Universidade de São Paulo

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Restauração de florestas tropicais em paisagens rurais: a influência do solo e cobertura florestal adjacente

Tropical forest restoration in rural landscapes: the influence of soil and adjacent forest coverage

Orientadora: Profa. Dra. Rozely Ferreira dos Santos

São Paulo

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RESUMO

Restauração de florestas tropicais em paisagens rurais: a influência do solo e cobertura florestal adjacente

A restauração ecológica tem sido requisitada a para proteção de biodiversidade e serviços ecossistêmicos. Este desafio é enfrentado com suporte de grandes avanços de ordem teórica e prática, bem como incentivos financeiros e políticas específicas. No entanto, ainda restam incertezas quanto aos fatores que influenciam a trajetória da restauração de florestas tropicais, comprometendo a eficiência no uso de recursos limitados. Visando contribuir para o desenvolvimento metodológico da restauração florestal, e favorecer a identificação de metas de restauração adequadas, estudamos o efeito de características do solo e do contexto de paisagem na restauração de Mata Atlântica, buscando respostas para três questões: Como as áreas disponíveis para restauração se estão distribuídas com relação ao gradiente de degradação, em uma região amplamente antropizada? Qual a importância de características do solo e da cobertura florestal no processo de recuperação? E qual é o efeito da idade de fragmentos adjacentes na regeneração que se estabele em restaurações florestais? Utilizando bases de dados geográficos e estatísticas de terras agrícolas, observamos que os projetos de restauração tendem a se estabelecer sobre paisagens altamente degradadas. Combinando informações de sensoriamento remoto, com a caracterização de solo e da vegetação, em áreas abrangidas pelo mesmo programa de restauração florestal, verificamos que a recuperação de biomassa é afetada pela granulometria, pela cobertura do florestal, e pela interação entre granulometria e composição química dos solos. Também verificamos que a idade da cobertura florestal adjacente afeta a frequência de diferentes atributos. Nossos resultados corroboram a necessidade de avaliação em escala detalhada para a previsão dos resultados da restauração, e sugerem aprimoramentos metodológicos. Considerando que, em paisagens rurais, a adjacência à florestas maduras e a disponibilidade de solos conservados tendem a ser recursos mais raros, as políticas de restauração de Mata Atlântica devem prever metas alternativas para as condições mais adversas, e técnicas para melhoria de condições do solo e conservação de remanescentes para possibilitar a recuperação de florestas tropicais em áreas adequadas.

Palavras-chave: *Agroecossistemas. Cobertura florestal. Efetividade. Filtros ambientais. Histórico de ocupação. Matas ciliares.*

ABSTRACT

Tropical forest restoration in rural landscapes: the influence of soil and adjacent forest coverage

Ecological restoration is addressing concerns surrounding threats to ecosystem services and biodiversity. Support for this endeavor comes from substantial conceptual and practical advances, and policy initiatives and monetary incentives. Still, it remains unclear what are the main factors influencing tropical forest restoration. This lack of knowledge can compromise the willingness to restore and waste limited resources. To improve the knowledge base and aid identification of appropriate restoration targets, we studied the effect of soil and landscape context on tropical forest restoration, focusing in three main questions. We first asked: How the potential land supply for restoration is spatially distributed in the range of disturbance contexts of a highly degraded tropical region? Secondly, we asked: How important are soil properties and forest adjacency for biomass uptake and community assembly during early tropical forest restoration? And at last: What is the effect of the age of adjacent forests patches on the forest regeneration established in restoration sites? Using georeferenced databases and rural lands statistics, we observed that forest restoration is likely to be located within highly degraded landscapes. Combining remote sensing, with soil and vegetation survey undertaken in forest restoration sites that were implemented by the same program, we found that biomass recovery is affected by soil texture, surrounding forest coverage and the interaction between soil texture and soil chemical composition. We also found that the age of surrounding forest coverage affected the regenerating plant community, influencing species groups relative density, as related to seed dispersal syndrome, seed size and habitat specialization. Our results corroborate the need for fine scale evaluations to predict restoration outcomes, and anticipate methodological refinement. Given projections for decreasing presence of old-growth forests and increasing soil degradation in tropical rural landscapes, restoration policies likely need to consider alternative restoration targets for adverse conditions, coupled with improving soil conditions and protecting forest remnants to allow moist tropical forest recovery in appropriate areas.

Keywords: *Agroecosystems. Land-use history. Effectiveness. Environmental filters. Forest cover. Riparian forests.*

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APRESENTAÇÃO

A restauração de Mata Atlântica tem contado com notável avanço ao longo das últimas décadas, devido a diversificação técnicas, a ênfase sob diferentes processos ecológicos e o desenvolvimento de diferentes abordagens para ampliação de diversidade (RODRIGUES et al., 2009). Estes avanços proporcionaram perspectivas promissoras, ou seja, de reversão no quadro de restrito sucesso verificado em períodos anteriores (WUETHRICH, 2007; RODRIGUES et al., 2009).

O desenvolvimento teórico-técnico foi acompanhado de mobilização social em torno da necessidade de ampliar esforços para restaurar habitats degradados, que internacionalmente culminou em metas globais como as estabelecidas pela Convenção de Diversidade Biológica de AIchi em 2010 e o desafio de Bonn-IUCN em 2011 (SUDING & HIGGS, 2015). As bases teórica e prática do processo de restauração ecológica esperadas pelos agentes sociais podem ser resumidas nas palavras de Alexander et al. (2011) que delimitam o que deve ser considerado para o cumprimento destas metas:

> *"A restauração ecológica é uma atividade intencional que inicia ou facilita a recuperação dos ecossistemas, restabelecendo uma trajetória benéfica de maturação que persiste ao longo do tempo. A ciência e a prática da restauração ecológica são focadas no restabelecimento de processos ecológicos pelos quais populações de espécies podem se auto-organizar em comunidades funcionais e persistentes, que se adaptam às condições de mudança e, ao mesmo tempo, fornecem serviços ecossistêmicos vitais. Além de restabelecer o funcionamento do ecossistema, a restauração ecológica também promove o restabelecimento de uma relação saudável entre os seres humanos e seus ambientes naturais, reforçando o vínculo indissolúvel entre natureza e cultura, e enfatizando os importantes benefícios que os ecossistemas prestam às comunidades humanas."*

Avanços técnicos e institucionais impulsionaram ações audaciosas, mobilizando expectativas que envolvem políticas de conservação em amplo contexto. De Groot (2013), por exemplo, afirma que mecanismos como REED+ e a compensação de emissões com sequestro de carbono são importantes para que metas globais de restauração sejam alcançadas. Já Maron et al. (2015) apontam a crescente preocupação em relação a "compensação da perda de biodiversidade", envolvendo a modalidade de compensação por restauração.

Em outras palavras, políticas públicas internacionais têm no bojo dos objetivos a serem alcançados, pretensões quanto à recuperação de biomassa e da composição biológica promovida por restaurações - condições básicas para atendimento dos processos ecológicos e serviços a serem alcançados. Expectativas semelhantes também são observadas no Brasil: as Resoluções da Secretaria do Meio Ambiente 30 de 2009 e 7 de 2017 são exemplos de antecipação de resultados de restauração. A Resolução SMA 30/2009 orienta projetos de reflorestamento para compensação de emissões de gases de efeito estufa, e estabelece que o "sequestro" máximo previsto nos projetos deve ser de 350 tCO_2 por hectare. Este "teto", ou valor máximo, é baseado em modelo calibrado com dados de vegetação remanescente (MARTINS et al., 2009). Já a Resolução SMA 7 de 2017, define a taxa para compensação de supressão de vegetação nativa, considerando o estágio sucessional da vegetação perdida e a classificação de sua localização quanto ao grau de prioridade para restauração. Como exemplo:

> *"§ 3º - No caso de vegetação primária ou vegetação sucessora em estágio avançado de regeneração:*
>
> *I - Áreas inseridas na categoria de Baixa Prioridade, do mapa "Áreas prioritárias para restauração de vegetação nativa", deverá ser compensada área equivalente a 2 (duas) vezes a área autorizada"*

Estes exemplos indicam que a restauração florestal é reconhecida como uma ação efetiva de resgate da biomassa, da riqueza e da diversidade florestal, bem como dos serviços ecossistêmicos advindos das mesmas. Porém, a "ecologia da restauração" reconhece limitações para a recuperação em condições de elevada

degradação. Na restauração florestal, solos degradados são apontados como limitantes ao crescimento da floresta, já uma grande limitação à recuperação da composição biológica é atribuída aos efeitos da perda e degradação de habitat (CHAZDON, 2008; SUDING & HOBBS, 2009). No entanto, as implicações destas relações ainda são pouco estudadas, uma vez que avanços neste campo requisitam a comparação de resultados em restaurações com histórico de implantação similar (SUDING, 2011).

