**SOIL PROPERTIES AND NEIGHBORING FOREST COVER AFFECT ABOVEGROUND BIOMASS AND FUNCTIONAL COMPOSITION DURING TROPICAL FOREST RESTORATION**

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## I-ABSTRACT

##### QUESTIONS

##### We studied the importance of soil properties and neighbouring forest cover in affecting plant community biomass and assembly during the tropical forest restoration process. We also investigated how compositional responses depended on traits expected to influence individual success.

##### LOCATION

##### Forest restoration sites (N=32) distributed across anthropogenic grasslands in six mixed-use agricultural watersheds in Eastern São Paulo state (Brazil).

##### METHODS

We identified and measured all woody individuals (DBH ≥5 cm) in four 200 m² plots per site. Then we translated these measurements into aboveground biomass (AGB), and related AGB variability to neighbouring forest cover, soil texture and chemical fertility with mixed effect models. We assessed the effect of these predictors on different species groups, arranged according to variation in wood density, tree height or habitat selectivity, through multivariate abundance models.

##### RESULTS

AGB ranged between 0 and 104.7 ton/ha (median of 10.4 ton/ha), with high variation within, as well as between, watersheds. Sand percentage, forest cover, and the interaction between soil nutrient concentrations and sand percentage were good predictors of measured AGB. The most parsimonious model projected a seven growing-seasons AGB recovery of 70.90 ton/ha, when a site is on fertile soils with 10% sand and surrounded by forest cover of 50%. In contrast, only 5.24 ton/ha is predicted on acidic-poor soils with 67% sand and 0% forest cover. Increasing forest cover favoured smaller trees and habitat-generalists while increasing sand percentage inhibited taller-species and forest-specialists. Sand percentage constrained softwoods in fertile soils.

##### CONCLUSION

Our results confirm that the likelihood of restoration to pre-disturbance conditions is constrained in contexts of higher degradation, such as when agricultural use adversely affects soil properties and/or motivates extreme deforestation. Lower AGB found on sandy soils suggests that forest recovery is sensitive to local drought intensification. Given regional projections for extended dry seasons, restoration approaches could consider targeting alternative reference states, rather than historical/undisturbed ones, under highly altered environments, while aiming to improve soil and microclimate conditions to allow moist tropical forest recovery where feasible.

###### Key words: Atlantic rainforest, disturbance, dispersal, environmental filters, landscape ecology, recovery, traits

## Nomenclature: Brazilian Flora 2020 (http://floradobrasil.jbrj.gov.br; accessed on 6 Jun 2016)

## II-INTRODUCTION

Conceptual and practical advances in the field of restoration ecology have encouraged the launch of forest restoration programs across the globe (Perring et al. 2015a, Suding et al. 2015). Restoration endeavours also occur in tropical hotspots for biological conservation (Calmon et al. 2011; Wuetrich, 2007), and native tree plantations are widely used as a central restoration technique (see Rodrigues et al. 2009; Lamb et al. 2005). However, restoration outcomes from these plantations can be highly variable and hard to predict (Holl & Zahawi 2014). Variability is likely due to regeneration processes being forged by the interplay of biotic and abiotic legacies (Flinn & Vellend, 2005; Hobbs et al. 2009), as well as varying disturbance regimes at the local and landscape levels (Suding, 2011; Holl & Aide, 2011). Consequently, to aid restoration practice, and better develop policy recommendations, we require a greater understanding of the major factors involved in successful forest recovery (Maron et al. 2012).

Forest restoration takes place as a sequence of interventions aimed to mitigate known obstacles for secondary succession (del Moral et al. 2007). Projects based in diverse native-tree-plantations initially target overcoming poor seed dispersal and manipulating species assembly by re-introducing a selected species pool and managing mortality rates (e.g. by reducing herbivory and controlling competition). Afterwards, the growth of the planted trees is expected to reestablish light competition, and facilitate recolonization through seed arrivals (Reid et al. 2015), and improve the establishment of old-growth forest species. However, the risk of incomplete transition from a tree plantation to a self-recovering connected forest can be high, and this disconnect is often attributed to a mixture of local and landscape constraints (Cramer et al. 2008; Suding 2011).

Locally, the main concerns are edaphic legacies induced by deforestation and agricultural land-use (Markewitz et al. 2004, Randrianarison et al. 2016). The negative effect of environmental legacies on the recruitment, growth and reproduction of species is referred to as environmental limitation (Baeten et al. 2009). For instance, forest recovery can be directly affected by lower water-holding capacity of sandy soils, exacerbated by agriculturally driven soil organic matter loss (Matson et al. 1997) or by livestock-mediated soil erosion, with mortality concentrated on certain species groups (Martinez-Garza et al.2013). Nonetheless, environmental changes may also promote an asymmetric effect on the species pool, and then a few species become overabundant, indirectly constraining forest recovery. As an example, successional inhibition has been attributed to fern overabundance on acidified soils in the Brazilian Atlantic Forest domain (Ribeiro et al. 2013). These early responses to environmental filters can also cause long-term implications for tropical forest succession. For example, Lebrija-Trejos et al. (2010) showed that structural development (i.e. crown area, basal area, and tree density) in tropical dry-forests shapes the local environment (i.e. light, temperature and moisture). This changed local environment altered the trajectory of community assembly through selecting species with certain functional traits.

