua Salud project was supported by The Smithsonian Tropical Research Institute, ForestGEO, Heising–Simons Foundation, HSBC Climate Partnership, Stanley Motta, SmallWorld Institute Fund, Frank and Kristin Levinson, the Hoch family, U Trust and Yale-NUS College and Singapore's Ministry of Education (IG16-LR004). MvB acknowledges support by The Future Cities Lab Global Program of the ETH-Singapore Centre, which is funded by National Research Foundation Singapore, by the National Parks Board of Singapore, and by Singapore's Ministry of Education (IG19_SG113). We would like to thank Johana Balbuena, Guillermo Fernandez, Julia Gonzalez, Miguel Nuñez, Anabel Rivas, Adriana Tapia, Daniela Weber, Estrella Yanguas, Federico Davies, and many interns and technicians for their help in collecting the Agua Salud data.

Statement of authorship

MvB, DC and JSH conceived the ideas. MvB and JSH designed and set up the field study. MvB, MB, and JSH collected the data. MvB analyzed the data and wrote the manuscript. All authors commented on and endorsed the manuscript.

References

Acevedo-Charry, O., & Aide, T. M. (2019). Recovery of amphibian, reptile, bird and mammal diversity during secondary forest succession in the tropics. *Oikos*, *128*(8), 1065–1078. https://doi.org/10.1111/oik.06252

Aide, T. M., & Cavelier, J. (1994). Barriers to Lowland Tropical Forest Restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology*, *2*(4), 219–229. https://doi.org/10.1111/j.1526-100X.1994.tb00054.x

Almond, Grooten, M., Bignoli, D. J., & Petersen, T. (Eds.). (2022). *Living Planet Report 2022 – Building a nature- positive society*. WWF, Gland, Switzerland. https://livingplanet.panda.org/en-GB/

Alroy, J. (2017). Effects of habitat disturbance on tropical forest biodiversity. *Proceedings of the National Academy of Sciences*, *114*(23), 6056–6061. https://doi.org/10.1073/pnas.1611855114

Anzures-Dadda, A., & Manson, R. H. (2007). Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. *Animal Conservation*, *10*(1), 69–76. https://doi.org/10.1111/j.1469-1795.2006.00074.x

Araujo Calçada, E., Closset-Kopp, D., Gallet-Moron, E., Lenoir, J., Rêve, M., Hermy, M., & Decocq, G. (2013). Streams are efficient corridors for plant species in forest metacommunities. *Journal of Applied Ecology*, *50*(5), 1152–1160. https://doi.org/10.1111/1365-2664.12132

Arroyo-Rodríguez, V., Melo, F. P. L., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., Norden, N., Santos, B. A., Leal, I. R., & Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: New insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, *92*(1), 326–340. https://doi.org/10.1111/brv.12231

Ashton, M. S., Gunatilleke, C. V. S., Singhakumara, B. M. P., & Gunatilleke, I. A. U. N. (2001). Restoration pathways for rain forest in southwest Sri Lanka: A review of concepts and models. *Forest Ecology and Management*, *154*(3), 409–430. https://doi.org/10.1016/S0378-1127(01)00512-6

Baraloto, C., Forget, P.-M., & Goldberg, D. E. (2005). Seed mass, seedling size and neotropical tree seedling establishment. *Journal of Ecology*, *93*(6), 1156–1166. https://doi.org/10.1111/j.1365-2745.2005.01041.x

Barlow, J., Gardner, T. A., Araujo, I. S., Ávila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Nunes-Gutjahr, A. L., Overal, W. L., … Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences*, *104*(47), 18555–18560. https://doi.org/10.1073/pnas.0703333104

Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Nally, R. M., Thomson, J. R., Ferraz, S. F. de B., Louzada, J., Oliveira, V. H. F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I. C. G., Aragão, L. E. O. C., Begotti, R. A., Braga, R. F., Cardoso, T. M., de Oliveira, R. C., Souza Jr, C. M., … Gardner, T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, *535*(7610), 144–147. https://doi.org/10.1038/nature18326

Bartoń, K. (2020). *MuMIn: Multi-Model Inference* (R package version 1.43.17) [R]. https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bello, C., Crowther, T. W., Ramos, D. L., Morán-López, T., Pizo, M. A., & Dent, D. H. (2024). Frugivores enhance potential carbon recovery in fragmented landscapes. *Nature Climate Change*, 1–8. https://doi.org/10.1038/s41558-024-01989-1

Bennett, A. F. (2003). *Linkages in the landscape: The role of corridors and connectivity in wildlife conservation*. IUCN - Thew World Conservation Union.

Boeschoten, L. E., van Breugel, M., Bailon, M., Balbuena, J., Nuñez, M., Cerezo, A., & Hall, J. S. (2021). Framework Species Approach Proves Robust in Restoring Forest on Fire Prone Invasive Grass: A Case Study from Panama. *Journal of Sustainable Forestry*, *40*(2), 197–215. https://doi.org/10.1080/10549811.2020.1746915

Borges, S. H., Tavares, T. do R. S., Crouch, N. M. A., & Baccaro, F. (2021). Sucessional trajetories of bird assemblages in amazonian secondary forests: Perspectives from complementary biodiversity dimensions. *Forest Ecology and Management*, *483*, 118731. https://doi.org/10.1016/j.foreco.2020.118731

Brancalion, P. H. S., Lamb, D., Ceccon, E., Boucher, D., Herbohn, J., Strassburg, B., & Edwards, D. P. (2017). Using markets to leverage investment in forest and landscape restoration in the tropics. *Forest Policy and Economics*, *85*, 103–113. https://doi.org/10.1016/j.forpol.2017.08.009

Brändel, S. D., Hiller, T., Halczok, T. K., Kerth, G., Page, R. A., & Tschapka, M. (2020). Consequences of fragmentation for Neotropical bats: The importance of the matrix. *Biological Conservation*, *252*, 108792. https://doi.org/10.1016/j.biocon.2020.108792

Brooks, M., E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Brudvig, L. A., Damschen, E. I., Tewksbury, J. J., Haddad, N. M., & Levey, D. J. (2009). Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of the National Academy of Sciences*, *106*(23), 9328–9332. https://doi.org/10.1073/pnas.0809658106

Bruun, H. H., & Ten Brink, D.-J. (2008). Recruitment advantage of large seeds is greater in shaded habitats. *Écoscience*, *15*(4), 498–507. https://doi.org/10.2980/15-4-3147

Burnham, K. P., & Anderson, D. R. (Eds.). (2004). *Model Selection and Multimodel Inference*. Springer. https://doi.org/10.1007/b97636

Busch, J., Engelmann, J., Cook-Patton, S. C., Griscom, B. W., Kroeger, T., Possingham, H., & Shyamsundar, P. (2019). Potential for low-cost carbon dioxide removal through tropical reforestation. *Nature Climate Change*, *9*(6), Article 6. https://doi.org/10.1038/s41558-019-0485-x

Camargo, P. H. S. A., Pizo, M. A., Brancalion, P. H. S., & Carlo, T. A. (2020). Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: Implications for restoration. *Journal of Applied Ecology*, *57*(12), 2329–2339. https://doi.org/10.1111/1365-2664.13697

