RESEARCH ARTICLE

Restoring tropical forest composition is more difficult, but recovering tree-cover is faster, when neighbouring forests are young

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Abstract

Context Neighbouring forests constitute biological sources that enable the succession from species-poor systems, such as tree-plantings, to highly diverse forests. However, old forest patches are becoming rare in tropical agricultural landscapes.

Objective We were interested in if, and how, spontaneous regeneration under tree-plantings reflects the age and the amount of the neighbouring forest cover. We anticipated that older forests promote a compositionally broader recovery in neighbouring tree-plantings, because older forests likely include disturbance-sensitive species, particularly within least deforested landscapes.

Methods We studied twenty-seven restoration sites implemented as tree-plantings in the Brazilian Atlantic Forest. We quantified the effects of age and amount of neighbouring forest cover on structural and compositional characteristics of the regeneration community (dbh < 5 cm). We used two landscape groups (presence, or absence, of forests older than 30 years.) with a similar areal range of forest cover, enabling the disentanglement of forest age from forest amount effects on regeneration community responses.

Results Surprisingly, we found that greater forest cover correlated with denser and more species-rich regeneration communities only when neighbouring forests were young. This pattern was promoted by non-vertebrate dispersed species. Regeneration communities in tree-plantings near to young forests had lower seed-mass and relative abundances of forest-specialists, compared to communities found near old forest patches.

Conclusion Regeneration is likely denser in landscapes of vast young-forest coverage. However, small-seeded and habitat-generalist species, frequently related to disturbance tolerance, tend to be dominant if old-growth forests are far away. This biased seed source appears to preclude the restoration of typical historic tropical forest composition.

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Introduction

During the last century, unprecedented extensive conversion of naturally forested areas to agricultural and urban areas spread throughout the tropics (Chazdon 2014). Since 2005, deforested areas cover most of the domains of tropical moist forests (Asner et al. 2009). Such drastic change in landscape composition increased risks of biodiversity loss and decline of ecosystem services, reinforcing the urgent need for forest-protective policies and restoration programs (Kueffer and Kaiser-Bunbury 2014; Suding et al. 2015). Correspondingly, large forest-restoration initiatives have included Brazilian deforested regions (Chazdon 2008; Durigan et al. 2013; Holl 2017). Forest restoration aims to lever secondary succession in degraded areas by employing approaches that may range from removal of anthropogenic disturbance to the intensive manipulation of species composition and abiotic conditions (Meli et al. 2017).

Active forest restoration is particularly recommended in severely deforested landscapes (Malhi et al. 2014), and typically involves native tree-plantings (Lamb et al. 2005; Rodrigues et al. 2009) because agricultural practices that are commonly adopted in crop-fields and pasture lands tend to eliminate tropical forest species from the seed bank (Lopez-Toledo and Martinez-Ramos 2011). These planted native trees are then expected to shelter regeneration communities, which comprise young descendants of planted trees together with individuals of the same and other species dispersed from neighbouring communities (Brancalion et al. 2010; Bertacchi et al. 2016; Reid et al. 2015). Planted trees increase seed arrivals by attracting seed dispersing animals, as recognized by the "applied nucleation" concept (i.e. triggering restoration with small vegetation patches as focal areas for recovery; Zahawi et al. 2013). Likewise, Catterall (2018) endorses attracted fauna as a restoration driver, rather than a passenger; although some animals can be much slower in occupying revegetated areas, such as the specialists of mature-growth habitats.

Arriving propagules play a crucial role in tropical forest recovery because planting a substantial fraction of the original diversity is unfeasible (Lamb et al. 2005). Accordingly, the role of nearby forest patches as biodiversity repositories has been recognised as a key asset for tropical forest restoration (Banks-Leite et al. 2014; Chazdon and Guariguata 2016; Crouzeilles and Curran, 2016; Molin et al. 2017). Essentially, forest restoration must take advantage from the biodiversity of natural habitats that is shared with surrounding anthropogenic habitat. Then, such functional connectivity may promote the local planted diversity to increasingly reflect the regional diversity (Ricklefs, 1987; Shackelford et al. 2017). In this context, the relevance of landscape forest-cover has been highlighted, because the arrival of diversity in restoration sites can be intensified or attenuated by landscape structure (Tscharntke et al. 2012).

Fostered by technical advances, the percentage of "landscape forest cover" has been used by spatial models addressing forest restoration as the single operational proxy for functional connectivity between natural habitats and habitats under recovery (e.g. Brancalion et al. 2019a, Rozendaal et al. 2019, and Strassburg et al. 2019). Typically, the amount of forest cover is calculated with remotely sensed tree-cover (Hansen et al. 2013). However, this remote sensing approach does not consider the quality of the forest cover e.g. age, species composition. Recent second-growth and old forests have been computed together as "forested areas".

At present, regenerating forests are the predominant form of forest cover in the tropics (Chazdon, 2014), as typically observed within the Brazilian Atlantic Forest domain (e.g. Lira et al. 2012; Ferraz et al. 2014). Second growth is vital for the recovery of degraded landscapes (Chazdon and Guariguata, 2016) and is rapidly expanding in the tropics, as a consequence of agricultural abandonment in terrains of lower farming capabilities (Asner et al. 2009). However, Gibson et al. (2011) have shown that regenerating forests are limited in taking on the role of old-growth forests since they present substantially lower biodiversity. These findings raise the question to what extent young secondary forest can replace old-growth forest patches in assisting forest restoration.