Alguns estudos no Brasil registram grandes diferenças de resultados na estrutura e composição de restaurações em condições semelhantes (e.g. MELO & DURIGAN, 2006; IGNÁCIO et al., 2007; MELO et al., 2007). Porém, informações sobre as origens destas diferenças ainda são escassas. O próprio insucesso de iniciativas anteriores apontadas por Wuethrich (2007) e Rodrigues et al. (2009) pode ter como uma das causas a falta de avaliação e remediação de importantes inibidores da recuperação. Essas considerações podem ser vistas como fortes indícios de que necessitamos acompanhar o desenvolvimento desses plantios de restauração na Mata Atlântica, de forma a orientar a busca por efetivo impacto positivo nas paisagens.

Nesse contexto, investigamos fatores que inibem a restauração de Mata Atlântica, buscando auxiliar o desenvolvimento de melhores procedimentos para o planejamento, implementação e manejo de restauração. Avaliamos a influência da textura e características químicas do solo onde foram estabelecidos plantios, assim como da quantidade e histórico da cobertura florestal adjacente imersa sob campos antrópicos. Também identificamos os padrões de recuperação da biomassa e da composição de espécies lenhosas em restaurações florestais, relacionados à características do solos e contextos de vizinhança. Os casos estudados foram implantados nos domínios de Mata Atlântica pelo Projeto de Recuperação de Matas Ciliares (PRMC), coordenado pela Secretaria do Meio Ambiente do Estado de São Paulo desde 2006.

Nossa expectativa é que os resultados possam incrementar os procedimentos adotados na restauração florestal em paisagens diversas e, por esse caminho, fortalecer a restauração como ferramenta de políticas de proteção de recursos naturais.

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Capitulo 1

Ecological restoration efforts in tropical rural landscapes: challenges and policy implications in a highly degraded region

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Abstract:

Ecological restoration has received increasing attention as international agreements have set ambitious goals to mitigate environmental change and reshape degraded landscapes. However, so far current advances on complying with these agreements are still modest. In particular, tropical forest restoration projects, implemented to conserve biodiversity and deliver ecosystem services, have had mixed success. Here we address the need for taking into account the spatial context of land available for restoration, to better inform policy given the results that can be expected from such large-scale restoration programs in tropical agricultural landscapes. Using a compendium of land voluntarily offered for restoration, we access the potential land supply and its characteristics for large-scale restoration programs in an emblematic heavily degraded tropical region: São Paulo state – Brazil. Using georeferenced databases and rural lands statistics, we show that the usually small parcels of land offered for restoration are low-priced with high potential for soil erosion, within landscapes predominantly used for livestock grazing and sugarcane cropping. Remnant native habitat is usually at great distances across these agricultural lands – on average nearly 500m to native habitat and over 4.5km to old growth forest. Such a scenario demands expensive restoration actions to assist an otherwise slow, or potentially non-existent, recovery process. This further demands significant contributions from risk exposure management and mitigation of degradation in adjacent habitat remnants and agricultural lands. It also indicates the necessity for a longer-term commitment among a broad set of social actors. Our findings, likely applicable to other densely populated tropical regions, suggest that land-use and restoration policies should acknowledge that the distance between implementing a restoration project, and achieving the ecological restoration, is still frequently long and uncertain.

Keywords: Tropical agroecosystems. Land-use change. Restoration policies. Global targets. Effectiveness.

1. INTRODUTION

Ecological restoration is increasingly gaining prominence as a means to address concerns around biodiversity loss and availability of ecosystem services (SUDING, 2011; TRABUCCHI et al., 2012; BRANCALION et al., 2013). Accordingly, extensive restoration endeavors have been implemented in degraded habitats, such as grasslands, wetlands, rivers and forests (JONSON 2010; KOEBEL & BOUSQUIN, 2014; MANSOURIAN & VALLAURI, 2014; THEILING et al., 2015). Large-scale restoration projects have also been proposed to recover neotropical hotspots for biological conservation (CHAZDON 2008; CALMON et al., 2011; DURIGAN et al., 2013), these regional programs are now interconnected by collaborative networks (ECHEVERRÍA et al., 2015), and commited to global agreements such as the 2010 Aichi Convention on Biological Diversity and the 2011 Bonn Challenge (SUDING et al., 2015). Efforts of such magnitude imply a substantial land use conversion. For instance, the global commitment of the Bonn Challenge embraces the restoration of 150 million hectares of degraded and deforested lands and the Aichi target encompasses the restoration of 15% of degraded ecosystems. In Brazil, rural land use legislation is compatible with these targets given that set-asides to be restored in Sao Paulo still encompass 1.9 million hectares (SOARES-FILHO, 2014). This legislative milieu persists despite the recent weakening of Brazilian forest protections (ALARCON et al., 2015). Restoration programs could also reverse the environmental degradation associated with the widespread non-compliance with habitat protection laws (PAYÉS et al., 2013; TERRA et al., 2014).

Conversion of deforested lands has been addressed using native tree plantations as a central restoration technique (LAMB et al., 2005; RODRIGUES et al., 2009). Generally, these interventions intend to foster regulating ecosystem services by converting agricultural fields into natural forests. However, the success of these plantations are still highly uncertain (COSTA et al., 2016; WUETHRICH, 2007), and varied outcomes have been reported for tropical forest restoration, even when similar protocols are implemented on different locations (MELO & DURIGAN, 2006; MELO et al., 2007; IGNÁCIO et al., 2007). This empirical evidence is consistent with theory, once it is taken into account that the recovery process is expected to be forged by the interplay of variable biotic and abiotic

legacies (FLINN & VELLEND, 2005; HOBBS et al., 2009) and also by disturbance regimes, which are often variable at local and landscape scales (HOLL & AIDE, 2011; SUDING, 2011). These finding strongly suggests that sustainable land use policies for these tropical rural areas need refining to take into account the distribution and characteristics of the land available for restoration.

Poverty and social conflicts are often found with the aforementioned altered environmental conditions in regions with demand for tropical forest restoration (CECCON et al., 2015). Financial support for restoration, from offsetting agreements and payments for ecosystem services (PES), seems opportune as a way to balance financial outcomes of restoration actions and resulting land use change. Nevertheless, while financial support seems suitable for these impoverished regions, the expected results of restoration actions are negotiated products, which can be controversial, especially when restoration is expected to be constrained by altered environmental conditions (see BULLOCK et al., 2011; MARON et al., 2012). Hence, identifying regions with adverse conditions for restoration, and their frequency, may aid strategic financial investment to maximize ecological returns. Attempting to bolster success of large-scale restoration, given the finite availability of resources, may also help negotiations and continued engagement within populated rural areas.

Soil degradation is an important variable to aid the anticipation of restoration results. Previous agricultural land-uses in tropical soils change their properties in different directions. Hunke et al. (2015) compared soil properties in different land-uses in the same region: pastures had soil that was more compacted and lower in total nitrogen than sugarcane plantations, while phosphorus and potassium were lost from sugarcane. They also observed considerable macronutrient accumulation under soybean plantations. Weill & Spavorek (2008) and Ferraz et al. (2013) recorded intensifying soil loss rates under sugarcane plantations. Rodrigues et al. (2011) documented that anthropogenic wet fields created by siltation double in frequency at sugarcane farms, compared to mixed-use landscapes. Clearly, the relation between soil distribution and land-use promotes different legacies for recovery, even though soil erosion legacy is widespread in tropical landscapes. For instance, studies show total soil loss in Brazil often

exceeds 50 t ha^{-1} y^{-1}, or 3.5 times the global mean, indicating this region as a global hotspot for soil loss (GUERRA et al., 2014).