At a broader scale, “helpful” neighbourhoods, such as well-forested landscapes, can be very beneficial to the restoration process (de Rezende et al. 2015). Ideally, neighbouring forests are functionally connected to the restoration site, and propagules are shared with restoration plantings through seed-rain (Barbosa & Pizo, 2006; Zahawi et al. 2013), but studies indicate that relatively short distances between forest patches pose an effective barrier to seed dispersal (Kauano et al. 2013; Souza et al. 2014). Other processes are also moderated by the landscape arrangement because forest surroundings tend to be moister and colder (Baker et al. 2014) and are more likely to obtain nutrients by lateral diffusion, for instance through animal translocation (Wolf et al. 2013) or litter fall. Overall, forest cover within a set radius of the target restoration site provides a good proxy of these neighbourhood effects on biomass recovery and community assembly.

Aboveground biomass (AGB) is a straightforward proxy to assess forest restoration success, and responses to environmental conditions, by combining forest-recovery outcomes in terms of stem density, tree growth and composition. Non-destructive AGB estimation is relatively well established for tropical forests (Ducanson et al. 2015), and empirical evidence indicates biomass as the main driver of changes in ecosystem process rates during tropical forest succession (Lohbeck et al. 2015). Hence, low AGB represents a poor restoration outcome, and in general, indicates poor conditions for restoration.

Total AGB combines primary production from different species groups in variable proportions, and in part, relative abundances respond to the scarcity or abundance of resources that favour alternative competitors (Lasky et al. 2014). Dominance in term of AGB is therefore expected to reflect environmental conditions, and quantifying these patterns may reveal local inhibitors for the restoration process. In particular, we expected softwood-species to be more likely to be excluded if pronounced drought is a key mortality driver, since denser woods enhance plant resistance to xylem cavitation, fire, wind, and grazing (Poorter & Markesteijn, 2008). In turn, favourable edaphic conditions support the development of productive forests, and maximum height (Hmax) then becomes an important trait associated with the competitive ability for light (Shamp & Aarssen, 2009). We also anticipated harsher restoration conditions to be less adverse for species of low specialization to mature forest environments. This prediction is also partly due to results that have shown the vulnerability of forest-specialists to deforestation and landscape fragmentation (Pardini et al. 2010; Banks-Leite et al. 2014).

In this study we assessed results from a Brazilian restoration program, to quantify the effect of edaphic conditions and the influence of neighbouring forest cover on biomass accumulation and its composition. Our main hypothesis is that total AGB recovery responds to local edaphic conditions and to the amount of forest cover in the neighbouring area. Also, we hypothesize that some species groups are particularly sensitive to local conditions, affecting the community assembly as a whole, and favouring generalists species more adapted to open anthropogenic woodlands.

## III-METHODS

### Study Area

In 2007 the PRMC program (“Projeto de Recuperação de Matas Ciliares”) started the implementation of over 500 restoration demonstration sites in private lands across São Paulo state, south-eastern Brazil (Wuetrich, 2007; Chazdon, 2008). For the present study, restoration sites were selected within the boundaries of the Serra do Mar coastal forests (Olson et al. 2001); these sites are underlain by granite-gneiss lithology in the “Atlantic plateau” geomorphic and botanical provinces (Scudeller et al. 2001). Restoration sites were situated within six watersheds, and distances between watersheds ranged from 30 to 150 km (Figure 1). Across the restoration sites, elevation ranges from 550 to 1510 m above sea level, annual precipitation ranges from 1400 to 1700 mm, and the dry season (average rainfall below 50 mm/month) varies between 3 and 5 months (Hijmans et al. 2005). Deforestation of these lands was stimulated by coffee cultivation in the early 19th century, exposing the soil to rainfall and increasing surface runoff and erosion. A few decades later, coffee plantations were replaced by dairy farming (Dean, 1991). The still prevalent pastures are now spread around scattered croplands, forestry plantations, as well as urban and forest patches.



*Figure 1- Eastern watersheds included in PRMC restoration program. Surveyed watersheds are located in the municipalities of Socorro (1), Joanópolis (3), Nazaré Paulista (4), Guaratinguetá (2), Cunha (5) and Paraibuna (6).*

### Study Design

Surveyed sites were selected through a structured screening. Different restoration protocols were tested by PRMC, but the subset of 32 sites considered here exclusively followed the central one: a species-rich tree plantation with the same (1666 trees/ha) density. After excluding sites with alternative protocols, we also excluded locations with extreme conditions on variables that are not modelled here, i.e. elevation, perimeter-area ratio, terrain slope and surface area. Then, we selected sites that had been established over anthropogenic grasslands, formerly used for grazing, with a minimum distance between sites of 1 km. Finally, we excluded watersheds with less than three eligible sites, leading to the analysed selection of 32 restoration sites from six watersheds.