Scarcity of neighbouring mature forests implies a compositional limitation to forest recovery (Holl 2007; Middendorp et al. 2016). Some species groups

tend to be particularly sensitive to heavy deforestation or degradation. For instance, the arrival of vertebrate-dispersed and large-seeded plants is more dependent on neighbouring old-growth forests (Lamb et al. 2005; Costa et al. 2012). A lack of large-seeded species in the seed rain of tree plantings can be persistent (Reid et al 2015), although de la Peña-Domene (2016) have shown that large-seeded trees from pre-existing forest patches can mitigate such constraints by enhancing the recolonization of adjacent sites. Moreover, younger forests have fewer reproductive trees of late-successional, forest-specialist species (Liebsch et al. 2008). The trend of increased rarity of these disturbance-sensitive species where neighbouring forests are young may be increased by heavy defaunation (Galetti et al. 2017) and by greater contribution from opportunistic non-forest trees in the seed rain (Zahawi et al. 2013).

Here, we evaluated the effect of amount and age of nearby forests, both derived from remotely-sensed estimates, on the regeneration communities that we observe during tropical forest restoration. We anticipated that regeneration communities growing underneath tree-plantings would present compositional limitations not only in highly deforested landscapes, but also in landscapes where mature forests are absent and neighbouring forest cover comprises young, second growth, forests. This compositional limitation would consist of reduced species richness, and a community composition dominated by generalist plant species rather than forest specialists, and lacking large-seeded and/or vertebrate dispersed species. We compared regeneration communities underneath tree-plantings from two groups, separated according to the age of neighbouring forest cover: neighbouring forest cover encompasses old forest patches; neighbouring forest cover is solely made up of young forest patches. The range of variation in the amount of neighbouring forest cover was similar for both age groups: young and old forest cover. We tested if larger and older forest cover promotes regeneration communities in restoration sites that are denser, more species-rich, and have an increased presence of vertebrate-dispersed, large seeded and forest-specialist species. Improved predictions on the effect of landscape composition will likely assist forest restoration planning in tropical agricultural landscapes by supporting the selection of more effective approaches.

Methods

Study area

The restoration program "Projeto de Recuperação de Matas Ciliares" (PRMC), coordinated by the Environmental Agency from São Paulo State, was launched in 2005 and established a milestone for Brazilian forest restoration policies. This unprecedented initiative included the implementation of over 500 demonstration sites distributed across the São Paulo state, which were set in private lands by regional working groups (Wuethrich 2007; Chazdon 2008). The present study was undertaken in the six Eastern watersheds covered by PRMC, comprising a 150-km-wide region (Online Resource 1 for study region map). All restoration sites we surveyed are located within the boundaries of the Atlantic-plateau geomorphological and botanical provinces (Scudeller et al. 2001) and the Serra do Mar coastal forests ecoregion (Olson et al. 2001). The agricultural expansion in this region of São Paulo state occurred in the nineteenth century promoting widespread and abrupt deforestation: deforested lands were used by agriculture and natural areas were degraded (Dean 1991). Currently, the land-use mosaic is vastly dominated by pastures, which typically enclose pockets of croplands, urban patches, commercial tree plantations, and tropical-forest of varied successional stages.

Sampling design

We conducted a vegetation survey and neighbouring forest cover assessment, having selected a group of 27 restoration sites, according to the protocol outlined below, from the 133 demonstration sites located within six watersheds. These watersheds are highly variable in area and number of restoration sites, which resulted in an uneven distribution of surveyed sites among watersheds (Fig. 1). Firstly, our screening process selected restoration projects that were implemented on former pasturelands with the following protocol: seedlings of over sixty species were planted in a regular density of 1667 seedlings/ha. Unfortunately, the list of planted species is taxonomically inaccurate due to the use of common names in the records so we are unsure about the exact planted composition at each site. However, it is likely that a similar composition was planted at each site, and we
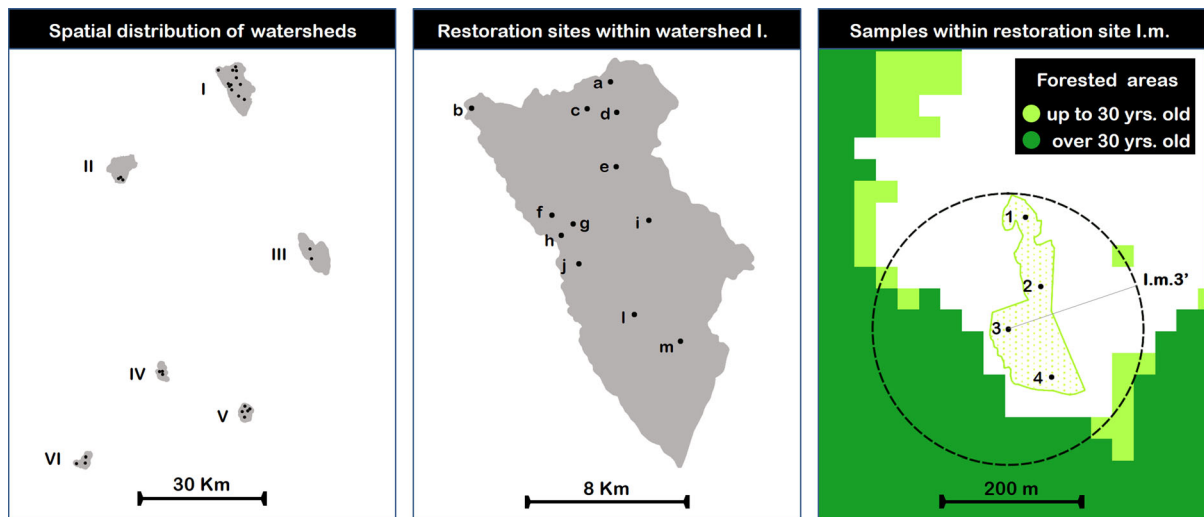
Fig. 1 Spatial structure of our sampling design. Spatial distribution of watersheds in our study region; restoration sites in a watershed; and vegetation-plots in a restoration site. The 200-m-buffer is shown for the vegetation plot 'I.m.3′ overlaying the raster resulting from the NDVI time series