It is also well established that the amount of remnant habitat in the restoration surroundings is crucial for supplying ecological functions (HOLL & AIDE 2011; TSCHARNTKE et al. 2012). During the restoration process, biotic connectivity is required for reintegrating remaing and/or reintroduced biota in to landscape dynamics, supporting recolonization of native biota and interaction with surrounding populations (BARBOSA & PIZO, 2006; PÜTZ et al., 2011; ZAHAWI et al., 2013). An absence of habitat adjacency is particularly restrictive for the recovery of highly diverse ecosystems, since the reintroduction of a relevant portion of the pre-disturbance species richness is likely unfeasible . Under isolation, biotic arrivals may only include ruderal species, that are abundant in the disturbed surroundings, indicating that a biotic threshold may have been surpassed (HOBBS et al., 2009). Finally, the landscape moderates the flow of energy, resources and organisms across habitats (TSCHARNTKE et al., 2012). Accordingly, landscape composition has a crucial role in influencing cross-habitat spillovers, for instance between regenerating forests and pastures or crops. Therefore, outcomes of the restoration measured in a particular land use context are unlikely to be accurately transferable to other landscapes with alternative compositions and/or configurations.

Despite the recognition of these three inter-related variables (i.e. land-use, habitat adjacency and soil loss) as key drivers of tropical forest restoration, the distribution and spatial relatedness among them, in relation to landscapes targeted by restoration programs, remains unknown. The literature provides rare examples of quantitative evaluation on this topic (e.g. CECCON et al., 2015), but to the authors' knowledge lacks spatially explicit approaches. This knowledge gap potentially hampers predictions and decision-making. Here, we address this knowledge gap by elucidating the landscape properties of land offered for restoration in Sao Paulo State. We then discuss the implications of our findings, on the geographical distribution of land available for restoration, in relation to restoration policies and practice.

2. METHODS

Our study region is the most populous Brazilian state, São Paulo. The state comprises 2.9 % of the national territory but supplies 32.6 % of Brazil's gross domestic product (IBGE, 2013). Human activities, while promoting the GDP, have exposed this region to severe deforestation, fragmentation and soil degradation (DEAN, 1997; HANSEN et al., 2013; GUERRA et al., 2014). Human land-uses encompass 83.6 % of the state (CETESB, 2012), mostly with assorted agricultural uses, settled over two biodiversity hotspots: Brazilian Atlantic Forest and the "Cerrado" savannas. The widespread ecological degradation in conjunction with its threatened biodiversity makes São Paulo state an ideal candidate for large-scale ecological restoration. The Riparian Forest Restoration Project (PRMC), coordinated by the environmental agency of São Paulo, was mainly intended for developing restoration policy, together with engaging and training local actors across the state (WUETRICH, 2007; CHAZDON, 2008). PRMC was predominantly focused on riparian forest restoration, but it also addressed the restoration of non-riparian areas.

To evaluate the geographical distribution of lands that are available for restoration we assessed the "restoration land bank of São Paulo", a management tool initially developed under the scope of "PRMC", to which private landholders voluntarily offer areas to restoration actions. We had access to a list from 2013 with 399 enrollments, encompassing 2,896 hectares from 87 municipalities. Surprisingly, 558 municipalities offered no enrollments. From 2014, this land bank was incorporated into the compulsory rural environmental cadastre (CAR), a much larger information system which endeavors to include all rural properties of Brazil. However, this system is still being implemented and so data were not available for the analysis herein. Furthermore, the spontaneous enrollments from 2013 provide a sample of engagement strictly related to a restoration program.

The enrollment records were incorporated in a geodatabase that included remnant habitat distribution from the São Paulo State Forest Inventory of Natural Vegetation (1:25,000) (IF 2010), and a map detailing susceptibility to soil loss in São Paulo State (1:500,000) (IPT 1994). The forest inventory we used (IF 2010) is a remote sensing product that classifies natural habitat patches according to

vegetation type and conservation status; from this base we extracted the location of: old-growth forests, early stages forests, and non-forest native vegetation. To evaluate the distance from native habitat across the agricultural matrix, the vegetation map was converted to raster data, with spatial resolution of 100m. Euclidean distances from each agricultural 100x100m cell to its nearest native vegetation patch were then calculated across the state. The geotechnical map combined predictions and systematic observations of local geotechnical events (e.g. rills and gullies) and from this base we extracted the susceptibility zones for soil loss due to erosion and landslide. To support the evaluation of land-use dynamics, including sugar cane expansion and average land price accounting for agricultural use, we accessed annual agricultural statistics between the years 2000 and 2013. Agricultural land-use and the land price for each agricultural suitability class was accessed from IEA (2014) and IEA (2015); these data are available at administrative region scale, which divides São Paulo into 40 units. Sugarcane cropping area from the season 2013-2014 was accessed at the municipal scale (645 units) using the CANASAT dataset (RUDORFF et al., 2010).

To evaluate the context of areas potentially available for restoration we first identified the general trends for São Paulo with statewide statistics, and then we compared the results to the municipal context of areas from the land-bank for restoration. To account for the size variability of areas that were registered in the land-bank, and the variability in size among municipalities, cumulative distribution curves were prepared for each explanatory variable (prevalence in area), including: remnant habitat coverage (habitat adjacency), the prevalence of soil erosion susceptibility classes (soil loss), and sugarcane crop(land-use). We then used non-parametric tests (Komolgorov-Smirnov two sample test) to verify if the resulting cumulative functions were distinct between treatments (statewide and land-bank sample). This procedure was implemented using the ‘ks.boot’ function (bootstrapping with 10,000 simulations) in the R package ‘Matching’ (SEKHON, 2011). However, trends observed at the administrative region scale (i.e. agricultural land use and land price) were not statistically tested due to the low number of samples (regional scale), as well as the prevalence of landslide risk zone.

3. RESULTS

The São Paulo Forest Inventory (IF 2010) indicates that old-growth forest, early successional forest, and non-forest (shrub-grassland) native vegetation cover 4.26%, 11.74%, and 1.67% of the state, respectively. The fact that the state has less than 18% native vegetation cover is worrisome from a native biodiversity conservation perspective, but this value also hides the clumped nature of its distribution (Figure 1). Consequently, in most municipalities within the state, natural habitat coverage is lower than 9.47% and old-growth forest coverage is lower than 1.17%.

We found remarkably lower native habitat coverage in regions with greater engagement to the restoration land-bank. Conspicuously, 34.0% of enrolled lands were found in municipalities with less than 4.5% native habitat coverage, while only 15.0% of state was within the same interval. Consistently, habitat coverage in 42.6% of state is up to 8.2% habitat coverage but the same condition comprises 72.3% of the land-bank. These example figures demonstrate significant differences on cumulative distributions, as confirmed with Komolgorov-Smirnov D-Statistic (K-S p-value = 0.0002, D=0.310). Across the agricultural matrix, the average distance to the nearest native habitat patch (old-growth forest, early stage forest, or non-forest native habitat) was 493 meters (**Erro! Fonte de referência não encontrada.**), while the average distance to the nearest old-growth forest patch was 4,540 meters.

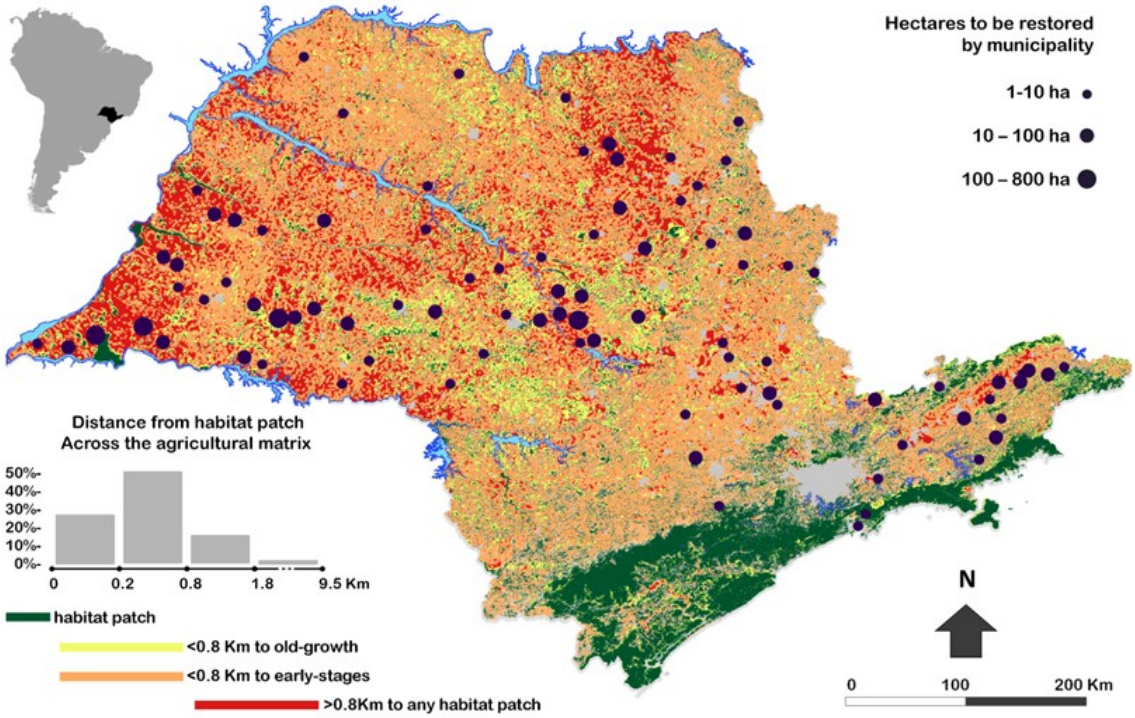

Figure 1.1 Enrollments for restoration (data from SMA, 2013) and distance from remnant habitat (data from IF, 2010). The spatial distribution of enrolled lands tends to be associated with greater distances from a habitat patch, in regions with lower native habitat coverage.