Restoration sites were implemented between the autumn of 2007 and the subsequent summer following similar protocols. Several local nurseries produced the seedlings; they adopted a broad species list and supplied individuals about 40 cm tall. Planting holes were prepared systematically before planting, typically in a 3 by 2 m grid and species were mixed at random. Dead saplings were replaced in the following growing-season, with species identity selected at random from the general planting list. Native and invasive grasses were controlled during the implementation phase, through herbicide application and manual control, but woody individuals were maintained. We note that detailed records of the species introduced at each site were taxonomically imprecise, and that the supply of species especially varied for replacement, but the mix of species was never planned to be different. It is therefore unlikely that there were major biases in planted species abundances among sites at project initiation. We have therefore assumed that the planted species-groups mix was essentially identical at all sites, and subsequent differences in growth and community assembly are due to site and landscape factors (Data for each species are listed in Appendix S1).

### Data Collection

These restoration trials were surveyed seven growing-seasons after the beginning of implementation. Four vegetation plots (4 x 50 m) were randomly demarcated within each restoration site. Woody individuals with diameter at breast height (DBH) ≥ 5 cm had their height and DBH recorded, and were identified to the species level; multi-stemmed individuals were included when the sum of cross-section areas at breast height was larger than the corresponding cut-off area (i.e. 19.6.cm²). Those that could not be consistently identified in the field had leaf/floral samples taken to allow further identification at the ESA herbarium (ESALQ-USP). We have adopted the minimum DBH of 5 cm as required by the allometric equation we used (Chave et al. 2014), as detailed further below.

Composite soil samples were taken inside each vegetation plot at 0-20 cm depth, by combining three sub-samples collected in the major axis of the parcel, at least 20 m apart from each other. These samples were analysed at IAC (Instituto Agronômico de Campinas), using their standard procedure for fertility and texture evaluation, which included pH (CaCl2); H+Al (potential acidity SMP-Buffer); P, K, Ca and Mg (Resin); Organic Matter (photometry), and Sand contribution (0.053-2.000 mm).

To assess the amount of habitat around the restoration sites, land-cover maps were produced using visual interpretation of orthophotos taken in 2005, two years before the plantings. The mapped area included an 800-m wide external buffer-zone for each restoration site, within which we measured the percentages of forest habitat cover from each plot at 0-200 m, 0-400 m and 0-800 m buffers; here we refer to the variable assessed through the resulting ratios as “forest cover”.

AGB of each surveyed tree was calculated with the allometric equation for AGB of tropical forests proposed by Chave et al. (2014). Accordingly, field measured tree height, and DBH was combined with specific wood density (WD) gathered from literature. Compiled data and references are presented in the Supplementary Information Appendix S1, in addition to WD information; this dataset included specific maximum height (Hmax) and a species categorization on specialization in moist-forests. Individual biomass was summed to give a plot level biomass estimate. We evaluated variability in plot-level estimates across restoration sites against predictor variables (i.e. soil properties and neighbouring forest cover).

We then investigated whether these same predictors had effects on the abundance of particular species groups in the restoration sites. Species were grouped on the basis of traits that we expected to influence assembly given the environmental conditions, as noted in the Introduction. Traits were wood density, height and habitat preference. Other traits could have been considered, but these were the traits that were best quantified among the surveyed species.

The median density of 0.58 g/cm3, observed among sampled species, was used as a cut-off density to group soft- and hard-woods. Likewise, 14 m, the median Hmax in our species poll, was adopted as the cut-off height to separate the groups of “shorter” and “taller” species. To classify sampled species according to habitat specialization, we first accessed the geographical distribution of identified species through the Global Biodiversity Information Facility (GBIF, 2016), and then we compared each occurrence map to the terrestrial ecoregions map (Olson et al. 2001). Species solely found within broadleaf tropical moist-forests domains, with no presence recorded at natural non-moist-forest habitats 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 scrublands.

### Data Analysis

#### Aboveground biomass

All data were analysed using R.3.2.0 (R foundation for Statistical Computing, Vienna, AT). Linear mixed models were used (*nlme* package, version 3.1-128, R-Core team) to evaluate the effects of edaphic conditions and forest cover on AGB density (ton/ha). For greater goodness of fit and to satisfy model assumptions on error distributions, we square-root-transformed AGB.

Forest cover expressed in percentages, soil chemical fertility and sand-percentage, were tested as fixed effects, as well as the interaction between chemical fertility and sand percentage. While forest cover and sand contribution were expressed in percentages, soil chemical properties needed to be translated into a single dichotomous categorical variable, given the correlation among chemical aspects, which collectively define broad groups of soil chemistry. To separate soil groups, we first quantified soil chemistry dissimilarity between sites using pairwise Gower distances, and then we performed hierarchical clustering of the sites based on the full dissimilarity matrix with average linkage using the *vegan* package (version 2.3-5, https://cran.r-project.org/web/packages/vegan). We retained two chemical-fertility groups: one of sites with soils that were richer in nutrients and less acidic (‘fertile soils’ hereafter), and the other included more acidic soils with lower nutrient concentrations (‘poor/acidic soils’ hereafter) (see Appendix S2). Then the mixed-effect model was completed by adding restoration site as a random term to capture between-site variation that was not explained by the other predictors.