assume this in our interpretation of our results. Secondly, we excluded sites that did not present any forest cover in a 200-m-wide buffer during the restoration implementation, as well as sites that presented values outside 1.5 times the interquartile range for: area (i.e. < 0.2 ha and > 2.2 ha), altitude (i.e. < 596 m and > 1508 m), annual precipitation (i.e. < 1370 mm and > 1735 mm) and slope (i.e. > 31%). Lastly, we set a minimum distance of 1 km between selected sites by discarding the most dissimilar neighbouring sites (again, on area, altitude, annual precipitation, and slope). To do so, we used the database from PRMC combined with climate models and the digital elevation model provided by World-Clim (Hijmans et al. 2005). The spatial structure of our sampling is presented in Fig. 1, and the location map, showing the wider Brazilian context, is presented in Online Resource 1.

Data collection

Vegetation data

We conducted vegetation surveys in the restoration tree plantations seven years after planting. We randomly located four coordinates within each restoration site to indicate the centre of each 200-m²-vegetation plot. Measured by the central coordinate, the average distance between vegetation plots from the same restoration site was 53.6 m. Then, inside each plot, a 100-m²-subplot was positioned with the same central point. Within the large plots, we quantified and identified all trees with diameter at breast height (dbh) ≥ 5 cm. In the subplot, we quantified and identified all woody individual taller than 0.5 m, with dbh < 5 cm. For multi-stemmed trees, the inclusion criterion was a combined basal area at breast height larger than 19.6 cm² i.e. an equivalent diameter of 5 cm. The cut-off dbh of 5 cm was set after exploratory field observations, in which we noted that systematically displayed individuals (clearly the planted ones) often presented dbh > 10 cm, and rarely < 7 cm. Thus, for our analysis, we assumed individuals of species of ≥ 5 cm dbh represented adults, and individuals of < 5 cm dbh represented juveniles of the regeneration community i.e. our focal response. As well as the regularity of spacing of the planted individuals of ≥ 5 cm dbh, they were also observed to be flowering/fruiting, in a manner not observed for those individuals of < 5 cm dbh. Given this, and the fact that seed banks of woody species are typically short lived in agricultural land, we are confident that we have accurately captured a description of the regeneration community, and that any variation in this community is driven by differing seed arrival and survival under tree plantings. Individuals that could not be consistently identified in the field had samples taken to allow further identification at the

ESA Herbarium (Department of Biology, ESALQ-USP). The nomenclature followed the database "Flora of Brazil 2020," according to the APG IV system (Chase et al. 2016).

Botanical databases were used to classify the identified species according to the seed-dispersal syndrome (by vertebrates or by non-vertebrates), seed mass (grams per seed) and habitat selectivity (moist-forest-specialist or habitat-generalists). We compiled information on seed-dispersal syndrome and seed mass from literature (references and species list presented in Online Resource 2). To classify species according to habitat selectivity, we first assessed the species geographical distribution through the Global Biodiversity Information Facility (GBIF; https://www.gbif.org accessed March 2017). We then compared each occurrence map to the terrestrial ecoregions map (Olson et al. 2001): species solely found within broadleaf tropical moist-forests domains were considered as "forest-specialists", while "generalist-species" presented a broader distribution that overlapped with moist-forest habitats but also included records from non-forest natural habitats such as tropical savannas and shrublands (Toledo et al. 2018a).

Remote sensing data: landscape predictor variables

Forest patches were mapped within a 200 m-buffer-zones around each vegetation plot; this distance is consistent with findings from Souza et al. (2014), Rezende et al. (2015) and Toledo et al. (2018a), which found substantial neighbourhood effects on forest patches in regenerating forests in distances up to 200 m. In addition, considering Tambosi et al (2014), the probability of several Atlantic Forest species dispersing across non-forested areas is likely halved by 50 m, and reduced by 75% across a distance of 100 m. Maps indicating the distribution of native forest were produced with the visual interpretation of colour orthophotos, with spatial resolution of 1 m, which were taken two years before the plantings. The natural forests have their boundaries vectorized at a scale of 1:4.000 with the software ArcGis 10.1. We assumed we had correctly delineated forest cover based on the photos: mapping activities did not include field validation i.e. ground-truthing.

The history i.e. the age class of these 'two-years-before-planting' forest patch areas was assessed by Normalized Difference Vegetation Index (NDVI)

(Rouse, 1973) using a time series of Landsat-5 images (spatial resolution of nearly 30 m) from the dry seasons of 1985, 2000 and 2014. We classified as "young forests" forest patches with low NDVI measured in images from 1985 and/or 2000. Patches with persistent high NDVI values (i.e. > 0.3) were considered as "old forests", even if they have expanded along the time series and became partially covered by younger second growth. The percentage of forest cover was then calculated with data from 2014, resulting in the values of "forest cover" we tested as a predictor in our models.