Enrollment for restoration took place in regions comprising all erosion susceptibility classes. Even so, the "very highly susceptible soil erosion" class, which covers 35.2% of the state, was found for 55.9% of enrolled lands, with significantly different distributions (K-S p-value = 0.002, D=0.35185). Conversely, 38.9% of the state is within municipalities of predominant high erosion potential, but only 19.1% of the enrolled lands were at same conditions leading to a significantly distinct distribution (K-S p-value = 0.0001, D=0.37313). However, similar distributions across the state and across the land bank was not rejected for low susceptibility to soil erosion (K-S p-value = 0.0702, D=0.23333). Ultimately, low susceptibility prevails at 19.8% of the state, and 19.7% of the land-bank.

Enrollment to the restoration land bank was generally concentrated in highly or very highly susceptible, erosion classes, and outside the landslide risk zone. Only 27.5% of offered lands were in municipalities with any landslide risk (compared to 36.7% of the state as a whole). In the opposite direction, remnant habitat coverage was concentrated in landslide risk zones, with 53% of this risk zone protected by natural habitat. In contrast, natural habitat only protects 8.9% of the

very highly susceptible erosion class (**Erro! Fonte de referência não encontrada.**).

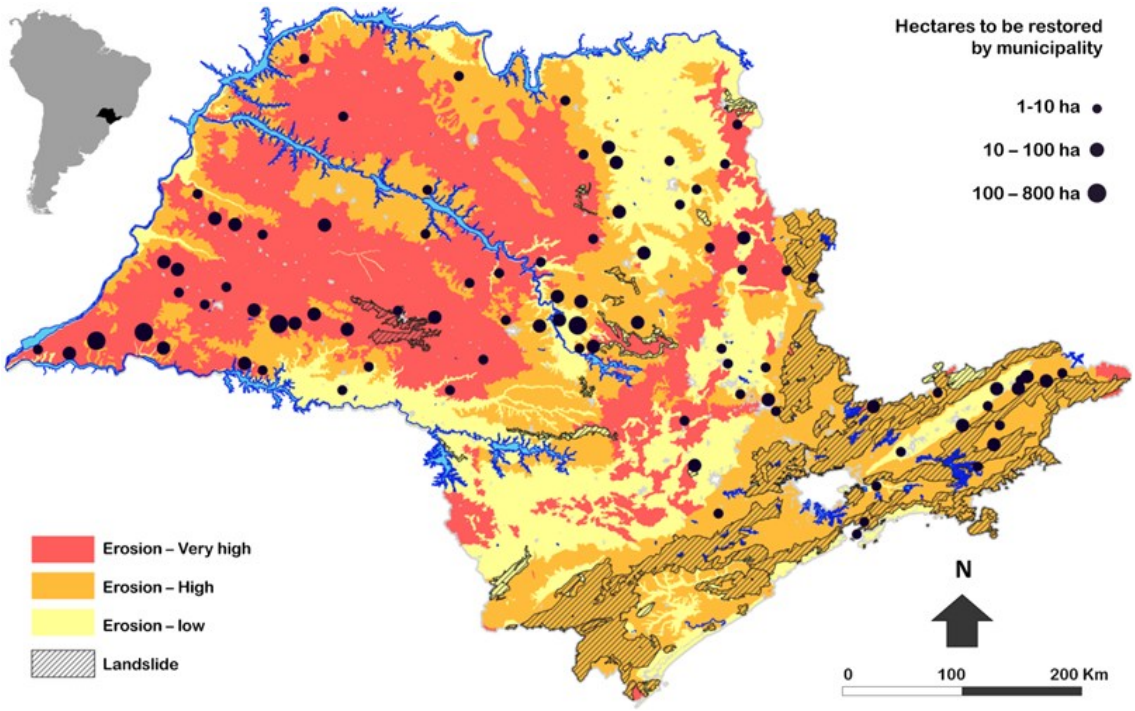

Figure 1.2 Enrollments for restoration (data from SMA 2013) plotted on the soil erosion map (data from IPT. 1994).

According to the agroeconomic database (IEA, 2015), between the years 2000 and 2013, the average annual rural land-use conversion was 381,607 hectares, affecting annually between 0.7% and 5.4% of the rural lands in São Paulo (Figure 1.3).

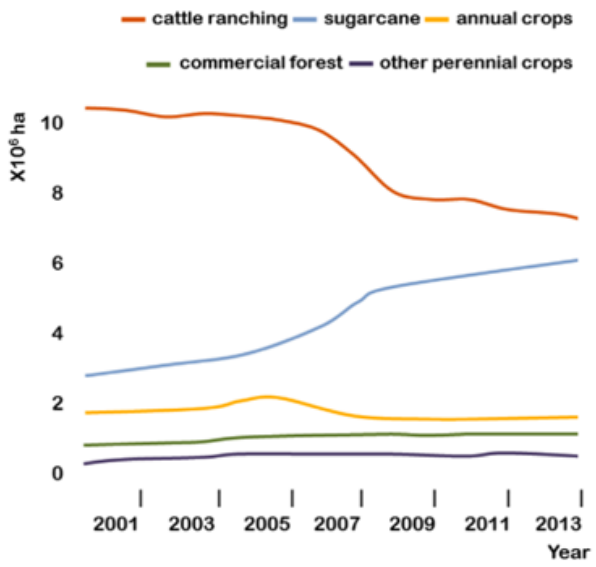

Figure 1.3 Agricultural land-use change in São Paulo State.

In 2013, 42.6% of the agricultural lands from São Paulo were used for cattle-ranching, and 36.8% for sugarcane cropping. Perennial crops, annual crops, and commercial forests represented only 3.5%, 9.9% and 7.2%, respectively, of the agricultural land-use. Livestock remained the major land use during the analyzed period, despite its decline in extent, while sugarcane cropping effectively doubled in extent and presented a clumped distribution. Enrollments to the land-bank were associated with slightly greater sugar-cane coverage as an effect of low enrollment at municipalities with less than 15% of sugarcane coverage, which comprises 41.9% of state area, but only 20.8% of the land-bank, resulting in significantly different distributions (K-S p-value = 0.009, D=0.2794). We estimated the average price of the enrolled lands at US$ 5,605 per hectare (SD=2,908), that is 26.9% cheaper than the average state-wide agricultural land price of US$ 7,663 per ha (SD=2,865).

4. Discussion

The urgency for restoration programs in highly degraded tropical regions, like the Brazilian state of São Paulo, is accompanied by adverse conditions for restoration. In our study region, available lands for restoration were predominantly associated with very low remnant native habitat coverage exacerbated by large distances to whatever habitat remained, commonly combined with very high soil erosion susceptibility. These characteristics are

suggestive of severe environmental constraints for ecological recovery in Sao Paulo state. Furthermore, given the similarity to the context described by Ceccon et al. (2015), such conditions are potentially commonplace in tropical agricultural landscapes. In addition, we also observed that land use by mechanized crops is expanding significantly, potentially increasing soil degradation and biological isolation. All these trends are reinforced by the profile of lands that are enrolled for restoration. At the current policy background, of interconnected multiscale restoration goals, results showed that unfavorable conditions for restoration prevailed in our study area, but most importantly, that conditions are highly variable within a territory that exemplifies a strongly human-modified tropical region.