To explore whether plot-level variation in biomass was derived from population differences (i.e. differences in stem density (trees/ha)), and/or average tree growth rates (i.e. differences in stem volume (cm3/tree)), models with the same fixed and random terms were fitted to these additional response variables. Likewise, we investigated if the evaluated environmental filters affected species richness, and/or diversity. Richness (a simple tally of the number of species in a plot) and Shannon diversity index (H’) were calculated at plot level, with R package “vegan”. Then, Shannon diversity was transformed to “effective species number” (exp(H’)), where species are weighted precisely by their abundances (Jost, 2006). We also tested if any of these models could be significantly improved by nesting within watershed as an additional random term, or by adding restoration site areal extent as a fixed term (restoration sites vary from 0.2 to 3.5 ha). However, the effect of including these variables was never significant, and they were dropped from the final presented models.

#### Plant community assemblage

As explained above, sampled species were bundled in contrasting groups according to specific wood density (≤0.58 g/cm3 or >0.58 g/cm3), specific Hmax (≤14 m or >14 m) and habitat preference (forest-specialists or generalists). Then we evaluated the particular effect of AGB predictors we have tested (i.e. forest cover, soil chemical group and sand percentage) on the relative abundance of each contrasting group. Pairwise comparison for each species grouping (i.e. WD, Hmax and habitat preference) was enabled through linear models for multivariate abundance data using the mvabund package (version 3.11.9, https://cran.r-project.org/web/packages/mvabund). Model-based analysis of multivariate abundance data was performed at the site scale, by considering average values for response and explanatory variables among the four plots of each one of the 32 restoration sites.

Only individuals identified at the species level were considered in these analyses, representing 84.9% of the total AGB surveyed. Species list, groups and references are presented in Appendix S1. Significance of the fitted effects were tested with ANOVA using adjusted p-values (9,999 permutations) and then predicted abundances were estimated, also using the mvabund package. Lastly, a Spearman’s rank correlation test was used to investigate whether there was association between traits-based groupings and if any considered group was related to higher or lower total biomass.

## IV-RESULTS

### Variation in potential explanatory variables and above ground biomass

Among the 128 plots, AGB ranged from zero to 104.7 ton/ha, with a median of 10.4 ton/ha. Averaging plots across restoration sites led to AGB ranging from 0.4 to 84.4 ton/ha (median = 12.0 t/ha). Stem density ranged from 0 to 1800 individuals/ha (median = 425.0 individuals/ha), thereby ranging between no recruitment at all, and 8% higher than the initial plantation density. In total 1216 individuals were sampled, 12 could not be identified due the condition of the plants, and 1092 were identified up to the species level. About half of species (53 of a total of 104 species) had fewer than four individuals in the entire survey.

Sand percentage ranged from 10% to 67% (median = 51.8%). The two soil categories based on acidity and nutrient concentrations (‘chemical fertility’ hereafter) contrasted better in Ca, Mg, and P concentrations (acidic/poor medians (in mmol/dm3): Ca = 6.0, Mg = 2.0 and P = 4.0; fertile medians: Ca = 25.0, Mg = 8.0, and P = 7.0). Also, “poor/acidic” soils presented a median pH of 4.2, (interquartile range, 4.0 to 4.3); while fertile soils presented a median pH of 4.8, (interquartile range, 4.5 to 4.9). Detailed information on the soil analysis is provided in the supplementary material (Appendix S2). Forest cover within the 200-m buffer ranged from 0% to 50% (median=10.4%), average forest cover for each restoration site for each of the buffer range is provided in Supplementary Material (Appendix S3).