The selection of 30 years as the cut-off considered models from Liebsch et al. (2008) and Poorter et al. (2016), which indicate that, from the 4th decade of forest recovery, increases in structural and compositional similarity to mature forest are likely to be minor. Finally, all plots were classified into two classes, according to the presence or absence of old forest in the surrounding buffer. This procedure resulted in the binary categorical predictor used in our models: young forest cover (young-FC, hereafter), and old forest cover (old-FC, hereafter). The young-FC group comprised 40 plots from 10 restoration sites, with an average forest cover of 15.6%, ranging up to 49.9%. Similarly, the old-FC group comprised 68 plots from 17 restoration sites, with an average forest cover of 18.4%, ranging up to 41.6%. The average "young forest gain" in the old-FC group (i.e. forest expansion during the past 30 yrs.) was 32.8%, ranging at plot level from 0% to 84.5% (data shown for each restoration site in the Online Resource 3).

Data analysis

Data analysis was performed with R.3.6.0. (R Foundation for Statistical Computing, Vienna, AT). Considering that vegetation plots were nested by watershed and restoration sites, linear mixed modelling (with nlme package version 3.1-139, R-Core Team) was used to assess the effects of age and amount of neighbouring forest-cover on six indicators of structural and compositional restoration of regeneration communities (DBH < 5 cm). The response variables analysed in the models were: a- stem density, b- observed species richness, c- stem density of vertebrate-dispersed species, d- stem density of non-vertebrate-dispersed species, e- community-weighted mean for seed mass (CWM-SM) and f- relative

abundance of moist-forest specialists; as measured at the plot level. We tested watershed, restoration site, and both watershed and restoration site as random factors in each model. We found that only considering the restoration sites provided the best combination on goodness of fit and model simplicity. Goodness-of-fit between models were compared with marginal and conditional R^2 (see Nakagawa et al. 2017) with MuMIn package version 1.43.6.

The effect of three predictors was assessed in these six models: percentage of forest cover in the 200 m-wide buffer, presence or absence of old (> 30 year old) fragments, and a third predictor, which is the analogous measure of the response variable, but obtained from the respective adult community (DBH ≥ 5 cm) (e.g. 'adult' stem density as a predictor of the regeneration stem density). We included the adult communities among the predictors so as to evaluate their direct influence on regeneration, potentially by means of their offspring. Thus, we evaluated stem density, observed species richness, density of vertebrate-dispersed trees, density of non-vertebrate-dispersed trees, CWM-SM, and relative abundance of forest-specialist trees—measured in adults above each regeneration community—as regeneration predictors. We also assessed the interaction between neighbouring forest age and forest cover because we expected the effect of forest age to be influenced by the amount of forest cover, for instance, old-growth species may become absent in 'old' forest patches in heavily deforested landscapes (Pardini et al. 2010; Banks-Leite et al. 2014). To satisfy the model assumptions on error distributions, CWM-SM was log-transformed, and relative abundance of forest-specialists was square-root transformed. Two plots without 'adult trees' (DBH ≥ 5 cm) were dropped in these last two models, because for these plots it was impossible to calculate seed-mass CWM and relative abundance of forest-specialists among 'adults'.

Results

Within the 200m²-plots, a total of 1033 trees with DBH ≥ 5 cm (here referred to as 'adults') belonging to 94 species were identified and measured. Two plots (out of 108) presented no adults. Correspondingly, in the 100m²-subplots, we catalogued 3199 small individuals (DBH < 5 cm, here referred to as 'juveniles')

belonging to 153 species. Every subplot presented juveniles. Fifteen species were only found among adults, while 74 species were solely sampled among juveniles. Plant conditions did not allow identification at the species level for 106 adults (10.7%) and 366 juveniles (11.4%).

Combining vegetation plot data with the literature survey on species traits provided additional context for the hypotheses we tested. We observed similar relative abundance of vertebrate-dispersed juveniles within young-FC and old-FC contexts (respectively, 58.6% and 60.2%), and both were slightly higher than relative abundances found with adults within young-FC and old-FC contexts (respectively, 40.3% and 51.3%). Juveniles presented smaller CWM of seed mass within young-FC (median = 0.061 g.; IQR = 0.031–0.124 g.) compared to old-FC (median = 0.097 g.; IQR = 0.048–0.257 g.); while adults presented greater and more variable CWM-SM within young-FC and old-FC (0.045 g./seed IQR = 0.020–0.223, and 0.071 g./seed IQR = 0.030–0.108, respectively). Also, it was notable that only 9.3% of adults and 7.5% of juveniles were categorised as forest-specialists in plots with young-FC, while forest specialists contributed 17.1% of adults and 13.2% of juveniles within old-FC.

Stem density and species richness

We did not find a significant association between stem densities of adults and juveniles (Table 1; p = 0.34). Forest age and amount significantly affected stem densities through their interaction: increasing forest cover related to greater juvenile stem density only within young-FC (Table 1, Fig. 2a). However, individually, neither forest age nor forest amount significantly affected juvenile stem densities (p = 0.99 and 0.34, respectively). The interaction between age and amount of forest cover was also a significant predictor of species richness in regeneration communities, with higher response values associated with higher forest cover only within young-FC (Table 1, Fig. 2). Nonetheless, for species richness, juvenile and adult communities were highly correlated (P = 0.001).