Carrasco-Rueda, F., & Loiselle, B. A. (2019). Do riparian forest strips in modified forest landscapes aid in conserving bat diversity? *Ecology and Evolution*, *9*(7), 4192–4209. https://doi.org/10.1002/ece3.5048

Carter, S., Herold, M., Avitabile, V., Bruin, S. de, Sy, V. D., Kooistra, L., & Rufino, M. C. (2017). Agriculture-driven deforestation in the tropics from 1990–2015: Emissions, trends and uncertainties. *Environmental Research Letters*, *13*(1), 014002. https://doi.org/10.1088/1748-9326/aa9ea4

Caughlin, T. T., Elliott, S., & Lichstein, J. W. (2016). When does seed limitation matter for scaling up reforestation from patches to landscapes? *Ecological Applications*, *26*(8), 2439–2450. https://doi.org/10.1002/eap.1410

Charles, L. S., Dwyer, J. M., & Mayfield, M. M. (2017). Rainforest seed rain into abandoned tropical Australian pasture is dependent on adjacent rainforest structure and extent. *Austral Ecology*, *42*(2), 238–249. https://doi.org/10.1111/aec.12426

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2351–2363. https://doi.org/10.1098/rstb.2011.0063

Chazdon, R. L., & Guariguata, M. R. (2016). Natural regeneration as a tool for large-scale forest restoration in the tropics: Prospects and challenges. *BIOTROPICA*, *48*(6), 716–730. https://doi.org/10.1111/btp.12381

Chazdon, R. L., Harvey, C. A., Komar, O., Griffith, D. M., Ferguson, B. G., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Breugel, M. V., & Philpott, S. M. (2009). Beyond Reserves: A Research Agenda for Conserving Biodiversity in Human-modified Tropical Landscapes. *Biotropica*, *41*(2), 142–153. https://doi.org/10.1111/j.1744-7429.2008.00471.x

Clark, J. S., LaDeau, S., & Ibanez, I. (2004). Fecundity of Trees and the Colonization–Competition Hypothesis. *Ecological Monographs*, *74*(3), 415–442. https://doi.org/10.1890/02-4093

Clark, J. S., Macklin, E., & Wood, L. (1998). Stages and Spatial Scales of Recruitment Limitation in Southern Appalachian Forests. *Ecological Monographs*, *68*(2), 213–235. https://doi.org/10.1890/0012-9615(1998)068[0213:SASSOR]2.0.CO;2

Coleman, E. A., Schultz, B., Ramprasad, V., Fischer, H., Rana, P., Filippi, A. M., Güneralp, B., Ma, A., Rodriguez Solorzano, C., Guleria, V., Rana, R., & Fleischman, F. (2021). Limited effects of tree planting on forest canopy cover and rural livelihoods in Northern India. *Nature Sustainability*, *4*(11), Article 11. https://doi.org/10.1038/s41893-021-00761-z

Cook-Patton, S. C., Drever, C. R., Griscom, B. W., Hamrick, K., Hardman, H., Kroeger, T., Pacheco, P., Raghav, S., Stevenson, M., Webb, C., Yeo, S., & Ellis, P. W. (2021). Protect, manage and then restore lands for climate mitigation. *Nature Climate Change*, *11*(12), 1027–1034. https://doi.org/10.1038/s41558-021-01198-0

Cook-Patton, S. C., Leavitt, S. M., Gibbs, D., Harris, N. L., Lister, K., Anderson-Teixeira, K. J., Briggs, R. D., Chazdon, R. L., Crowther, T. W., Ellis, P. W., Griscom, H. P., Herrmann, V., Holl, K. D., Houghton, R. A., Larrosa, C., Lomax, G., Lucas, R., Madsen, P., Malhi, Y., … Griscom, B. W. (2020). Mapping carbon accumulation potential from global natural forest regrowth. *Nature*, *585*(7826), Article 7826. https://doi.org/10.1038/s41586-020-2686-x

Corbin, J. D., & Holl, K. D. (2012). Applied nucleation as a forest restoration strategy. *FOREST ECOLOGY AND MANAGEMENT*, *265*, 37–46. https://doi.org/10.1016/j.foreco.2011.10.013

Corlett, R. T. (2016). Ecological Roles of Animals in Tropical Forests. In L. Pancel & M. Köhl (Eds.), *Tropical Forestry Handbook* (pp. 503–510). Springer. https://doi.org/10.1007/978-3-642-54601-3_54

Craven, D., Hall, J. S., Berlyn, G. P., Ashton, M. S., & van Breugel, M. (2015). Changing gears during succession: Shifting functional strategies in young tropical secondary forests. *Oecologia*, *179*(1), 293–305. https://doi.org/10.1007/s00442-015-3339-x

Crouzeilles, R., Beyer, H. L., Monteiro, L. M., Feltran-Barbieri, R., Pessôa, A. C. M., Barros, F. S. M., Lindenmayer, D. B., Lino, E. D. S. M., Grelle, C. E. V., Chazdon, R. L., Matsumoto, M., Rosa, M., Latawiec, A. E., & Strassburg, B. B. N. (2020). Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. *Conservation Letters*, *13*(3), e12709. https://doi.org/10.1111/conl.12709

Crouzeilles, R., Curran, M., Ferreira, M. S., Lindenmayer, D. B., Grelle, C. E. V., & Rey Benayas, J. M. (2016). A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications*, *7*(1), Article 1. https://doi.org/10.1038/ncomms11666

Cubiña, A., & Aide, T. M. (2001). The Effect of Distance from Forest Edge on Seed Rain and Soil Seed Bank in a Tropical Pasture1. *Biotropica*, *33*(2), 260–267. https://doi.org/10.1111/j.1744-7429.2001.tb00177.x

Dalling, J. W., Muller-Landau, H. C., Wright, S. J., & Hubbell, S. P. (2002). Role of dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology*, *90*(4), 714–727. https://doi.org/10.1046/j.1365-2745.2002.00706.x

Dave, R., Saint-Laurent, C., Murray, L., Antunes Daldegan, G., Brouwer, R., De Mattos Scaramuzza, C. A., Raes, L., Simonit, S., Catapan, M., García Contreras, G., Ndoli, A., Karangwa, C., Perera, N., Hingorani, S., & Pearson, T. (2019). *Second Bonn Challenge progress report: Application of the Barometer in 2018*. IUCN, International Union for Conservation of Nature. https://doi.org/10.2305/IUCN.CH.2019.06.en

Daws, M. I., Gaméné, C. S., Glidewell, S. M., & Pritchard, H. W. (2004). Seed mass variation potentially masks a single critical water content in recalcitrant seeds. *Seed Science Research*, *14*(2), 185–195. https://doi.org/10.1079/SSR2004168

de la Peña-Domene, M., Martínez-Garza, C., & Howe, H. F. (2013). Early recruitment dynamics in tropical restoration. *Ecological Applications*, *23*(5), 1124–1134. https://doi.org/10.1890/12-1728.1