The supply of lands for restoration is oriented towards degraded and cheaper regions, corroborating with the “leftover for set aside” trend reported for terrestrial protected areas by Joppa & Pfaff (2009) and marine reserves by Devillers et al. (2015). Cheaper lands do provide an opportunity for either a greater extent of restoration, or higher-cost restoration activities, since less money is involved in the initial purchase of land. Additionally, the focusing of restoration in more degraded areas also contradicts the argument that ecological restoration competes for strategic areas with agricultural production (see also MARTINELI et al. 2010; LAPOLA et al., 2014; STRASBURG et al., 2014). However, this trend makes large-scale restoration even more challenging, due to the predominance of adverse conditions associated with degraded areas, as we discuss below.

The scarceness of natural habitat coverage and the observed predominance of long distances between habitat patches are far worse than thresholds evidenced by ecological studies. Pardini et al. (2010), for example, developed a model focused on the effects of forest fragmentation on local and regional diversity, with data from the Brazilian Atlantic Forest. They demonstrated the occurrence of an abrupt landscape-wide loss of forest-specialist species when deforestation surpasses a threshold ratio between 31% and 11% of natural habitat coverage, undermining ecological resilience and management effectiveness. Figures from our study indicate that most of the available landscapes for restoration are far too deforested in comparison to this critical band, habitat coverage greater than 31% was only found in 14.3% of São Paulo. Moreover, old growth forest coverage

greater than 31% was only found in 3.9% of the state. In addition to these areal threshold effects, Kauano et al. (2013) recorded a greater tree diversity increase in restoration projects that were closer than 200m from a forest remnant; an identical critical distance for ecological recovery was found by Souza et al. (2014) and Rezende et al. (2015). However, only 28.3% of all agricultural lands in São Paulo were found within 200m of habitat patches, in a region where the mean distance from the nearest habitat patch was found to be 2.5 times higher than the critical distance verified by these cited studies. These figures indicate that strong support from spontaneous recovery reported for other regions (e.g. REZENDE et al., 2015) cannot be taken for granted in most of the study area. Still, an exception was clearly observed at the domains of steep slopes, on the landslide risk zone, where natural habitat has been spared due to low agricultural land suitability. The overwhelming majority of regions with very poor habitat coverage suggests that resemblance to natural areas is unlikely to be achieved through forest succession in a representative portion of available lands for ecological restoration.

Cost effectiveness is also affected by connectivity loss. Reducing restoration costs by adopting less interventional approaches, such as nucleation strategies (ZAHAWI et al. 2013), is likely to be more successful where connectivity is present. However, our results indicate that this favorable situation is rare. This caveat is even greater considering that a large proportion of existing remnant habitat is relatively recent second-growth forest (LIRA et al., 2012) that is an already simplified version of the ‘ancestor’ pristine habitat (EWERS et al. ,2013), and we found in the used database that only a quarter of remaining forest is classified as “old-growth”. In addition, severe defaunation affects ongoing seed dispersal in this region (GALETTI et al. 2013). Hence, biological conditions for a species-rich tropical forest succession tend to be far from ideal in highly deforested regions, with unreliable support from spontaneous regeneration, requiring expensive and arduous interventions as plantations of native trees, that will likely result in persistently narrowed biodiversity (CHAZDOM, 2008; BENAYAS et al., 2009).

Similar concerns apply to restoration at degraded soils: higher costs are involved, and especially, much longer recovery may be unavoidable. Severe soil degradation is commonly observed in tropical landscapes, as evidenced with

gullies, rills, and silted streams. Sugarcane plantations are a mechanized crop system related to higher soil loss rates, and these plantations are expanding at the expense of cattle ranching, in turn related to significantly lower soil loss; and this land use change is taking place in a region with extensive areas of very high susceptibility to soil erosion. Furthermore, mechanization of crops such as sugarcane tends to lead to the occupation of flat land, pushing pastures to steep areas (RUDORFF et al. 2010), which can then also engender increased soil loss. Taking that into account, soil degradation is a general constraint for restoration projects whether the land was previously cropped or grazed. With degraded soil conditions, investing in standard agronomic interventions, such as liming and compost incorporation, and biological mediation of soil recovery, have shown promising results for ecological restoration (KARDOL & WARDLE, 2010; AMPOORTER et al., 2011; ROA-FUENTES et al., 2015; ZAHAWI et al., 2015; PERRING et al., 2015). However, soil recovery is recognized as a time demanding process in restoration projects (AMAZONAS et al., 2011; BONINI & ALVES, 2011), and slow soil recovery may persist for decades or centuries.

Unquestionably, this longer recovery increases exposure to several risks, and restoration planning in the light of degraded soil conditions should then consider natural and human-induced disturbance regimes in the longer term (e.g. fire, silting, land use turnover). Reducing risks with extended isolation from such disturbances makes projects more arduous and expensive (ZAHAWI et al., 2014). Crucially, restoration sites are open systems, for good or ill, and such openness is magnified in the longer-term. Therefore, surrounding land-use may become a major ally or an important antagonist in the recovery process. Thus, a large-scale restoration agenda should also consider degradation control in conservation areas, and adoption of best practices in agricultural areas (e.g. windbreaks, soil conservation, agroforestry schemes, and toxic inputs reduction).

In our study area, the land use context presented a sharing of dominance on agricultural land use for sugarcane plantations and pastures, offering an illustrative example of contrasting matrices. Although cattle-ranching and sugarcane crops are basically monocultures of exotic grasses, their agronomic particulars impart different ecological consequences. Poor restoration outcomes verified in Northeastern Brazil were partly attributed to the low biological

permeability of the surrounding sugarcane plantations by Costa et al. (2016). Large monocultural fields can be particularly hostile for native regenerating species, and sugarcane is harvested even before flowering, weakening plant-animal interactions. In contrast, livestock production includes semi-natural habitats with variable densities of native species, and have a historical compatibility to bocages - landscapes comprising small fields compartmentalized by a woody network - which improves their connectivity and diversity (see JAMONEAU et al., 2011; CASTRO & VAN DEN BERG, 2013). The effects these different agricultural properties have on restoration outcomes require further observational and experimental studies; nevertheless, the chances of improving ecosystem functioning at pastures seems much more promising, if compared to sugarcane agronomic options. Hence, the proliferation of large monocultural fields, as promoted by the biofuel industry in Brazil (FERREIRA FILHO & HORRIDGE, 2014), can be considered challenging for restoration programs, given reports of greater soil loss and the potentially greater ecological contrast.

Sustainable land use planning needs to consider that under the severely constraining contexts, observed in a large portion of our study area, restoration outcomes tend not to provide all the services of healthy ecosystems (PALMER & FILOSO, 2009; REY BENAYAS et al., 2009). Likewise, offsetting schemes must take into account that the partial recovery provides distinct habitats that are unable to replace the historic ones (MARON et al. 2012). However, the acknowledgment of constraining conditions for restoration should not discourage restoration programs. Although constraints may arguably prevent successful achievement of classical restoration goals, additional partially recovered habitats will likely aid overall ecosystem functioning and improve resilience of communities and ecosystems to environmental change. Then, the improved conditions will support “strict restoration” (sensu SHACKELFORD et al. 2013) in adjacent less disturbed areas, and may increase the viability of remaining habitat and the sustainability of agricultural systems (see TSCHARNTKE et al., 2012; HOBBS et al., 2014). Furthermore, taking into account constraints to classical restoration enables focusing on the recovery of ecological functions that may be achieved more feasibly (MARON et al., 2012) although further studies are required on the modelling of restoration benefits (e.g. BIRCH et al., 2010;

TAMBOSI et al., 2014) and trade-offs among functions (e.g. PERRING et al., 2012). In our study, the entire set of variables presented high spatial heterogeneity. Hence, acknowledging local and regional adversities makes it possible to select a realistic set of ecosystem functions and services that can be recovered. Conversely, unrealistic expectations may promote a twofold undesirable result. As well as the waste of resources by falling short of ecological goals, disappointment undermines long-term commitment among different social actors (i.e. farmers, local NGOs, rural extensionists and governmental agencies), breaking the forces required to implement a broad and integrated restoration agenda.