After separating individuals according to seed dispersal syndrome, we found that none of the tested variables was a good predictor of density for vertebrate-dispersed juveniles. Only a marginally significant association was found with forest cover amount (Fig. 2c). Densities of vertebrate dispersed juveniles

Table 1 Effects of-forest cover amount, forest cover age, adult community, and interaction between age and amount; on the regeneration communities for stem density, species richness, stem density of vertebrate-dispersed species, and stem density of non-vertebrate species

Model–regeneration communities	Predictors	Estimates	DenDF	F-value	p-value
a. Stem density	Forest cover (%)	55.85	78	0.001	0.976
$R^2_{LMM(c)} = 0.8125$	Forest age ($\geq$ 30yrs instead of $<$ 30yrs)	10.13	25	0.000	0.999
$R^2_{LMM(m)} = 0.1193$	Stem density (dbh $\geq$ 5 cm)	0.18	78	0.914	0.342
	Interaction forest cover and age	− 69.99	78	5.816	0.018*
b. Species richness	Forest cover (%)	17.97	78	0.851	0.359
$R^2_{LMM(c)} = 0.7454$	Forest age ($\geq$ 30yrs instead of $<$ 30yrs)	2.90	25	0.111	0.741
$R^2_{LMM(m)} = 0.2496$	Species richness (dbh $\geq$ 5 cm)	0.34	78	11.714	0.001**
	Interaction forest cover and age	− 20.43	78	7.371	0.008*
c. Vertebrate dispersed density	Forest cover (%)	34.30	78	3.86	0.053
$R^2_{LMM(c)} = 0.7894$	Forest age ($\geq$ 30yrs instead of $<$ 30yrs)	4.36	25	0.062	0.806
$R^2_{LMM(m)} = 0.0813$	Vertebrate dispersed density (dbh $\geq$ 5 cm)	0.06	78	0.062	0.804
	Interaction forest cover and age	− 22.01	78	0.953	0.332
d. Non vertebrate-dispersed density	Forest cover (%)	15.83	78	0.623	0.432
$R^2_{LMM(c)} = 0.3801$	Forest age ($\geq$ 30yrs instead of $<$ 30yrs)	5.73	25	0.088	0.769
$R^2_{LMM(m)} = 0.1319$	Non vertebrate-dispersed density (dbh $\geq$ 5 cm)	0.30	78	3.493	0.065
	Interaction forest cover and age	− 33.59	78	7.048	0.010*

ANOVA table resulting from linear mixed models with conditional R^2 (fixed and random factors) and marginal R^2 (fixed factors only). Significant effects are marked with asterisks: ** $p<0.005$, * $p<0.05$

presented a small variance within restoration sites, and a large variance between restoration sites, which was strongly related to random factors acting at the site level, but not to the fixed variables (i.e. forest cover amount and age, and density of vertebrate dispersed adults) (Table 1). In turn, densities of non-vertebrate dispersed juveniles, compared to vertebrate-dispersed, were more weakly related to random factors and more strongly related to fixed factors (Table 1). We found a significant effect from the interaction between forest cover amount and forest cover age, in which higher densities of non-vertebrate dispersed juveniles related to more forested landscapes only within young-FC contexts (Fig. 2d).

Disturbance sensitive traits: seed mass and habitat selectivity

We found significantly higher CWM seed mass among juveniles in landscapes with old forest. Such association between older nearby forests and larger seeds reflected changes in absolute densities for both extremes: small-seeded, and large-seeded, species.

For instance, juveniles from all species with seed mass below 0.001 g. presented average densities of 408/ha for young-FC, and 243/ha for old-FC, while the average density of juveniles from all species with seed mass above 1 g. was found as 105/ha for young-FC and 225/ha for old FC. In addition, CWM of seed mass in the regeneration community correlated to the seed mass observed among adults (Table 2a and Fig. 3a).

Similarly, we found higher relative abundance of forest-specialists in regeneration communities when old forests were nearby, and when the relative abundance of forest-specialists was higher in the adult communities (Table 2 and Fig. 3b). The average density of forest-specialist individuals was smaller within young-FC (165.0/ha) than within old-FC (389.7/ha); while generalists species were slightly rarer within old-FC (2572.1/ha) as compared to sites within young-FC (2797.5/ha).
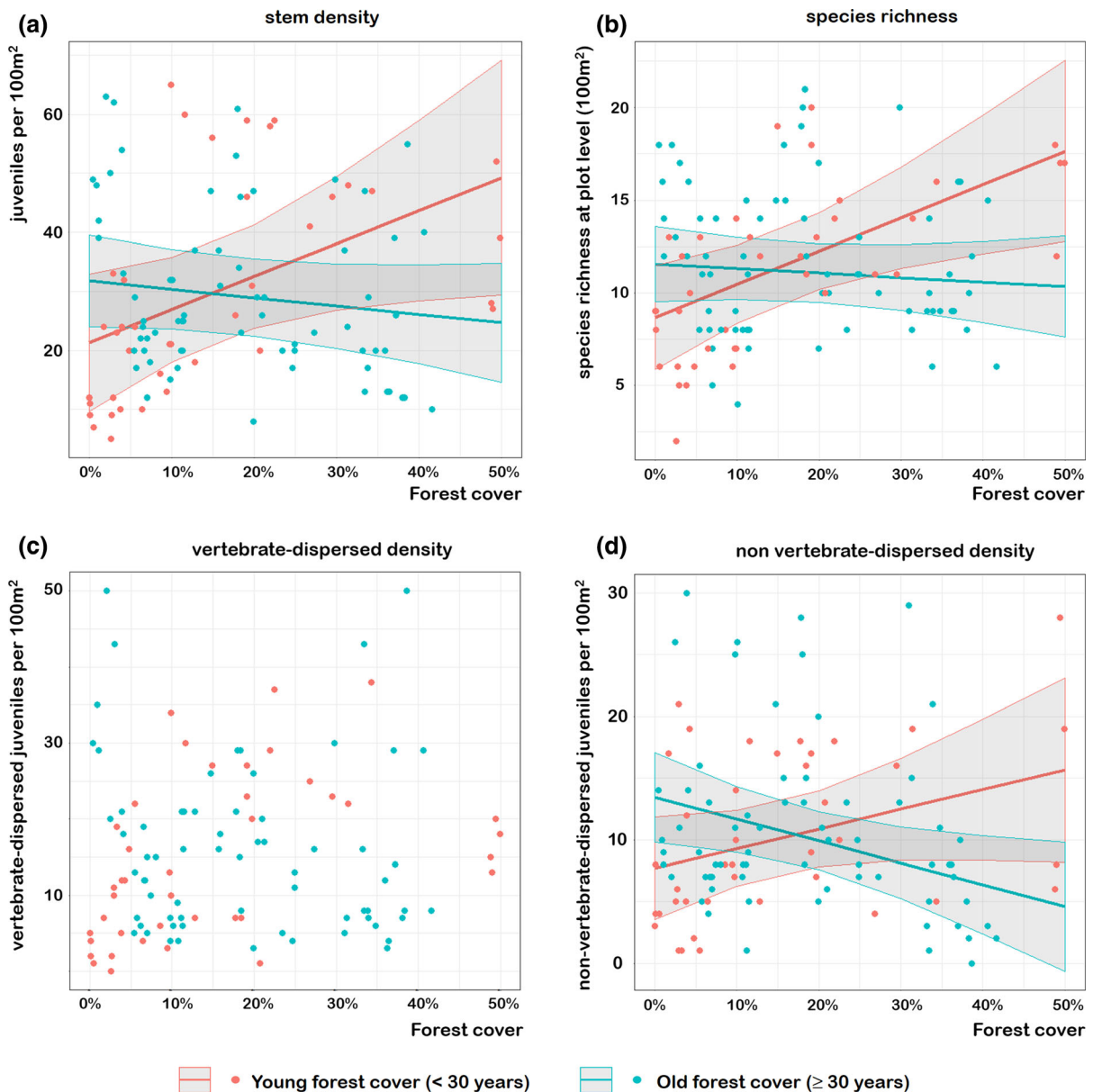
Fig. 2 Observed densities in juveniles (dbh < 5 cm) per 100m² plot (a, c and d) and species richness (b), as a function of forest cover amount and age (coloured points). Lines show models predictions (Table 1) ± 95% confidence intervals for young and old forest cover contexts. For these projections, we set the analogous measurement of the respective predictor in the adult communities (dbh ≥ 5 cm) at the observed median value (i.e. 7.5 for "a.", 5.0 for "b." and 3.0 for "d.". No prediction was made for "c" (vertebrate-dispersed stem densities) due to the lack of association with evaluated factors