Decaëns, T., Martins, M. B., Feijoo, A., Oszwald, J., Dolédec, S., Mathieu, J., Arnaud de Sartre, X., Bonilla, D., Brown, G. G., Cuellar Criollo, Y. A., Dubs, F., Furtado, I. S., Gond, V., Gordillo, E., Le Clec'h, S., Marichal, R., Mitja, D., de Souza, I. M., Praxedes, C., … Lavelle, P. (2018). Biodiversity loss along a gradient of deforestation in Amazonian agricultural landscapes. *Conservation Biology*, *32*(6), 1380–1391. https://doi.org/10.1111/cobi.13206

Dent, D. H., & Estrada-Villegas, S. (2021). Uniting niche differentiation and dispersal limitation predicts tropical forest succession. *Trends in Ecology & Evolution*, *36*(8), 700–708. https://doi.org/10.1016/j.tree.2021.04.001

Dent, D. H., & Joseph Wright, S. (2009). The future of tropical species in secondary forests: A quantitative review. *Biological Conservation*, *142*(12), 2833–2843. https://doi.org/10.1016/j.biocon.2009.05.035

DeWalt, S., Maliakal, S., & Denslow, J. (2003). Changes in vegetation structure and composition along a tropical forest chronosequence: Implications for wildlife. *FOREST ECOLOGY AND MANAGEMENT*, *182*(1–3), 139–151. https://doi.org/10.1016/S0378-1127(03)00029-X

Dosch, J. J., Peterson, C. J., & Haines, B. L. (2007). Seed rain during initial colonization of abandoned pastures in the premontane wet forest zone of southern Costa Rica. *Journal of Tropical Ecology*, *23*(2), 151–159. https://doi.org/10.1017/S0266467406003853

Edwards, D. P., Cerullo, G. R., Chomba, S., Worthington, T. A., Balmford, A. P., Chazdon, R. L., & Harrison, R. D. (2021). Upscaling tropical restoration to deliver environmental benefits and socially equitable outcomes. *Current Biology*, *31*(19), R1326–R1341. https://doi.org/10.1016/j.cub.2021.08.058

Elliott, S., Tucker, N. I. J., Shannon, D. P., & Tiansawat, P. (2022). The framework species method: Harnessing natural regeneration to restore tropical forest ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1867), 20210073. https://doi.org/10.1098/rstb.2021.0073

Estoque, R. C., Myint, S. W., Wang, C., Ishtiaque, A., Aung, T. T., Emerton, L., Ooba, M., Hijioka, Y., Mon, M. S., Wang, Z., & Fan, C. (2018). Assessing environmental impacts and change in Myanmar's mangrove ecosystem service value due to deforestation (2000–2014). *Global Change Biology*, *24*(11), 5391–5410. https://doi.org/10.1111/gcb.14409

Estrada-Villegas, S., Stevenson, P. R., López, O., DeWalt, S. J., Comita, L. S., & Dent, D. H. (2022). Animal seed dispersal recovery during passive restoration in a forested landscape. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1867), 20210076. https://doi.org/10.1098/rstb.2021.0076

Finegan, B. (1996). Pattern and process in neotropical secondary rain forests: The first 100 years of succession. *Trends in Ecology & Evolution*, *11*(3), 119–124. https://doi.org/10.1016/0169-5347(96)81090-1

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (Third edition). SAGE.

Garate-Quispe, J., Velásquez Ramírez, M., Becerra-Lira, E., Baez-Quispe, S., Abril-Surichaqui, M., Rodriguez-Achata, L., Muñoz-Ushñahua, A., Nascimento Herbay, P., Fernandez-Mamani, Y., Alarcon-Aguirre, G., Herrera-Machaca, M., Hilares Vargas, L., Corvera Gomringer, R., & del Castillo Torres, D. (2023). Influence of Distance from Forest Edges on Spontaneous Vegetation Succession Following Small-Scale Gold Mining in the Southeast Peruvian Amazon. *Diversity*, *15*(6), Article 6. https://doi.org/10.3390/d15060793

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, *12*(6), 561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. a., Bradshaw, C. J. a., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*(7369), 378–381. https://doi.org/10.1038/nature10425

Gilroy, J. J., Edwards, F. A., Uribe, C. A. M., Haugaasen, T., & Edwards, D. P. (2014). Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. *Journal of Applied Ecology*, *51*(5), 1337–1346. https://doi.org/10.1111/1365-2664.12284

González-Castro, A., Yang, S., & Carlo, T. A. (2019). How does avian seed dispersal shape the structure of early successional tropical forests? *Functional Ecology*, *33*(2), 229–238. https://doi.org/10.1111/1365-2435.13250

Gratzer, G., Pesendorfer, M. B., Sachser, F., Wachtveitl, L., Nopp-Mayr, U., Szwagrzyk, J., & Canham, C. D. (2022). Does fine scale spatiotemporal variation in seed rain translate into plant population structure? *Oikos*, *2022*(2). https://doi.org/10.1111/oik.08826

Hall, J. S., Kirn, V., & Yanguas-Fernández, E. (2015). *Managing Watersheds for Ecosystem services In the Steepland Neotropics*. Inter-American Development Bank.

Hall, J. S., Plisinski, J. S., Mladinich, S. K., van Breugel, M., Lai, H. R., Asner, G. P., Walker, K., & Thompson, J. R. (2022). Deforestation scenarios show the importance of secondary forest for meeting Panama's carbon goals. *Landscape Ecology*, *37*(3), 673–694. https://doi.org/10.1007/s10980-021-01379-4

Harvey, C. A., Komar, O., Chazdon, R., Ferguson, B. G., Finegan, B., Griffith, D. M., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Breugel, M. V., & Wishnie, M. (2008). Integrating Agricultural Landscapes with Biodiversity Conservation in the Mesoamerican Hotspot. *Conservation Biology*, *22*(1), 8–15. https://doi.org/10.1111/j.1523-1739.2007.00863.x

Hassler, S. K., Zimmermann, B., van Breugel, M., Hall, J. S., & Elsenbeer, H. (2011). Recovery of saturated hydraulic conductivity under secondary succession on former pasture in the humid tropics. *Forest Ecology and Management*, *261*(10), 1634–1642. https://doi.org/10.1016/j.foreco.2010.06.031

Hilje, B., Sánchez, N. V., Bayne, E. M., & Sánchez-Azofeifa, A. (2020). Bird Assemblage Recovery in a Chronosequence of Tropical Dry Forests in Costa Rica. *Forests*, *11*(6), Article 6. https://doi.org/10.3390/f11060629

Holl, K. D. (1999). Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture: Seed Rain, Seed Germination, Microclimate, and Soil1. *Biotropica*, *31*(2), 229–242. https://doi.org/10.1111/j.1744-7429.1999.tb00135.x

Howe, H. F., & Smallwood, J. (1982). Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics*, *13*(1), 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

Huanca Nuñez, N., Chazdon, R. L., & Russo, S. E. (2021). Seed-rain–successional feedbacks in wet tropical forests. *Ecology*, *102*(7), e03362. https://doi.org/10.1002/ecy.3362

Ismail, S. A., Ghazoul, J., Ravikanth, G., Kushalappa, C. G., Uma Shaanker, R., & Kettle, C. J. (2017). Evaluating realized seed dispersal across fragmented tropical landscapes: A two-fold approach using parentage analysis and the neighbourhood model. *New Phytologist*, *214*(3), 1307–1316. https://doi.org/10.1111/nph.14427