### Biomass Model

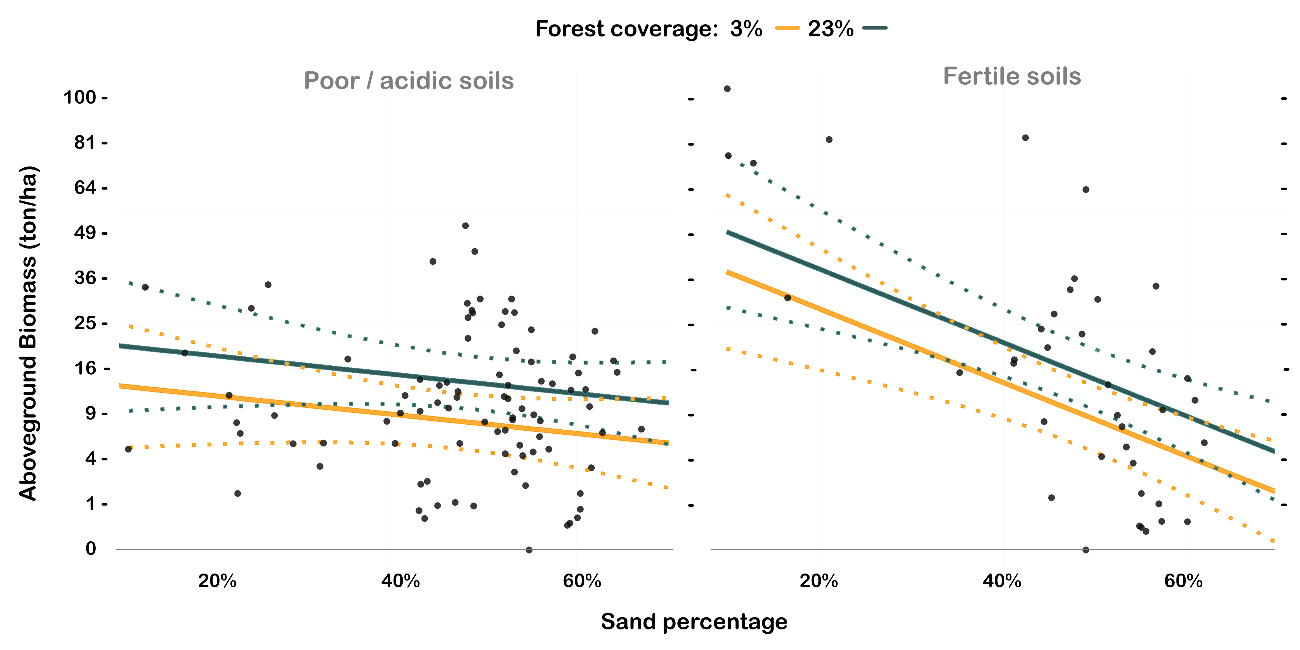
AGB was significantly influenced by environmental factors acting at a local scale. In particular, AGB decreased as sand percentage increased, but the effect depended on chemical fertility. The effect of increasing sand percentage was minor on acidic/poor soils because they showed low AGB along the entire sand-percentage gradient, but the decline in AGB was strong on fertile soils (Table 1; Figure 2). On the other hand, neither chemical fertility nor sand percentages presented any significant interactions with forest cover. AGB also increased as forest cover increased within 200 m of the site. Interestingly, no significant effect from forest cover was detected with enlarged buffer zones. The absence of a significant forest cover effect with 400-m and 800-m buffer zones was observed with AGB, tree density, and mean stem volume as response variables (results not shown).

Survival of planted species at the restoration sites appeared to drive AGB variability: stem density was related to the same set of explanatory variables as AGB. In contrast, growth of trees (as represented by stem volume) was only influenced by forest cover and, surprisingly, not by the edaphic factors at any given site. This is despite the fact that higher stem volumes of any given individual will be associated with higher AGB for any given wood density.

AGB correlated strongly with species richness and Shannon diversity (exp(H’)); however, species richness and Shannon diversity were solely associated with the interaction between sand percentage and chemical fertility and were not associated with any single environmental predictors (Table 1).

Table 1 *Effects of soil sand percentage, soil fertility group and forest cover on the plot-level biomass (ton/ha), stem density (trees/ha), stem volume (average cm³/tree) and Shannon diversity. Results show an ANOVA table resulting from linear mixed models; see text for model structure.*

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| *Response* |  | *Predictor* | *denDF* | *F-value* | *p-value* |  |
| *Biomass (square root)* |  | Sand(%) | 92 | 8.756 | 0.004 | \*\* |
|  | Soil group | 92 | 0.424 | 0.516 |  |
|  | Forest coverage | 92 | 11.979 | <0.001 | \*\* |
|  | Sand:Soil | 92 | 5.458 | 0.022 | \* |
|  |  |  |  |  |  |  |
| *Stem density* |  | Sand(%) | 92 | 9.814 | 0.002 | \*\* |
|  | Soil group | 92 | 0.082 | 0.776 |  |
|  | Forest coverage | 92 | 3.910 | 0.051 | . |
|  | Sand:Soil | 92 | 8.040 | 0.006 | \*\* |
|  |  |  |  |  |  |  |
| *Average stem volume (square root)* |  | Sand(%) | 90 | 3.162 | 0.079 |  |
|  | Soil group | 90 | 2.665 | 0.106 |  |
|  | Forest coverage | 90 | 12.859 | <0.001 | \*\* |
|  | Sand:Soil | 90 | 0.856 | 0.357 |  |
|  |  |  |  |  |  |  |
| *Species richness* |  | Sand(%) | 90 | 2.899 | 0.092 |  |
|  | Soil group | 90 | 0.239 | 0.626 |  |
|  | Forest coverage | 90 | 1.036 | 0.311 |  |
|  | Sand:Soil | 90 | 7.808 | 0.006 | \*\* |
|  |  |  |  |  |  |  |
| *Shannon (exponential)* |  | Sand(%) | 90 | 1.76697 | 0.187 |  |
|  | Soil group | 90 | 0.9645 | 0.329 |  |
|  | Forest coverage | 90 | 0.64872 | 0.423 |  |
|  | Sand:Soil | 90 | 4.43311 | 0.038 | \* |

**

*Figure 2 - Observed biomass (sqrt-transformed) as a function of soil sand percentage for the two soil chemical-fertility groups (points). Lines show model predictions (Table 1) +/- 95% confidence intervals for 3% and 23% forest cover (interquartile extremes in the surveyed data).*

### Community Models

Tree community-composition responded to environmental context. Sand percentage affected all trait groupings. AGB from softwoods, taller-species and forest-specialists negatively correlates with sand percentages. Moreover, the resulting model predicts the absence of forest-specialists once the sand fraction is over 55%, despite the substantial contribution from forest-specialists to the total AGB predicted for fertile non-sandy soils (>30%).