Discussion

Despite marked quantitative and compositional differences found among regeneration communities growing beneath native tree-plantings, overall records indicate a meaningful forest recovery. Across all sites, we identified 168 species and found an average of 3391 stems per hectare, which reveals a nearly threefold increase for woody species richness and a nearly twofold increase for stem density, found seven years after the plantation of 60 species in a density of 1667 seedlings/ha. Still, similar initial restoration

Table 2 Effects of the forest cover amount, forest age, and adult community on the regeneration communities on the regeneration communities' CWM seed mass and the relative abundance of forest specialists

Model–regeneration Communities	Predictors	Estimates	DenDF	F-value	p-value
a. CWM seed mass	Forest cover (%)	2.15	76	2.66	0.107
$R^2_{LMM(c)}$ = 0.5334	Forest age (≥ 30yrs instead of < 30yrs)	0.80	25	4.38	0.047*
$R^2_{LMM(m)}$ = 0.2069	CWM seed mass (dbh ≥ 5 cm)	0.19	76	12.37	0.001**
	Interaction forest cover and age	− 1.13	76	0.35	0.557
b. Relative abundance of forest specialists	Forest cover (%)	− 0.44	76	2.16	0.146
$R^2_{LMM(c)}$ = 0.3992	Forest age (≥ 30yrs instead of < 30yrs)	− 0.66	25	8.58	0.007*
$R^2_{LMM(m)}$ = 0.1940	Rel. abund. of forest specialists (dbh ≥ 5 cm)	0.15	76	4.58	0.036*
	Interaction forest cover and age	0.29	76	0.82	0.369

ANOVA table resulting from linear mixed models with conditional R^2 (fixed and random factors) and marginal R^2 (fixed factors only). Significant effects are marked with asterisks: ** $p<0.005$, * $p<0.05$
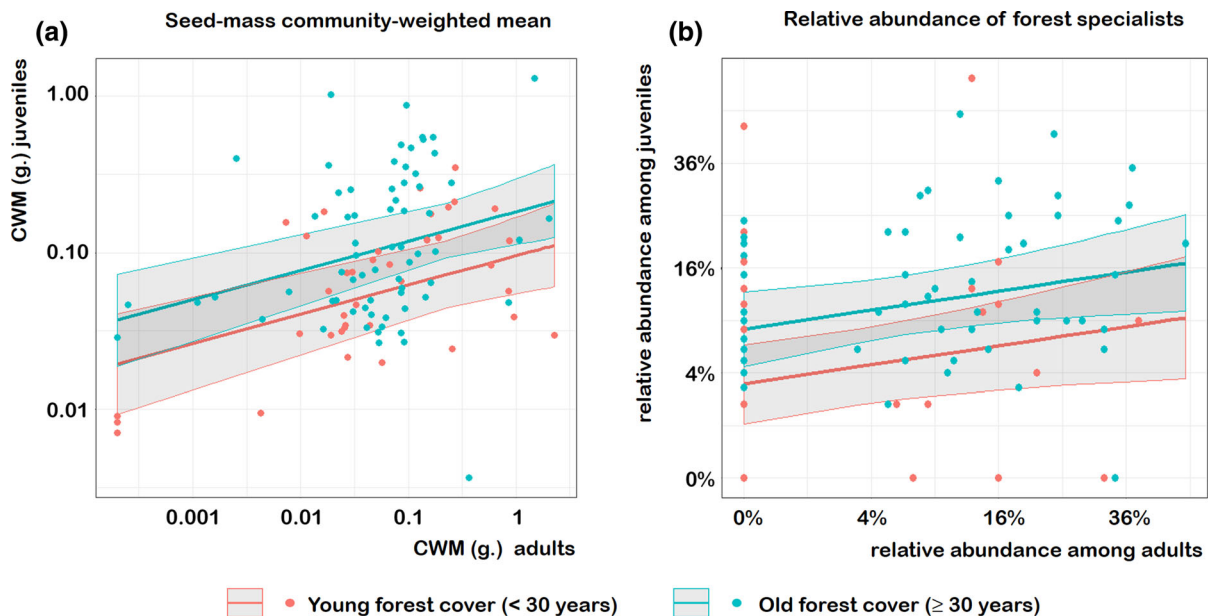
Fig. 3 Observed CWM-SM in regeneration communities as a function of CWM-SM among adults (a), and relative density of forest-specialists among juveniles as a function of the relative abundance of forest-specialists among adults (b). Lines show models predictions (Table 1) ± 95% confidence intervals for young and old forest cover contexts. For these projections, we set the forest cover to the observed medium value (i.e. 13.75%)