Jakovac, C. C., Junqueira, A. B., Crouzeilles, R., Peña-Claros, M., Mesquita, R. de C. G., & Bongers, F. (2021). The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biological Reviews*, *96*(4), 1114–1134. https://doi.org/10.1111/brv.12694

Jones, F. A., & Muller-Landau, H. C. (2008). Measuring long-distance seed dispersal in complex natural environments: An evaluation and integration of classical and genetic methods. *Journal of Ecology*, *96*(4), 642–652. https://doi.org/10.1111/j.1365-2745.2008.01400.x

Jones, M. E., & Davidson, N. (2016). Applying an animal-centric approach to improve ecological restoration. *Restoration Ecology*, *24*(6), 836–842. https://doi.org/10.1111/rec.12447

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*(5), 592–599. https://doi.org/10.1111/1365-2435.12345

Kulikowski, A. J., Zahawi, R. A., Werden, L. K., Zhu, K., & Holl, K. D. (2022). Restoration interventions mediate tropical tree recruitment dynamics over time. *Philosophical*

Transactions of the Royal Society B: Biological Sciences, *378*(1867), 20210077. https://doi.org/10.1098/rstb.2021.0077

Laborde, J., Guevara, S., & Sánchez-Ríos, G. (2008). Tree and shrub seed dispersal in pastures: The importance of rainforest trees outside forest fragments. *Http://Dx.Doi.Org/10.2980/1195-6860(2008)15[6:TASSDI]2.0.CO;2*. https://doi.org/10.2980/1195-6860(2008)15[6:TASSDI]2.0.CO;2

Lai, H. R., Chong, K. Y., Yee, A. T. K., Tan, H. T. W., & van Breugel, M. (2020). Functional traits that moderate tropical tree recruitment during post-windstorm secondary succession. *Journal of Ecology*, *108*(4), 1322–1333. https://doi.org/10.1111/1365-2745.13347

Lai, H. R., Craven, D., Hall, J. S., Hui, F. K. C., & van Breugel, M. (2021). Successional syndromes of saplings in tropical secondary forests emerge from environment-dependent trait–demography relationships. *Ecology Letters*, *24*(9), 1776–1787. https://doi.org/10.1111/ele.13784

Lai, H. R., Hall, J. S., Batterman, S. A., Turner, B. L., & van Breugel, M. (2018). Nitrogen fixer abundance has no effect on biomass recovery during tropical secondary forest succession. *JOURNAL OF ECOLOGY*, *106*(4), 1415–1427. https://doi.org/10.1111/1365-2745.12979

Lai, H. R., Hall, J. S., Turner, B. L., & van Breugel, M. (2017). Liana effects on biomass dynamics strengthen during secondary forest succession. *Ecology*, *98*(4), 1062–1070. https://doi.org/10.1002/ecy.1734

Lasky, J. R., & Keitt, T. H. (2012). The Effect of Spatial Structure of Pasture Tree Cover on Avian Frugivores in Eastern Amazonia. *Biotropica*, *44*(4), 489–497. https://doi.org/10.1111/j.1744-7429.2012.00857.x

Lebrija-Trejos, E., Pérez-García, E. a., Meave, J. a., Poorter, L., & Bongers, F. (2011). Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology*, *27*(05), 477–489. https://doi.org/10.1017/S0266467411000253

Lennox, G. D., Gardner, T. A., Thomson, J. R., Ferreira, J., Berenguer, E., Lees, A. C., Mac Nally, R., Aragao, L. E. O. C., Ferraz, S. F. B., Louzada, J., Moura, N. G., Oliveira, V. H. F., Pardini, R., Solar, R. R. C., Vaz-de Mello, F. Z., Vieira, I. C. G., & Barlow, J. (2018). Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. *Global Change Biology*, *24*(12), 5680–5694. https://doi.org/10.1111/gcb.14443

Lima, L. S., Coe, M. T., Soares Filho, B. S., Cuadra, S. V., Dias, L. C. P., Costa, M. H., Lima, L. S., & Rodrigues, H. O. (2014). Feedbacks between deforestation, climate, and hydrology in the Southwestern Amazon: Implications for the provision of ecosystem services. *Landscape Ecology*, *29*(2), 261–274. https://doi.org/10.1007/s10980-013-9962-1

Link, A., & Fiore, A. D. (2006). Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. *Journal of Tropical Ecology*, *22*(3), 235–246. https://doi.org/10.1017/S0266467405003081

Lippke, B., Puettmann, M., Oneil, E., & Dearing Oliver, C. (2021). The Plant a Trillion Trees Campaign to Reduce Global Warming – Fleshing Out the Concept. *Journal of Sustainable Forestry*, *40*(1), 1–31. https://doi.org/10.1080/10549811.2021.1894951

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martinez-Ramos, M., Meave, J. A., Paz, H., Perez-Garcia, E. A., Romero-Perez, I. E., Tauro, A., & Bongers, F. (2013). Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, *94*(6), 1211–1216.

Luck, G. W., & Daily, G. C. (2003). Tropical Countryside Bird Assemblages: Richness, Composition, and Foraging Differ by Landscape Context. *Ecological Applications*, *13*(1), 235–247. https://doi.org/10.1890/1051-0761(2003)013[0235:TCBARC]2.0.CO;2

Martin, M. P., Woodbury, D. J., Doroski, D. A., Nagele, E., Storace, M., Cook-Patton, S. C., Pasternack, R., & Ashton, M. S. (2021). People plant trees for utility more often than for biodiversity or carbon. *Biological Conservation*, *261*, 109224. https://doi.org/10.1016/j.biocon.2021.109224

Martínez-Ramos, M., Pingarroni, A., Rodríguez-Velázquez, J., Toledo-Chelala, L., Zermeño-Hernández, I., & Bongers, F. (2016). Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica*, *48*(6), 745–757. https://doi.org/10.1111/btp.12382

Matsuo, T., Martínez-Ramos, M., Bongers, F., van der Sande, M. T., & Poorter, L. (2021). Forest structure drives changes in light heterogeneity during tropical secondary forest succession. *Journal of Ecology*, *109*(8), 2871–2884. https://doi.org/10.1111/1365-2745.13680

Mayhew, R. J., Tobias, J. A., Bunnefeld, L., & Dent, D. H. (2019). Connectivity with primary forest determines the value of secondary tropical forests for bird conservation. *Biotropica*, *51*(2), 219–233. https://doi.org/10.1111/btp.12629

McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H., & Santamaria, L. (2012). Seed dispersal in changing landscapes. *Biological Conservation*, *146*(1), 1–13. https://doi.org/10.1016/j.biocon.2011.09.018

Mendenhall, C. D., Shields-Estrada, A., Krishnaswami, A. J., & Daily, G. C. (2016). Quantifying and sustaining biodiversity in tropical agricultural landscapes. *Proceedings of the National Academy of Sciences*, *113*(51), 14544–14551. https://doi.org/10.1073/pnas.1604981113