Forest cover in the 200 m buffer affected AGB predictions for all trait groupings except wood density. AGB from shorter-species and generalist-species positively correlates with forest cover. In contrast, chemical fertility, alone, was not a good predictor of AGB for any of these groups. However, the interaction between fertility and sand percentage was highly significant for WD groups. The negative effect of sand percentages on softwood AGB was highly significant on fertile soils, and non-significant on acidic/poor soils (Table 2 and Figure 3).

No clear correlation was found between species groupings. AGB share between WD groups did not correlate to habitat selectivity or Hmax ratios, despite the preponderance of softwood-species among forest-specialists (18:26 spp.) and of hardwoods among shorter species (28:51 spp.). Still, a moderate correlation was found between AGB shares of forest specialists and taller species, and hence between generalists and shorter species ratios (Spearman ρ = 0.525, p=0.002), which is consistent with preponderance of shorter-species among habitat-generalists (47:78 spp.), and of taller-species among forest-specialists (18:26 spp.). Surprisingly none of these groupings was a good predictor of total AGB. The biomass share between WD and Hmax groups weakly correlated to total AGB (ρ = 0.375, p=0.035 and Spearman ρ = 0.356, p=0.046, respectively) but not to habitat-selectivity groups.

*TABLE 2 - Anova results for linear model fits for the multivariate abundance data, with species groups as responses. “global test” shows the overall effects of the predictors on the multivariate abundance data, whereas the “univariate test” shows effects of the predictors on the individual species groups.*

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *Predictor* | *"Global test"* | | |  |  | *Univariate test* | | | | |  |
|  | *Wood density groups (WD)* | | | |  | *WD ≤ 0.58 g/cm3* | |  | *WD > 0.58 g/cm3* | |  |
|  | Res. df | F | Pr(>F) |  |  | F | Pr(>F) |  | F | Pr(>F) |  |
| *Sand %* | 30 | 8.1 | 0.0373 | \* |  | 5974 | 0.0483 | \* | 2126 | 0.1525 |  |
| *Forest coverage %* | 29 | 7646 | 0.0350 | \* |  | 4796 | 0.0697 | . | 2.85 | 0.0995 |  |
| *Soil group* | 28 | 2181 | 0.3504 |  |  | 1528 | 0.4056 |  | 0.653 | 0.4296 |  |
| *Sand:Soil* | 27 | 13973 | 0.0037 | \*\* |  | 13693 | 0.0029 | \*\* | 0.279 | 0.5920 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  | *Maximum height groups (Hmax)* | | | |  | Hmax ≤ 14m | |  | Hmax > 14m | |  |
|  | Res. df | F | Pr(>F) |  |  | F | Pr(>F) |  | F | Pr(>F) |  |
| *Sand %* | 30 | 11299 | 0.0153 | \* |  | 2008 | 0.1666 |  | 9291 | 0.011 | \* |
| *Forest coverage %* | 29 | 10548 | 0.0183 | \* |  | 9287 | 0.0105 | \* | 1262 | 0.274 |  |
| *Soil group* | 28 | 0.102 | 0.9464 |  |  | 0.075 | 0.9508 |  | 0.028 | 0.9508 |  |
| *Sand:Soil* | 27 | 6063 | 0.0768 | . |  | 3293 | 0.1512 |  | 2769 | 0.1512 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  | *Habitat selectivity groups* | | | |  | *Forest specialists* | |  | *Generalists* | |  |
|  | Res. df | F | Pr(>F) |  |  | F | Pr(>F) |  | F | Pr(>F) |  |
| *Sand %* | 30 | 18.73 | 0.0042 | \*\* |  | 17206 | 0.0024 | \*\* | 1531 | 0.2226 |  |
| *Forest coverage %* | 29 | 6879 | 0.0473 | \* |  | 0.829 | 0.3699 |  | 6.05 | 0.0399 | \* |
| *Soil group* | 28 | 0.669 | 0.7134 |  |  | 0.241 | 0.7617 |  | 0.428 | 0.7617 |  |
| *Sand:Soil* | 27 | 5962 | 0.0722 | . |  | 3415 | 0.1549 |  | 2546 | 0.1549 |  |



*Figure 3 – AGB as a function of sand percentage with species grouped by wood density, maximum height and habitat selectivity. Predictions within observed range for two soil conditions (fertile soils and poor/acidic), and two forest cover percentages in a 200 m buffer (interquartile extremes in our sampling).*

## V-DISCUSSION

Assessing the varying results from the restoration program PRMC, and investigating their relationships with local environmental context, provides the opportunity to refine general predictions for tropical forest restoration. Combining plot-level estimates to the site scale confirmed our observations that restoration outcomes ranged from open fields to dense regenerating forests. The average vegetation presents the appearance of an early stage low-stature woodland as indicated by a mean stem density of 475 trees/ha, with relatively small average tree size (averages: height = 6 m, DBH = 11 cm). AGB accumulation was particularly constrained by sandy soils, and by lower forest cover within 200 m of the restoration site. These factors also promoted particular patterns of community assembly, and critically both are often intensified by agricultural land-use. Notably, our results suggest that unfavourable environmental contexts are not exceptions in areas designated for restoration (given the low median AGB across plots). Instead, such conditions can be prevalent, which will have marked effects on the cost-efficiency and success-rates of large restoration programs previously announced for tropical forests (Calmon et al. 2011, Durigan et al. 2013). Lastly, in the light of ecological theory, we discuss the role of environmental drivers in engendering variability in AGB accumulation and community composition, focusing on how our results can assist successful restoration programs.