interventions resulted in markedly variable trajectories. The relation between such quantitative and compositional differences and the surrounding landscape revealed some unexpected patterns, but also corroborated some predictions grounded by previous studies. We discuss these relationships, together with the practical implications of our findings.

Regeneration density and species richness

The relevance of considering the influence of the neighbouring forest history was corroborated by the significant effect of the interaction between forest age and forest cover on the density and the species richness of juveniles. Here, the general expectation of denser seed rain in landscapes of greater forest cover leading

to a denser and richer regeneration (Holl 2007; but see Charles et al. 2019), was supported in the context of young forest cover, but not around forests that were older than 30 years. Such a pattern suggests two possibilities: higher old forest cover is not consistently improving the seed arrival in restoration sites; and/or seed rain around old forests are not resulting in the establishment of denser or richer communities due to limitations on germination and seedling survival (Reid and Holl 2013).

The possibility of regeneration communities being affected by variation in seed arrival due to dispersal limitation is consistent with our results. We found the correlation between the amount of forest cover and the density of regeneration communities to be dependent on the dispersal syndrome. Accordingly, the rarity of non-vertebrate-dispersed trees is increased markedly when young Brazilian Atlantic Forests gets older (Liebsch et al. 2008). On the other hand, the studied region is marked by heavy forest fragmentation (Toledo et al. 2018b) and defaunation, with negative consequences on seed dispersal (Galetti et al. 2013, 2017). Defaunation can play a crucial role in the recovery of tropical forests because the vast majority of tropical trees are dispersed by animals (Howe and Smallwood 1982). Thus, populations of numerous animal-dispersed species may sometimes be trapped inside forest patches by the local absence of their dispersers, which limits the cross-habitat spill-lover of zoochoric species. Hence, in comparison to young-forest seed rains, old-forest seed-rains are likely least related to anemochoric trees, and more affected by defaunation.

It is well documented that the early stages of regeneration of tropical forests is driven by strict filters, resulting from the shortage of tree cover (Brancalion et al. 2019b). As well as forest age and forest cover, we used 'adult' densities as predictors of tree cover at each restoration site. Unexpectedly, we found that adult stem densities did not provide significant effects on juvenile densities, neither for vertebrate-dispersed species nor for non-vertebrate-dispersed species. Perhaps, the range of 'adult' stem densities will increase in the future, revealing the expected effect on juvenile densities. The average 'adult' stem density in our sample was 478 individuals per hectare, while Brancalion et al. (2019b) compared stem densities up to 3333 ind/ha.

The establishment of regeneration communities could also be influenced by limiting physico-chemical and biological conditions at the sites, which can elevate mortality rates due to e.g. dessication, competition and predation (Reid and Holl 2013). We intended that our sampling design reduced the variation in such conditions. However, our analysis indicates that the relevance of tested predictors of densities and species richness (i.e. forest cover amount, forest-cover age and adult community density and composition) was mild compared to other factors varying between restoration sites, as demonstrated by the difference between conditional and marginal R^2 values. In other words, the simplicity of the few predictors we used comes at the expense of a greater explanation of variance by fixed factors. It is possible that variables such as soil properties outweighed forest amount and age in explaining regeneration patterns (Table 1). Alternatively, or additionally, some unexplained variance could be related to the relative abundance of forest ages in the landscape, successional variation within forest age groups, and/or unmeasured forest configuration. Presumably, these features have been accounted at the restoration site level as random factors. Different scales at which to include forest cover and forest age (i.e. beyond the 200 m buffer we considered) could also lead to changed insights, perhaps depending on the dispersal capabilities of surrounding species. Interestingly, considering other buffers with our data would compromise the analysis we performed here: too small a buffer (e.g. 100 m) would lead to zero forest cover in the surrounding landscape for 42 plots, out of the 108 in total, while too great a buffer (e.g. 800 m) would mean that all landscapes had some 'old' forest. Regardless, our results suggest that knowing the age of surrounding forest, in addition to its cover, provides insight into the composition and structure of regeneration communities in restoration sites. This emphasises a likely requirement for future studies to consider more nuanced landscape descriptors and that using multiple aspects of forest cover data to predict ecological responses is a valuable tool for ecologists and/or restoration practitioners. We fully expect the suggested approach to be workable for restoration planners.