Metcalfe, D. J., & Grubb, P. J. (1995). Seed mass and light requirements for regeneration in Southeast Asian rain forest. *Canadian Journal of Botany*, *73*(6), 817–826. https://doi.org/10.1139/b95-090

Mitchell, S. L., Edwards, D. P., Bernard, H., Coomes, D., Jucker, T., Davies, Z. G., & Struebig, M. J. (2018). Riparian reserves help protect forest bird communities in oil palm dominated landscapes. *Journal of Applied Ecology*, *55*(6), 2744–2755. https://doi.org/10.1111/1365-2664.13233

Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T., & Westoby, M. (2007). Global patterns in seed size. *Global Ecology and Biogeography*, *16*(1), 109–116. https://doi.org/10.1111/j.1466-8238.2006.00259.x

Moore, R. P., Robinson, W. D., Lovette, I. J., & Robinson, T. R. (2008). Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters*, *11*(9), 960–968. https://doi.org/10.1111/j.1461-0248.2008.01196.x

Moran, C., Catterall, C., Green, R., & Olsen, M. (2004). Functional variation among frugivorous birds: Implications for rainforest seed dispersal in a fragmented subtropical landscape. *Oecologia*, *141*(4), 584–595. https://doi.org/10.1007/s00442-004-1685-1

Moran, C., & Catterall, C. P. (2014). Responses of Seed-Dispersing Birds to Amount of Rainforest in the Landscape around Fragments. *Conservation Biology*, *28*(2), 551–560. https://doi.org/10.1111/cobi.12236

Muscarella, R., & Fleming, T. H. (2007). The Role of Frugivorous Bats in Tropical Forest Succession. *Biological Reviews*, *82*(4), 573–590. https://doi.org/10.1111/j.1469-185X.2007.00026.x

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, *15*(7), 278–285. https://doi.org/10.1016/S0169-5347(00)01874-7

Neumann-Cosel, L., Zimmermann, B., Hall, J. S., van Breugel, M., & Elsenbeer, H. (2011). Soil carbon dynamics under young tropical secondary forests on former pastures—A case study from Panama. *Forest Ecology and Management*, *261*(10), 1625–1633. https://doi.org/10.1016/j.foreco.2010.07.023

Ngo Bieng, M. A., Delgado-Rodríguez, D., Vilchez-Mendoza, S., López-Sampson, A., García, E., Sepúlveda, N., & Somarriba, E. (2022). Tree diversity in a tropical agricultural-forest mosaic landscape in Honduras. *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-21280-7

Ogden, F. L., Crouch, T. D., Stallard, R. F., & Hall, J. S. (2013). Effect of land cover and use on dry season river runoff, runoff efficiency, and peak storm runoff in the seasonal tropics of Central Panama. *Water Resources Research*, *49*(12), 8443–8462. https://doi.org/10.1002/2013WR013956

Oksanen, J. F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinnPierre, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community Ecology Package* (2.5-7) [Computer software]. https://CRAN.R-project.org/package=vegan

Palma, A. C., Goosem, M., Fensham, R. J., Goosem, S., Preece, N. D., Stevenson, P. R., & Laurance, S. G. W. (2021). Dispersal and recruitment limitations in secondary forests. *Journal of Vegetation Science*, *32*(1), e12975. https://doi.org/10.1111/jvs.12975

Pardini, R., de Souza, S. M., Braga-Neto, R., & Metzger, J. P. (2005). The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biological Conservation*, *124*(2), 253–266. https://doi.org/10.1016/j.biocon.2005.01.033

Pendrill, F., Gardner, T. A., Meyfroidt, P., Persson, U. M., Adams, J., Azevedo, T., Bastos Lima, M. G., Baumann, M., Curtis, P. G., De Sy, V., Garrett, R., Godar, J., Goldman, E. D., Hansen, M. C., Heilmayr, R., Herold, M., Kuemmerle, T., Lathuillière, M. J., Ribeiro, V., … West, C. (2022). Disentangling the numbers behind agriculture-driven tropical deforestation. *Science*, *377*(6611), eabm9267. https://doi.org/10.1126/science.abm9267

Pignataro, A. G., Levy-Tacher, S. I., Aguirre-Rivera, J. R., Nahed-Toral, J., González-Espinosa, M., González-Arzac, A., & Biganzoli, F. (2017). Natural regeneration of tree species in pastures on peasant land in Chiapas, Mexico. *Agriculture, Ecosystems & Environment*, *249*, 137–143. https://doi.org/10.1016/J.AGEE.2017.08.020

Piotto, D., Craven, D., Montagnini, F., Ashton, M., Oliver, C., & Thomas, W. W. (2019). Successional, spatial, and seasonal changes in seed rain in the Atlantic forest of southern Bahia, Brazil. *PLOS ONE*, *14*(12), e0226474. https://doi.org/10.1371/journal.pone.0226474

Pohlman, C. L., Tng, D. Y. P., & Florentine, S. K. (2021). Do primary rainforest tree species recruit into passively and actively restored tropical rainforest? *Forest Ecology and Management*, *496*, 119453. https://doi.org/10.1016/j.foreco.2021.119453

Poorter, L., Craven, D., Jakovac, C. C., van der Sande, M. T., Amissah, L., Bongers, F., Chazdon, R. L., Farrior, C. E., Kambach, S., Meave, J. A., Muñoz, R., Norden, N., Rüger, N., van Breugel, M., Almeyda Zambrano, A. M., Amani, B., Andrade, J. L., Brancalion, P. H. S., Broadbent, E. N., … Hérault, B. (2021). Multidimensional tropical forest recovery. *Science*, *374*(6573), 1370–1376. https://doi.org/10.1126/science.abh3629

Poorter, L., & Rose, S. A. (2005). Light-dependent changes in the relationship between seed mass and seedling traits: A meta-analysis for rain forest tree species. *Oecologia*, *142*(3), 378–387. https://doi.org/10.1007/s00442-004-1732-y

Portela, R., & Rademacher, I. (2001). A dynamic model of patterns of deforestation and their effect on the ability of the Brazilian Amazonia to provide ecosystem services. *Ecological Modelling*, *143*(1), 115–146. https://doi.org/10.1016/S0304-3800(01)00359-3

R Core Team. (2020). *R: A Language and Environment for Statistical Computing* (4.0.3) [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Rand, T. A., West, N. M., Russell, F. L., & Louda, S. M. (2020). Post-dispersal factors influence recruitment patterns but do not override the importance of seed limitation in populations of a native thistle. *Oecologia*, *193*(1), 143–153. https://doi.org/10.1007/s00442-020-04656-2

Reid, J. L., Holl, K. D., & Zahawi, R. A. (2015). Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications*, *25*(4), 1072–1082. https://doi.org/10.1890/14-1399.1

Ripperger, S. P., Kalko, E. K. V., Rodríguez-Herrera, B., Mayer, F., & Tschapka, M. (2015). Frugivorous Bats Maintain Functional Habitat Connectivity in Agricultural Landscapes but Rely Strongly on Natural Forest Fragments. *PLOS ONE*, *10*(4), e0120535. https://doi.org/10.1371/journal.pone.0120535

Rogers, H. S., Donoso, I., Traveset, A., & Fricke, E. C. (2021). Cascading Impacts of Seed Disperser Loss on Plant Communities and Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *52*(1), 641–666. https://doi.org/10.1146/annurev-ecolsys-012221-111742

Rüger, N., Schorn, M., Kambach, S., Chazdon, R. L., Farrior, C., Meave, J., Muñoz, R., Breugel, M. V., Amissah, L., Bongers, F., Craven, D., Hérault, B., Jakovac, C. C., Norden, N., Poorter, L., Sande, M. V. D., Wirth, C., Delgado, D., Dent, D., … Lopez, O. (2023). Successional shifts in tree demographic strategies in wet and dry Neotropical forests. *Global Ecology and Biogeography*, *36*(6), 1002–1014. https://doi.org/10.22541/au.165123910.08650742/v1

Ružička, M. (1958). Anwendung mathematisch–statisticher Methoden in der Geobotanik (synthetische Bearbeitung von Aufnahmen). *Biologia, Bratislava*, *13*, 647-661.