### Aboveground Biomass responses

The extensive database analysed by Poorter et al. (2016) indicates an average AGB recovery of 122 ton/ha during the first twenty years of neotropical secondary forests, with higher AGB yields in the first years. Hence the expected AGB recovery in the seven growing seasons investigated here would be around or above 40 ton/ha. However, we observed an average seven growing-seasons AGB accumulation of 16 ton/ha, suggesting that recovery conditions are largely poor in the studied rural landscapes. Our analysis pointed to forest cover and sand percentage as major drivers of AGB recovery; chemical fertility, in turn, did not affect AGB recovery by itself, but it was involved with an interaction with sand percentage.

Our model results predict low AGB recovery on sandy soils regardless of chemical fertility, with similar performance on non-sandy acidic/poor soils. However, much higher AGB is predicted for non-sandy fertile soils. Accordingly, Holl & Zahawi (2014) attributed a supporting role for soil chemical-fertility on tropical forest recovery. Also, Poorter et al. (2016) reported a minor effect of chemical-fertility on AGB uptake, compared to water availability. This pattern is possibly dynamic given that forest growth both affects and is influenced by soil properties (Honnay et al. 2002; Lebrija-Trejos et al. 2010). Even so, this interdependent relation (growing forests and soil underneath them) raises an interesting point: diverging recovering trajectories may perpetuate if differences in edaphic conditions persist along the recovery process. Therefore, long-term assessments are needed to properly investigate if initially diverse recovering forests will converge in the future, as expected by practitioners.

Sandier soils are associated with higher seedling mortality due to lower water-holding capacity (Hallett et al. 2014). Interestingly, in our study, sand percentage was highly significant as a predictor of stem densities, but was not significant for average stem size, suggesting a stronger link to mortality rates as compared to growth rates. This reinforces the argument that the connection between observed sand percentage and AGB is likely due to drought mortality. Webb et al. (2005) found diminishing rainy days correlating to decreasing forest cover across São Paulo state. At the broader scale, tree mortality and forest die-off intensification have been associated with “hotter drought”, which can be attenuated at “buffered-refugia” if landscape heterogeneity provides climate relicts where growing trees have cooler-moister conditions (Allen et al. 2015). It seems reasonable to assume that hotter drought is intensified by the agricultural matrix in the studied region, and that soil heterogeneity can amplify or attenuate water shortage. Our results suggest that patches of non-sandy soils are favourable for AGB recovery due to better moisture regulation, possibly at levels that are closer to those found under tropical forests and gaps.

If human-induced drought intensification is such an important recovery driver, perhaps the effective spontaneous recovery reported for landscapes with greater forest cover (de Rezende et al. 2015; Zahawi et al. 2013; de la Peña-Domene et al. 2014) results from greater microclimate buffering, where proximity to forest relicts ameliorates microclimatic differences between forests and open grasslands. Still, we found no significant interaction between forest cover and sand percentage, which could indicate climatic buffering. Similarly, we found no significant interaction between forest cover and soil fertility, showing no evidence of nutrient buffering by lateral diffusion. In this case, it is suggested that the consistent forest cover effect that we observed is most likely related to biotic connection, e.g. through seed dispersal.

Intriguingly, the amount of forest cover in the 200 m buffer was the most significant predictor of AGB. This pattern was related to the average size of trees, but not with the number of trees. Hence if, as our data indicate, there is no significant interaction between forest cover and soil properties, larger trees in forested landscapes may not be related to favourable edaphic conditions, but possibly result from particular species assemblages, with greater abundance of species that grow faster during early forest recovery, as we discuss in the following section

### Tree community assemblage

Strong correlations were observed between AGB and species richness, as well as between AGB and exp(H), adding weight to the perspective that restoring diversity is important for AGB recovery (Perring et al. 2015b). Here, effective species number exp(H’) and species richness were consistently higher in non-sandy fertile soils. Moreover, functional composition presented some clear responses to environmental variables, by means of tree-assemblage singularities.

In our observations, softwood-species were highly prevalent, and taller-species presented a minor dominance in conditions of higher AGB recovery, which is consistent with findings from Rüger et al. (2012), relating higher intrinsic growth rates to taller stature and lower WD among tropical trees. Similar relations were found by Wright et al. (2010) for fast-growing and short-lived species, given they are light-demanding pioneer tropical trees, particularly benefiting from faster growth rates, which is consistent with early stages here surveyed. Biomass share among WD groups also indicated that softwood species are more sensitive to sand percentage, supporting the sand-drought relation, which is also reflective of lower endurance to drought in softwood species (Poorter & Markesteijn 2008). However, softwood species were predicted to be always rare in poor/acidic soils, regardless of sand percentage. We did not observe taller-species prevalence in productive forest (as indicated by fertile soils), as would be predicted by increased light competition (Shamp & Aarssen 2009). This lack of a relationship may be attributed to the early stage we surveyed, when growth speed is more important to AGB composition than the achievable height or longevity. However, under unfavourable edaphic conditions, reduced contributions from taller and/or softwood species is potentially a persistent pattern, given that the reduced AGB uptake evident under these conditions is still far smaller than expectations for tropical forest succession.