Financial costs can also affect the commitment to restoration. Adverse environmental conditions require expensive restoration interventions (as discussed earlier), and indeed, this assumption finds support through ongoing initiatives. A realistic cost baseline is provided by the “Atlantic Forest Restoration Initiative - National Bank for Economic and Social Development” (BNDES 2016), in which the first 14 forest restoration projects (total of 2,683 ha) were contracted after a competitive selection, with an average cost of US$7,501.00/ha. Extrapolating this comparatively high average cost (see de GROOT et al, 2013) to the São Paulo one million hectares target (WUETHRICH, 2007; CHAZDON, 2008) results in a direct spend of US$7.5 billion in implementation costs, to be hosted by rural land assets evaluated in US$4.6 billion, as estimated with data from IEA (2014). Clearly, an effort of such magnitude requires strong public commitment, and it is worth mentioning that the one million hectare target can be considered modest for biodiversity conservation. Even if all restoration actions were successful at restoring all targeted facets of native biodiversity, the result of such a great achievement would only improve the natural habitat coverage to just over 20%, still far below than the supposed safe zone of 30% coverage found by Pardini et al. (2010). Even so, the magnitude of such targets dwarfs any ongoing restoration action, as well as the few thousand hectares voluntarily enrolled for restoration elucidated by this study.

The poor engagement, as found in the land bank, poses a critical obstacle for large-scale restoration, and this challenge arguably goes hand in hand with high costs and uncertainty around benefits. Therefore, while the magnitude of the

restoration targets is consistent with ecological requirements, we found no evidence that these targets can be fulfilled in a few decades. Enrollments and achievements so far, indicate that this in an endeavor for some generations of restoration ecologists and landscape planners. In this direction, continuity of restoration programs, such as PRMC, is a vital resource, these experiences may add weight to evidences of restoration benefits for ecosystem services and respective communities (e.g. de GROOT et al., 2013; GRAND-CLEMENT et al., 2013), justifying the costly efforts that are needed. Furthermore, given the acknowledged uncertainties involved in the restoration process, combining long-term monitoring and adaptive management can be particularly beneficial, as a means of increasing the quality of decision making and improving restoration effectiveness (see SHULTZ, 2008).

5. CONCLUSION

In the last decades, restoration ecology has experienced remarkable progress and encouraged ambitious proposals (SUDING 2011; PERRING et al., 2015; SUDING et al., 2015). However, we found that restoration actions in the region of São Paulo, an illustrative environmentally degraded tropical region, are still far from taking place on a scale proportional to that required by habitat protection policies. Willingness to restore tends to be higher at degraded and inexpensive areas, where restoration efforts are likely to face outcome limitations, higher intervention costs and the need to manage risk over the long term. We point out that this challenging scenario likely constitutes a disengaging factor, which needs to be confronted by diminishing uncertainties and highlighting restoration benefits to the broader community. Recent advances converge to the suggestion that some major obstacles to ecological restoration can be overcome by considering the boundaries and surroundings of restoration sites as key elements to be planned and managed, taking into account their respective biophysical and cultural assets, and our reflections on São Paulo state indicate that this perspective is particularly valuable in highly degraded regions. Still, reversing negative projections for ecological restoration in densely occupied tropical regions is likely a long-term assignment, requiring constancy and resilience also from the policy environment. In the meantime, engagement is likely to gain appeal

and momentum, since the demand for endangered ecosystem services is also higher in these populated regions.

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Capitulo 2

Soil properties and adjacent forest coverage affect aboveground biomass and functional composition during tropical forests restoration.

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Abstract:

QUESTION

Understanding the main factors influencing tropical forest restoration at small scales, and the ecosystem consequences of variation in these factors, is key to developing effective restoration strategies. We studied the importance of soil properties and native habitat adjacency in affecting plant community biomass and assembly during the restoration process.

LOCATION

Forest restoration sites (N=32), established using the same protocol, 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=5cm) in four 200m2 plots per site. We translated these measurements into aboveground biomass (AGB), then related biomass variability to adjacent forest coverage (200m buffer), site fertility and soil properties with multilevel models. We also investigated the effect of these predictors on the abundance of different species groups, arranged according to variation in major traits (wood density, tree height) or habitat preference (moist forest specialists vs generalists), 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 coverage, and the interaction between soil nutrient concentrations and sand percentage were good predictors for biomass recovery. The most parsimonious model projected a six-year AGB recovery of 70.90 ton/ha, when a site is on fertile soils with 10% sand, and surrounded by forest coverage of 50%. In contrast, only 5.24 ton/ha is predicted on acidic-poor soils with 67% sand and 0% surrounding forest coverage. Increasing surrounding forest coverage favored smaller trees and habitat-generalists while increasing sand percentage inhibited taller species and moist-forest specialists. Sandy soils, when found on otherwise fertile sites, constrained softwoods.

CONCLUSION

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 fertility has been degraded and/or extreme deforestation has taken place. Lower biomass 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 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. Recovery. Traits.

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

1. INTRODUCTION

Substantial conceptual and practical advances in the field of restoration ecology have encouraged the launch of targeted forest restoration programs across the globe (PERRING et al. 2015b, SUDING et al. 2015). These restoration endeavors also take place in tropical hotspots for biological conservation (CALMON et al., 2011; WUETRICH, 2007), and, in this context, native tree plantations are now

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 levers, 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 therefore 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, controlling competition and mitigating post-disturbance environmental filters). Afterwards, the growth of the introduced trees is expected to reestablish light competition, facilitate immigrant arrivals (REID et al., 2015), and improve the establishment of old-growth species. But 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, QUINTON et al., 2010, 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). Such limitation can emerge because of direct physiological effects of the novel environment on the trees, but also through indirect effects, if the competitive interactions between species are altered and a few species become overabundant. For instance, successional inhibition has been attributed to fern overabundance on acidic disturbed soils in the Brazilian Atlantic forest domain (RIBEIRO et al., 2013). Forest recovery can also be constrained by lower water holding capacity of sandy soils, exacerbated by agriculturally driven soil organic matter loss (MATSON et al., 1997). Martinez-

Garza et al. (2013) showed drastic drought mortality of seedlings, concentrated in certain species groups, in a forest restoration experiment undertaken in sandy soils eroded by tropical livestock.

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 the landscape scale, connectivity is required for coupling the planted communities with landscape-scale ecological dynamics (BARBOSA & PIZO, 2006; PÜTZ et al., 2011; ZAHAWI et al., 2013). Within landscapes with sufficient natural vegetation (of the target type), spontaneous regeneration can take place vigorously after reducing disturbance (DE REZENDE et al., 2015). However, dispersal limitation is generally thought to be important, since studies indicate that relatively short cross-matrix distances pose an effective barrier to seed dispersal (KAUANO et al., 2013; SOUZA et al., 2014). Furthermore, available remnants may be too disturbed to act as an effective source of propagules (CHAZDON, 2008). Forest adjacency can also affect microclimate and nutrient flux, since climatic buffering can make the forest surroundings moister and colder (BAKER et al., 2014), and the forest patches can export nutrients by lateral diffusion, for instance through animal translocation (WOLF et al., 2013) or litter fall.

Aboveground biomass (AGB) is a straightforward proxy to assess forest restoration success, by combining forest recovery outcomes in terms of stem density, tree growth and functional 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 biomass represents a poor restoration outcome, and is expected to indicate poor conditions for restoration. Total AGB is made up of diverging yields from different species groups. Different relative abundances could reflect the scarcity

or abundance of resources that favour alternative competitors (LASKY et al., 2014). AGB share among species groups is therefore also expected to respond to different environmental conditions, and tropical forest restoration practices will be enabled by quantifying these patterns.

In this study we assessed results from a Brazilian restoration program, in order to quantify the effect of edaphic conditions and the influence of the adjacent forest coverage on biomass accumulation and tree composition. We hypothesize that total AGB recovery responds to both local edaphic conditions and the amount of neighbouring forest coverage; and that some species groups are especially affected, shaping community assembly. Understanding factors that influence tropical forest recovery can help us to improve predictions for forest restoration in agricultural regions of the humid tropics, guide species choice, and avoid wasted effort.

2. METHODS

2.1. 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 the state of São Paulo, in south eastern Brazil. Site selection resulted from regional workshops mainly intended for developing restoration policy, and also for training and engaging local actors (WUETRICH, 2007; CHAZDON, 2008). Sites were located in 15 watersheds scattered throughout a 780 km swath of land crossing the state from east to west, using a minor part of each farm engaged. The present study only surveyed eastern sites, which are all located within the boundaries of the Serra do Mar coastal forests (OLSON et al., 2001) in the "Atlantic plateau" geomorphic and botanical provinces (SCUDELLER et al., 2001).