Sánchez-Montoya, M. M., Datry, T., Ruhi, A., Carlson, S. M., Corti, R., & Tockner, K. (2023). Intermittent rivers and ephemeral streams are pivotal corridors for aquatic and terrestrial animals. *BioScience*, *73*(4), 291–301. https://doi.org/10.1093/biosci/biad004

San-José, M., Werden, L. K., Joyce, F. H., Reid, J. L., Holl, K. D., & Zahawi, R. A. (2022). Effects of landscape structure on restoration success in tropical premontane forest. *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-16542-3

Seidler, T. G., & Plotkin, J. B. (2006). Seed Dispersal and Spatial Pattern in Tropical Trees. *PLOS Biology*, *4*(11), e344. https://doi.org/10.1371/journal.pbio.0040344

Shono, K., Cadaweng, E. A., & Durst, P. B. (2007). Application of Assisted Natural Regeneration to Restore Degraded Tropical Forestlands. *Restoration Ecology*, *15*(4), 620–626. https://doi.org/10.1111/j.1526-100X.2007.00274.x

Sinacore, K., García, E. H., Finkral, A., Van Breugel, M., Lopez, O. R., Espinosa, C., Miller, A., Howard, T., & Hall, J. S. (2023). Mixed success for carbon payments and subsidies in support of forest restoration in the neotropics. *Nature Communications*, *14*(1), 8359. https://doi.org/10.1038/s41467-023-43861-4

Stevenson, P. R. (2011). The Abundance of Large Ateline Monkeys is Positively Associated with the Diversity of Plants Regenerating in Neotropical Forests. *Biotropica*, *43*(4), 512–519. https://doi.org/10.1111/j.1744-7429.2010.00708.x

Stoner, K. E., Vulinec, K., Wright, S. J., & Peres, C. A. (2007). Hunting and Plant Community Dynamics in Tropical Forests: A Synthesis and Future Directions. *Biotropica*, *39*(3), 385–392. https://doi.org/10.1111/j.1744-7429.2007.00291.x

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6

Tang, Q., Liang, G., Lu, X., & Ding, S. (2014). Effects of corridor networks on plant species composition and diversity in an intensive agriculture landscape. *Chinese Geographical Science*, *24*(1), 93–103. https://doi.org/10.1007/s11769-014-0659-4

Tarabon, S., Dutoit, T., & Isselin-Nondedeu, F. (2021). Pooling biodiversity offsets to improve habitat connectivity and species conservation. *Journal of Environmental Management*, *277*, 111425. https://doi.org/10.1016/j.jenvman.2020.111425

Tewksbury, J. J., Levey, D. J., Haddad, N. M., Sargent, S., Orrock, J. L., Weldon, A., Danielson, B. J., Brinkerhoff, J., Damschen, E. I., & Townsend, P. (2002). Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences*, *99*(20), 12923–12926. https://doi.org/10.1073/pnas.202242699

Tucker, M. A., Busana, M., Huijbregts, M. A. J., & Ford, A. T. (2021). Human-induced reduction in mammalian movements impacts seed dispersal in the tropics. *Ecography*, *44*(6), 897–906. https://doi.org/10.1111/ecog.05210

Turnbull, L. A., Coomes, D., Hector, A., & Rees, M. (2004). Seed Mass and the Competition/Colonization Trade-off: Competitive Interactions and Spatial Patterns in a Guild of Annual Plants. *Journal of Ecology*, *92*(1), 97–109.

Turner, I. M. (2008). *The ecology of trees in the tropical rain forest* (Digitally pr. version). Cambridge Univ. Press.

van Breugel, M., Bongers, F., & Martinez-Rarnos, M. (2007). Species dynamics during early secondary forest succession: Recruitment, mortality and species turnover. *Biotropica*, *39*(5), 610–619. https://doi.org/10.1111/j.1744-7429.2007.00316.x

van Breugel, M., Bongers, F., Norden, N., Meave, J. A., Amissah, L., Chanthorn, W., Chazdon, R. L., Craven, D. J., Farrior, C. E., Hall, J. S., Hérault, B., Jakovac, C. C., Lebrija-Trejos, E. E., Miguel, M.-R., Muñoz, R., Poorter, L., Rüger, N., van Der Sande, M. T., & Dent, D. H. (2024). Feedback loops drive ecological succession: Towards a unified conceptual framework. *Biological Reviews*. https://doi.org/10.1111/brv.13051

van Breugel, M., Craven, D., Lai, H. R., Baillon, M., Turner, B. L., & Hall, J. S. (2019). Soil nutrients and dispersal limitation shape compositional variation in secondary tropical forests across multiple scales. *Journal of Ecology*, *107*(2), 566–581. https://doi.org/10.1111/1365-2745.13126

van Breugel, M., Hall, J. S., Craven, D., Bailon, M., Hernandez, A., Abbene, M., & van Breugel, P. (2013). Succession of Ephemeral Secondary Forests and Their Limited Role for the Conservation of Floristic Diversity in a Human-Modified Tropical Landscape. *PLoS ONE*, *8*(12), e82433. https://doi.org/10.1371/journal.pone.0082433

Verheyen, K., & Hermy, M. (2001). The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology*, *89*(5), 829–840. https://doi.org/10.1046/j.0022-0477.2001.00596.x

Veryard, R., Wu, J., O'Brien, M. J., Anthony, R., Both, S., Burslem, D. F. R. P., Chen, B., Fernandez-Miranda Cagigal, E., Godfray, H. C. J., Godoong, E., Liang, S., Saner, P., Schmid, B., Sau Wai, Y., Xie, J., Reynolds, G., & Hector, A. (2023). Positive effects of tree diversity on tropical forest restoration in a field-scale experiment. *Science Advances*, *9*(37), eadf0938. https://doi.org/10.1126/sciadv.adf0938

Vieira, D. L. M., Rodrigues, S. B., Jakovac, C. C., Da Rocha, G. P. E., Reis, F., & Borges, A. (2021). Active Restoration Initiates High Quality Forest Succession in a Deforested Landscape in Amazonia. *Forests*, *12*(8), 1022. https://doi.org/10.3390/f12081022