Above-ground biomass from forest-specialists presented a high sensitivity to sand concentration, and this can be considered particularly challenging for biodiversity conservation because the pool of species which better represents the restoration target are predicted to disappear where sand percentage is greater than 55%. Also, the rarity of forest specialists in sandier, and consequently drier, environments may be a pattern that persists into the future, because the positive effect from forest cover was only significant for generalist-species and shorter trees; then forest-specialist-species are unlikely to arrive from neighbouring forests.

In part, the local diversity we have surveyed reflects the status of regional diversity (following Ricklefs, 1987), and we note that a large proportion of current Atlantic Forest is relatively recent second growth (Lira et al. 2012), favouring short-living and fast-growing pioneer species. Pardini et al. (2010) showed an abrupt loss of forest-specialist taxa (but not habitat generalists), in landscapes where Brazilian Atlantic Forest cover was reduced to between 31% and 11%. In the present study, half of the landscapes were above 11% forest cover, and only 3 in 32 restoration sites presented more than 31% of forest cover. Therefore, the positive correlation between forest cover and the relative abundance of habitat generalist-species is the expected pattern since remnant forests are largely disturbed and because high forest cover rates (e.g. >50%) were never found in our study region.

A lower regional level of diversity, together with poor dispersal, implies the surpassing of a biotic threshold for recovery (Hobbs et al. 2009). On the other hand, the general absence of endemic old-growth forest-species on sandy soils could indicate an abiotic threshold to recovery. These ideas require further testing, accompanied by monitoring of restoration sites. Future studies could also benefit from the compositional description of neighbouring forests, together with target restoration sites being surrounded by greater variation in forest cover than investigated here (Table SI3). If sufficient variation in both these variables could be assessed, i.e. multiple community compositions at multiple different forest covers, it may be possible to segregate the importance of dispersal limitation and reduced regional diversity on the success of restoration in target sites.

### Implications for restoration planners and practitioners

Palmer et al. (1997) highlight the importance of finding the appropriate spatial scale for successfully restoring ecosystem function. Our AGB model demonstrates the relevance of recovery drivers operating at the local scale: there was no influence of forest cover at radii of 400 and 800 m, while there was significant variation in AGB, which reflected the large variation in soil properties among watersheds. Similarly, Holl & Zahawi (2014) have pointed that edaphic conditions may greatly vary across short distances in a tropical region. Also, Rezende et al. (2015), Kauano et al. (2013) and Souza et al. (2013) reported the limited reach of benefits from remnant habitat proximity (up to 200 m). These findings indicate that landscape heterogeneity within 200 m must be assessed in restoration actions.

Restoration practitioners can easily assess the environmental predictors we evaluated in this study in the pre-implementation phase, i.e. when planning where and what to restore. Simple mitigation actions may be effective in some conditions, but these require tests and observation. Restoration assessment standards (e.g. Chaves et al. 2015) can be usefully applied to boost this learning process, along with updating and fine-tuning outcome predictions. For example, predictive models could be improved by quantifying the effect of techniques to increase soil water-holding capacity (e.g. organic matter or biochar incorporation) or ameliorate the microclimate (e.g. windbreaks or buffering woody agriculture) on restoration success. Also, acknowledging the land-use legacy effect on ecosystem recovery may also indicate how current agricultural practices can avoid creating hostile environments for future recovery (e.g. by implementing soil conservation and habitat protection practices).

## VI-CONCLUSION

We have shown that sandy soils can severely constrain tropical forest restoration, that favourable soil chemical properties are highly effective at promoting AGB in non-sandy soils, and that neighbouring forest cover consistently supported woody biomass recovery. Along with total AGB response, the tree-community composition changed with varying environmental conditions. In these early stages of recovery, biomass from softwoods and forest-specialist species was particularly sensitive to sand percentage, and AGB from small trees and generalist species was the most positively affected by forest cover. Notably, forest specialist-species were absent in drought-prone sites whenever sand percentage increased above 55%. Our results corroborate the need for fine-scale evaluations to predict restoration outcomes and suggest that degradation associated with agricultural practices constrains the likelihood of restoration to pre-disturbance conditions, particularly where soil has been degraded and/or massive deforestation has been carried out. When abiotic conditions are favourable, native tree planting may likely be a successful technique depending on biological drivers of forest succession. However, further abiotic disturbance implies the necessity of manipulating edaphic conditions, coupled with the long-term presence of alternative communities. Given projections for increasing drought in this region, across scales, alternative restoration targets must be considered for drought-prone conditions.

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### **Supporting information**

**Appendix S1.** Species list and species grouping classification

**Appendix S2.** Statistics of soil chemical variables within soil groups

**Appendix S3.** Geographic information for surveyed restoration sites