Compositional indicators of disturbance sensitivity

We have observed that the lack of neighbouring old-forests compromises, in comparison to historical conditions, the compositional recovery of forests under restoration. Habitat-generalists and small-seeded species (e.g. *Baccharis dracunculifola*, *Myrcine coriacea*, *Schinnus terebentifolia* and *Vernonanthura polyanthes*) dominated regeneration communities in restoration sites with young neighbouring forest cover. These results are consistent with theoretical predictions of dependence between local diversity and the landscape species pool (Rickflefs 1987, Tscharntke et al. 2012). Indeed, forest-specialist juveniles were rarer in restoration sites within landscapes where forests were completely absent 10–30 years earlier. In turn, large-seeded juveniles were rarer in young forests, whereas large-seeded seedlings are more competitive under shady conditions beneath mature forests (Foster and Janson 1985; Lohbeck et al. 2015). Also, large-seeded zoochoric trees require large frugivores to recolonize young forests, and large seed dispersers tend to become locally extinct under conditions of extreme deforestation (Galetti et al. 2017).

Furthermore, these patterns that relate to seed-mass and habitat-selectivity are likely connected to a broader functional trend: studies have reported increased rarity of 'disturbance-sensitive' trees (Tabarelli et al. 2004) as well as the overabundance of 'disturbance-tolerant' trees (Prieto et al. 2014) resulting from forest fragmentation. Forest specialists are more sensitive to degradation as a result of specialization to narrow environmental niches, characterized by dark understorey with relatively stable humidity and temperature (Edwards et al. 2014). In contrast, Laurance et al. (2018) include fast growing pioneer trees among the 'disturbance-lovers', which are habitat generalist that are common within young second growth (Liebsch et al. 2008) and the anthropogenic matrix (Lopez-Toledo and Martinez-Ramos 2011; Zahawi et al. 2013; Reid et al. 2015).

We have observed that these generalist species tend to dilute populations of disturbance-sensitive tree species, as predicted by the 'concentration and dilution hypothesis' (Tscharntke et al. 2012), in well-forested landscapes that only presented young forests. Such a pattern supports a concerning possibility: remotely sensed data indicating regional expansions of tropical forests, as verified by Lira et al. (2012), Rezende et al. (2015), Rudel et al. (2016), and Molin et al. (2017) may sometimes reveal the rise of impoverished forests, lacking species groups that are particularly targeted by restoration programs. Thus, robust areal recovery of the forest-cover may not be followed by a comprehensive ecological recovery in heavy degraded landscapes. In other words, ecological inferences based on satellite data require ground-truthing through biological surveys, particularly in vastly deforested rural landscapes, in which forest cover tends to be increasingly impoverished in forest-specialist species (Tabarelli et al. 2008; Pardini et al. 2010; Benchimol et al. 2017).

Implications for restoration practices

Our models indicate that greater stem density and species richness are related to higher forest cover when young forests are nearby, which is promoted by abundant non-vertebrate-dispersed trees. Proximity to young forest patches is therefore opportune when fast tree-cover recovery is among the targets of the restoration intervention, for instance in classic goals related to reducing soil erosion and landslide risks (Stanturf et al. 2014).

We observed composition of adult communities consistently affecting the species assemblage in the respective regeneration communities, as observed with species richness, CWM of seed mass, and relative abundance of forest specialist (p = 0.001, p < 0.001, and p = 0.036; respectively). These results corroborate that the planted species-pool can mitigate, or intensify, limitations from the surrounding diversity. Consequently, high diversity tree-plantings (Rodrigues et al. 2009; Brancalion et al. 2010) can alleviate constraints resulting from the loss of functional connectivity between restoration sites and mature forests. In this case, the selection of species for restoration plantings should be carefully planned in favour of vulnerable species (Hooper et al. 2005; Brancalion et al. 2018), in spite of seed/seedling market tendencies, which privileges small seeded species (Brancalion et al. 2018). We highlight this idea on account of the increasing weight of recommendation in the literature that tropical forest restoration be focused on passive, rather than active, restoration (e.g. Chazdon and Uriarte 2017; Meli et al. 2017, but see

Reid et al. 2018; and Gardon et al. 2020). Our results ground the recommendation of active restoration on sites that are too far from old-growth forests (i.e. distance > 200 m), in which manipulating the species pool is likely necessary.

Predictive models on tropical forest recovery have been developed to assist global and national scale conservation policies. In particular, findings from Brancalion et al. (2019a), Rozendaal et al. (2019), and Strassburg et al. (2019) supported the amount of neighbouring forest cover as a good predictor of forest recovery. Perhaps their models could also be improved by accounting for the age of the forest patches. However, these three studies adopted a 5-km buffer to measure the forest cover. Presumably, they have captured a different set of social, abiotic and ecological drivers of forest recovery that are also related to the landscape forest cover, but that are better detected at a considerably larger scale. Our findings are better suited for restoration planning in landscape scale, which ideally happens after global and national guidelines have been followed.

Conclusion

We evaluated tree communities that resulted from similar native-tree plantings in landscapes with old forests, and landscapes comprising young forests only. We found that faster recovery of tree cover and species richness is likely to take place in landscapes with a considerable amount of young forests (i.e. > 25% of land-cover), due an increased regeneration of non-vertebrate dispersed, small seeded, and habitat generalist trees. However, disturbance-sensitive species i.e. vertebrate dispersed, moist-forest specialists are more likely to be missing in the absence of nearby old forests. Our results demonstrate that the history of neighbouring forests (i.e. amount of cover and age) is valuable information for landscape restoration planners.

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