Vincent, J. R., Curran, S. R., & Ashton, M. S. (2021). Forest Restoration in Low- and Middle-Income Countries. *Annual Review of Environment and Resources*, *46*(1), 289–317. https://doi.org/10.1146/annurev-environ-012220-020159

Wendt, A. L., Chazdon, R. L., & Vargas Ramirez, O. (2022). Successional trajectories of seed dispersal mode and seed size of canopy tree species in wet tropical forests. *Frontiers in Forests and Global Change*, *5*. https://www.frontiersin.org/articles/10.3389/ffgc.2022.946541

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., … Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Wijdeven, S., & Kuzee, M. (2000). Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecology*, *8*(4), 414–424. https://doi.org/10.1046/j.1526-100x.2000.80056.x

Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, *91*(12), 3664–3674. https://doi.org/10.1890/09-2335.1

Wright, S. J., Zeballos, H., Domínguez, I., Gallardo, M. M., Moreno, M. C., & Ibáñez, R. (2000). Poachers Alter Mammal Abundance, Seed Dispersal, and Seed Predation in a Neotropical Forest. *Conservation Biology*, *14*(1), 227–239. https://doi.org/10.1046/j.1523-1739.2000.98333.x

Wunderle, J. (1997). The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *FOREST ECOLOGY AND MANAGEMENT*, *99*(1–2), 223–235. https://doi.org/10.1016/S0378-1127(97)00208-9

Zahawi, R. A., Werden, L. K., San-José, M., Rosales, J. A., Flores, J., & Holl, K. D. (2021). Proximity and abundance of mother trees affects recruitment patterns in a long-term tropical forest restoration study. *Ecography*, *44*(12), 1826–1837. https://doi.org/10.1111/ecog.05907

Zimmerman, J., Pascarella, J., & Aide, T. (2000). Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *RESTORATION ECOLOGY*, *8*(4), 350–360. https://doi.org/10.1046/j.1526-100x.2000.80050.x

Supplementary Information SI1

Vegetation inventories in the Agua Salud area

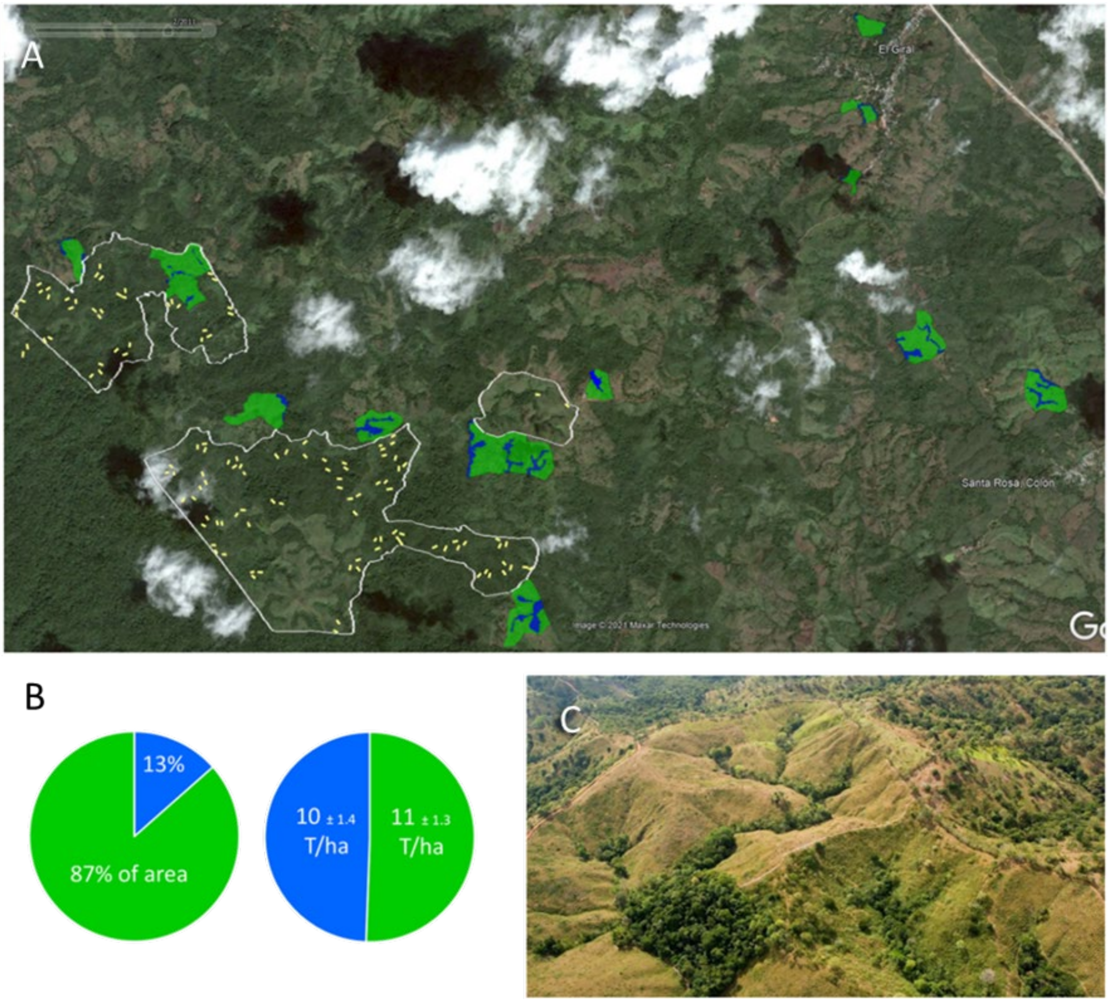

Figure S1. Trees in pastures. (A) Full tree inventory of 15 pastures, including all non-forest trees in the open pasture area (green-shaded areas) and streamside forest fragments that bordered or crossed these pastures (blue-shaded). (B) Mean percentage of the total pasture area covered by the forest fragments and open pasture (left-hand pie chart) and mean percentage of total tree above ground biomass in forest fragments and open pastures (right –hand pie chart). Colors as in A. The plots of the long-term secondary forest dynamics study are indicated by the small yellow rectangles.

Vegetation inventories in the Agua Salud area included:

1. the 54 secondary forests sites, each with two 20x50m plots, that were mentioned in the Method section of the main text, including the 45 study sites, four additional secondary forest sites in which the two plots differed in age, and five additional sites for which we did not have an exact age (but at least >50 year).
2. The inventory of the streamside secondary forest fragments, as described in the main text.
3. Four 1-ha plots in the adjacent Soberania National Park sites, all secondary forests >100y old.

4. A full inventory of 15 pastures. The pastures were located in the Agua Salud study Area and the adjacent area around the town of Giral (Fig. S1). Total sampled area was 138 ha, and included open grass land and. All trees with a diameter at breast height of 10cm were measured and identified in the open grass land areas within the pasture (living fences and isolated trees) and in the strips of streamside forests fragments along the streams (CFFs) that bordered or crossed the these pastures (unpublished data M. van Breugel & J.S. Hall). On average, 13% of each pasture was covered by the forest fragments, but these forest fragments contained about 50% of the total aboveground tree biomass (Fig. S1B). The average density of pasture trees was 58 ha^{-1} (±23 SD).