Thirty-two eastern sites spanned six watersheds included in PRMC, within the upper Paraiba do Sul River Basin and the upper Tiete River Basin. Watersheds are underlain by granite-gneiss lithology, and comprise two mountain-ranges with crystalline parent material: "Serra do Mar" and "Serra da Mantiqueira" (Figure 2.1). Distances among each watershed vary between 30 km and 150 km. Across

the restoration sites, elevation ranges from 550 to 1510 meters above sea level, but annual precipitation ranges only from 1400 to 1700 mm, and the dry season (average monthly precipitation below 50mm) varies between 3 and 5 months (HIJMANS et al., 2005) during late autumn and winter. Early agricultural uses of these lands took place during the 19th Century (DEAN, 1991), and exposed a heterogeneous soil surface with varying slopes to the rainy summers. Nowadays, land coverage is dominated by pasture, surrounding scattered cropland, as well as urban and forest patches.

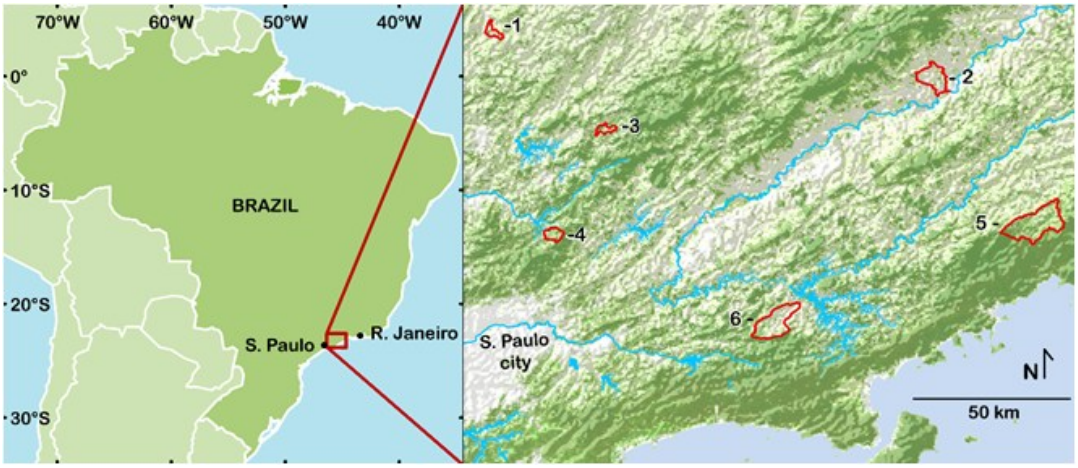

Figure 2.1 Eastern watersheds included in PRMC restoration program. Within Alto Tietê river basin, surveyed watersheds are located at the municipalities of Socorro (1), Joanópolis (3) and Nazaré Paulista (4). The Paraiba do Sul river basin comprised the watersheds located at Guaratinguetá (2), Cunha (5) and Paraibuna (6).

2.2. Study Desing

The PRMC tested different restoration protocols across São Paulo state, but the thirty-two selected sites presented here exclusively followed the main one: A species-rich tree plantation with a density of 1666 individuals per hectare. Several local nurseries produced the seedlings; they followed a broad species list and supplied individuals about 40 cm tall. Planting holes were prepared systematically prior to planting, typically in a 3 by 2 meters grid and species were mixed at random. Dead saplings were replaced, generally one year after project initiation. During replacement, species identity was 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 most spontaneous 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 made the reasonable assumption 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.

A structured screening process resulted in the final selection of the thirty-two sites presented here. Restoration sites were (1) as similar as possible with regard to variables that are not modelled here (e.g., elevation, perimeter to area ratio) and (2) were replicated at least three times within watersheds. So, after excluding restoration sites with alternative protocols, we also excluded locations with extreme conditions regarding elevation, perimeter-area ratio, terrain slope, and surface area (i.e. from 0.2ha to 3.5ha). Then, we considered 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. This resulted in the selection of the 32 restoration sites from six watersheds.

2.3. Data Colection

Four vegetation plots (4m x 50m) were randomly installed within each restoration site. Woody individuals with diameter at breast height (130cm; DBH) > 5 cm had their height and DBH recorded, and were identified to the species level; multistemmed individuals were included when the combined basal area was larger than the cutoff 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 (Department of Biology, ESALQ-USP).

Composite soil samples were taken from each vegetation plot at 0-20cm depth, by combining three sub-samples collected along the larger central axis, with a minimum distance of 20 m from each other. These samples were analyzed 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 (Resin), K (Resin), Ca (Resin), Mg (Resin); Organic Matter (photometry), and Sand contribution (0.053 - 2.00 mm).

Literature data were gathered to classify the identified species according to wood density (WD), maximum height (Hmax) and geographical distribution (the list of species, grouping data, and references are presented in the supplementary information Appendix S1). WD was combined with field measured tree height and DBH to calculate aboveground tree biomass using the allometric equation for tropical forests proposed by Chave et al. (2014). Then, WD and Hmax groups were investigated as environmental filtering indicators. Higher WD is typically found in species well adapted to dry conditions, since denser woods enhance plant resistance to xylem cavitation, fire, wind, and grazing, which are important causes of plant mortality in drier and more open plant communities (POORTER & MARKESTEIJN, 2008). On the other hand, favorable edaphic conditions support the development of productive forests, and Hmax thus becomes important as a trait associated with competitive ability for light (SHAMP & AARSSEN, 2009). The median value among identified species was used as the cut-off point (14 meters for Hmax; and 0.579 g/cm³ for WD) to separate contrasting levels within groups.

We were also interested whether harsher environmental conditions are as constraining to tree species with a broad geographical distribution, as they are to moist-forest specialist trees. To test it, we first accessed the geographical distribution of identified species through the Global Biodiversity Information Facility database (GBIF, 2016). Distribution records were then compared with the terrestrial ecoregions map (OLSON et al., 2001) to enable classification of species in two groups: the “moist-forest specialists” includes species distributed inside broadleaf tropical moist forests domains, with no presence recorded at natural non-moist forest habitats; and the “habitat generalists” group includes species with a broader distribution that overlapped with moist forest habitats, but also included records from non-forest natural habitats such as tropical savannas and scrublands.

To assess forest coverage in the surrounding landscape, land cover maps were produced for each site using visual interpretation of orthophotos taken in 2005, two years before the initiation of restoration projects. The mapped area included an 800 m wide external buffer zone for each restoration site, within which we

measured the forest coverage percentage from each plot at 0-200m, 0-400m and 0-800m buffers.

2.4. DATA ANALYSUS

ABOVEGROUND BIOMASS

All data were analyzed 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 adjacent forest coverage on the above-ground biomass density (ton/ha). For greater goodness of fit and to satisfy model assumptions on error distributions, we square root transformed sand percentage and the above-ground biomass. Soil chemical properties, sand contribution, forest coverage and their interaction were tested as fixed effects, while restoration site was added as a random term to capture between-site variation that was not explained by the other predictors. We also investigated whether biomass variability and community assembly were significantly affected by nesting within watershed as a random term. However, their inclusion was never significant across all models, justifying their removal from selected models.

Soil chemical variables were highly correlated among each other and collectively define broad groups of soil chemistry. We first quantified the variation in soil chemistry between sites using pairwise Gower distances and performed hierarchical clustering of the sites based on the full dissimilarity matrix (with average linkage using the vegan package, version 2.3-5, R-Forge). We retained two soil groups: one group of sites that was clearly less acidic and richer in nutrients (‘fertile soils’ hereafter), and another group which included more acidic soils with lower nutrient concentrations, with a few exceptions of high concentrations of potassium (K) and organic matter concentrations (‘poor/acidic soils’ hereafter) (see Appendix S 2).

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)), the same models were fitted to these response variables. In addition, we also 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 diversity (as indicated by their relative abundances) were calculated at plot level. The Shannon diversity index (H) was calculated with R package “vegan”, and transformed to an “effective species number” (exp(H)), where species are weighted precisely by their abundances (JOST, 2006).