Total number of species, including morphospecies, is 953, and the total number of species that were identified to species is 811.

Supplementary Information SI2

Plot-level environmental variables

Basal area

We used basal area (m^2 ha^{-1}), and not age, as our primary variable representing ecological succession because, while it relates strongly to forest age, it has been found to be a better predictor of successional changes in environmental variables, stand dynamics, and species composition. To account for difference in sample area, tree basal area was scaled to the plot level according to sample effort per size class (i.e., woody plant individuals that were not lianas and with 1 cm ≤ DBH < 5 cm were counted double in our calculation of species abundances).

Light

Data on understory light was estimated from 11 hemispherical photographs per plot, taken at 5 m intervals along the central 50-m axis of the plots, at 1.5 meter above soil level. Data from van Breugel *et al*. (2013).

Soil nutrients

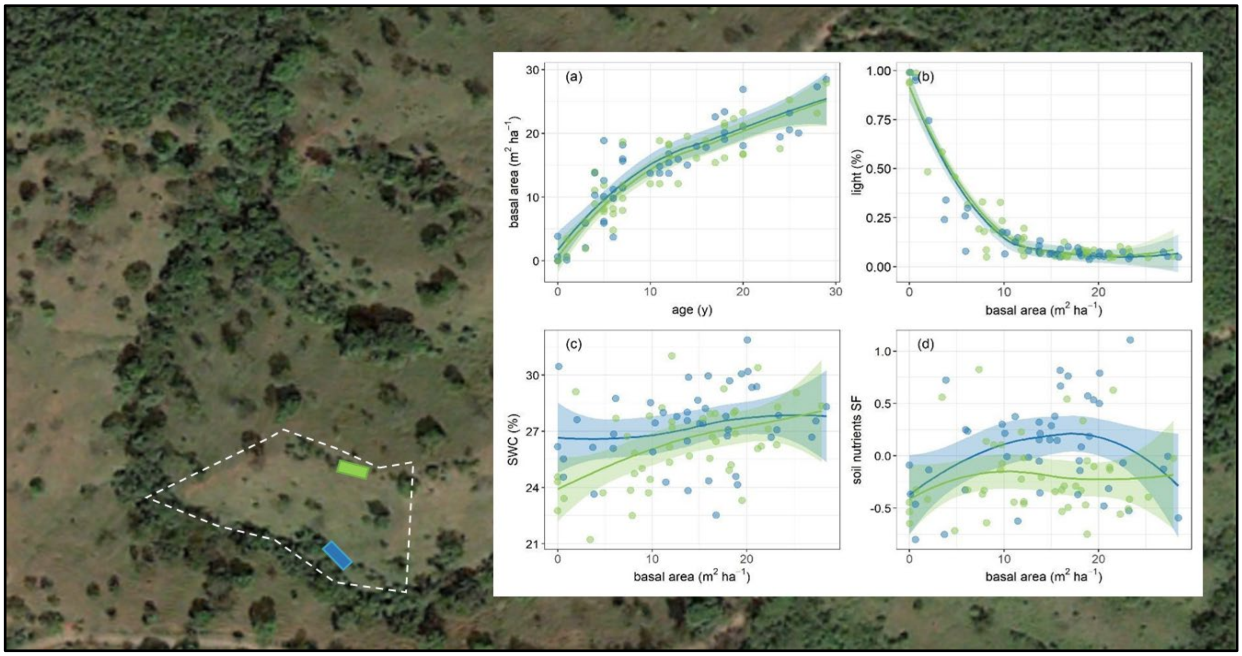

Figure S2. Variation in stand structure and environmental conditions across and within 45 secondary forest sites along a successional gradient. In each site, two plots were laid out on a hill slope within pastures abandoned between 0-32 y ago, one at the bottom of the slope adjacent to older stream-side forest and one at the top of the slope. Green and blue rectangles, dots and lines represent upper and lower slope plots, respectively. Lines and shade areas plot loess regression models with 95% confidence intervals. (**A**) stand basal area (m2ha-1). (**B**) Understory light (%). (**C**) Soil fertility (the first principle component of a soil nutrient PCA). (**D**) Gravimetric soil water content (%).

We used soil fertility data from van Breugel *et al*. (2019), which was obtained as follows: Soil samples (0--15 cm) were collected in 2010 at five different locations in each plot. These samples were bulked and thoroughly mixed per plot and concentrations of extractable (plant-available) nutrients (P, K, Ca, Mg, Cu, Fe, Mn, Zn) and the potential toxin Al were determined by Mehlich-III extraction (Mehlich, 1984). Total N was determined by dry combustion using an elemental analyzer (Thermo Flash 1112, Bremen, Germany). To identify the nutrients that contributed most to the variation across the landscape, a principal component analysis (PCA) was run using the function 'rda' of R package 'vegan' (Oksanen *et al*. 2020). Between-plot dissimilarity in soil nutrients was calculated using Euclidean distances, with nutrient concentrations centered and scaled to standard deviation prior. A second PCA was run with the five elements with factor loadings on the first PC < -1 (Al) or > 1 (P, Ca, Mg, and Cu). In our analyses, we used the plot loadings on the first PC as explanatory variable. This PC explains 27% of the variation and suggests a soil fertility gradient ranging from low to very low nutrient concentrations, combined with increasing concentrations of extractable Al -- a potential toxin - for both slope positions. See van Breugel *et al*. (2019), supporting Information, figures S1-S4 for more details.

Gravimetric soil water content

We used unpublished data M. van Breugel & J.S. Hall. During the dry period of December 2009--April 2010, 10-cm deep soil cores were collected at 10 points per plot every two weeks. Soil samples were wrapped in aluminum foil and transported in Ziplock bags to the lab to avoid water loss. Per sample, the gravimetric soil water content (SWC, %) was determined and plot means were calculated for each census. For this study, we used for each plot the lowest of the bi-weekly dry-season SWC means as explanatory variable – rather than the SWC at the end of the dry season – for two reasons: (i) It took two weeks to collect the soil samples across all plots, which means that collection dates differ among plots. (ii) During the 2009-2010 dry period, occasional and spatially heterogeneous rainfall events occurred across the study area. As a consequence of both points, the census with longest previous period without rainfall varied among plots.

References

Mehlich, A. (1984). Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. *Communications in Soil Science and Plant Analysis* 15(12): 1409–1416. DOI: 10.1080/00103628409367568

Oksanen, J. F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinnPierre, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). vegan: Community Ecology Package (2.5-7). https://CRAN.R-project.org/package=vegan

van Breugel, M., Hall, J. S., Craven, D., Bailon, M., Hernandez, A., Abbene, M., & van Breugel, P. (2013). *Succession of Ephemeral Secondary Forests and Their Limited Role for the Conservation of Floristic Diversity in a Human-Modified Tropical Landscape*. PLoS ONE 8(12): e82433. DOI: 10.1371/journal.pone.0082433

van Breugel, M., Craven, D., Lai, H. R., Baillon, M., Turner, B. L., & Hall, J. S. (2019). *Soil nutrients and dispersal limitation shape compositional variation in secondary tropical forests across multiple scales*. Journal of Ecology 107(2): 566–581. DOI: 10.1111/1365-2745.1312