PLANT COMMUNITY ASSEMBLAGE

We analyzed the association between biomass within the three separate species groups (WD, Hmax and habitat preference) and potential explanatory environmental variables through linear models for multivariate abundance data using the mvabund package (Wang et al. 2012), version 3.11.9. We compared response variables of total biomass across a group, and at each level when groups were separated by their median value, per restoration site, with explanatory variables of mean site level environmental values (sand percentage, fertility grouping, fertility-sand % interaction, and forest coverage in the 200 m buffer). Only individuals identified at the species level were considered in these analyses, representing 84.9% of the total biomass surveyed. Species list, groups and references can be found in Appendix S1. Significance of the fitted effects were tested with anova using adjusted p-values (9,999 permutations), and then predicted abundances (in biomass) were estimated, also using the mvabund package. In addition, a Spearman’s rank correlation test was used to investigate whether there was an association among traits-based groupings, and also if any considered trait was related to higher or lower total biomass.

3. RESULTS

3.1. 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 (average = 475.0 individuals), thereby 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. Most of the species (53 of a total of 104 species) had fewer than 4 individuals in the entire survey.

Sand percentage ranged from 10% to 67% (average = 47.4%), and forest coverage within the 200m buffer ranged from 0% to 50% (average = 14.5%). The most contrasting variables between the poor/acidic soil group and the more fertile soil group were the concentrations of Ca, Mg, and P, with poor/acidic soils on average having well under half their corresponding fertile soil values (acidic/poor means (in mmolc/dm3): Ca = 8.1, Mg = 2.4 and P = 5.9; fertile means: Ca = 29.3, Mg = 10.3, and P = 15.1). In addition, “poor/acidic” soils presented a median pH of 4.2, (between q25=4.0 and q75=4.3); while fertile soils presented a median pH of 4.8, (between q25=4.5 and q75=4.9). Detailed information on the soil analysis is provided in the supplementary material (Appendix S2).

3.2. Biomass Model

AGB was significantly influenced by environmental factors acting on a local scale. In particular, AGB decreased as sand percentage increased, but the effect depended on soil chemical fertility. The effect 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 and Figure 5). Biomass also increased as surrounding forest coverage increased within 200m of the site. Interestingly, given that the narrower buffer is part of any wider buffer and therefore other buffer ranges are correlated, there was no significant effect of forest coverage within 400 and 800 m of the site for biomass, tree density, and mean stem volume as responses (results not shown).

Survival of planted species at the restoration sites appeared to drive the variation in biomass 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 surrounding forest coverage 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 biomass 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 soil group, and were not associated with any single environmental predictors (Table 2.1).

Table 2.1 Effects of soil sand percentage, soil fertility group and surrounding forest coverage on the plot-level biomass (ton/ha), stem density (trees/ha), stem volume (average cm^3/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	*

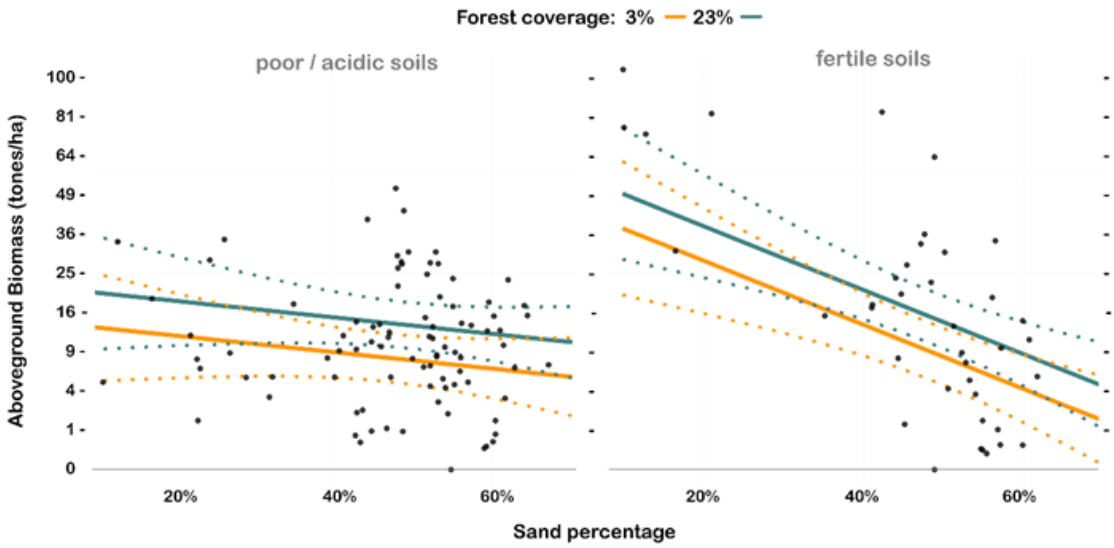

Figure 2.2 Observed biomass (sqrt-transformed) as a function of soil sand percentage for the two contrasting soil fertility groups (points). Lines show model predictions (table 1) +/- 95% confidence intervals for 3% and 23% forest coverage (interquartile extremes of in our sampling).

3.3. Community Models

Tree community-composition responded to environmental context. We found significant effects of sand percentage in all trait-groupings. Biomass predictions for traits groups were, in general, greatly supported by adjacent forest cover data, except for the marginal significance found with wood density. In contrast, soil fertility, alone, was not a good predictor for the share of biomass between species groups. However, the interaction between fertility and sand percentage was highly significant for wood density groups, but unimportant for the others groupings (Table 2.2 and Figure 2.3).

Biomass share between wood density groups was mostly affected through the interaction between soil groups and sand percentage: soft wooded biomass (WD < 0.58 g/cm³) was negatively affected by sand percentage at fertile soils. Between maximum height groups, sand percentage and forest percentage shared a similar importance in being good predictors of biomass increases, especially due to the negative effect of sand percentage on taller trees (Hmax>14m), and the positive effect of forest coverage on shorter trees. Habitat generalists benefited from adjacent forest coverage. Forest specialists, meanwhile, were highly constrained by sand percentages: at fertile soils with low sand percentage, forest specialists are predicted to provide a high contribution to the total biomass (>30%), but this contribution was predicted to decline to 0 once sand was over 55%.

Biomass share between WD groups was not correlated to habitat selectiveness or Hmax ratios. However, a moderate correlation was found between maximum height groups and habitat selectiveness: biomass share from generalist species positively correlated to biomass share from shorter species (Spearman $\rho = 0.525$, $p=0.002$), consequentially the same relation was found between forest specialists and taller species. In addition, significant weak positive correlations were found between total biomass and WD groups (Spearman $\rho = 0.375$, $p=0.035$) and Hmax groups (Spearman $\rho = 0.356$, $p=0.046$), but not between total biomass and the habitat selectiveness group. It is worth mentioning that from the 26 forest-specialists species, 18 are from the taller group, while from the 70 habitat-generalist species, 47 are from the shorter group (see supplementary information Appendix S 1).

Table 2.2 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. Analysis of variance for linear models of biomass share among species groups.

Predictor	*"Global test"*				*Univariate test*					
	Wood density groups (WD)				*WD < 0.58 g/cm³*			*WD > 0.58 g/cm³*		
	Res.Df	val(F)	Pr(>F)		F value	Pr(>F)		F value	Pr(>F)	
Sand %	30	8.100	0.037	*	5.974	0.048	*	2.126	0.153	
forest coverage %	29	7.646	0.035	*	4.796	0.070	·	2.850	0.100	
Soil group	28	2.181	0.350		1.528	0.406		0.653	0.430	
Sand:Soil	27	13.973	0.004	**	13.693	0.003	**	0.279	0.592	
	Maximum height groups (H_{max})				Hmax <14m.			Hmax≥14m.		
	Res.Df	val(F)	Pr(>F)		F value	Pr(>F)		F value	Pr(>F)	
Sand %	30	11.299	0.015	*	2.008	0.167		9.291	0.011	*
forest coverage %	29	10.548	0.018	*	9.287	0.011	*	1.262	0.274	
Soil group	28	0.102	0.946		0.075	0.951		0.028	0.951	
Sand:Soil	27	6.063	0.077	.	3.293	0.151		2.769	0.151	
	Habitat selectiveness groups				*Forest specialists*			*Generalists*		
	Res.Df	val(F)	Pr(>F)		F value	Pr(>F)		F value	Pr(>F)	
Sand %	30	18.730	0.004	**	17.206	0.002	**	1.531	0.223	
forest coverage %	29	6.879	0.047	*	0.829	0.370		6.050	0.040	*
Soil group	28	0.669	0.713		0.241	0.762		0.428	0.762	
Sand:Soil	27	5.962	0.072	.	3.415	0.155		2.546	0.155	

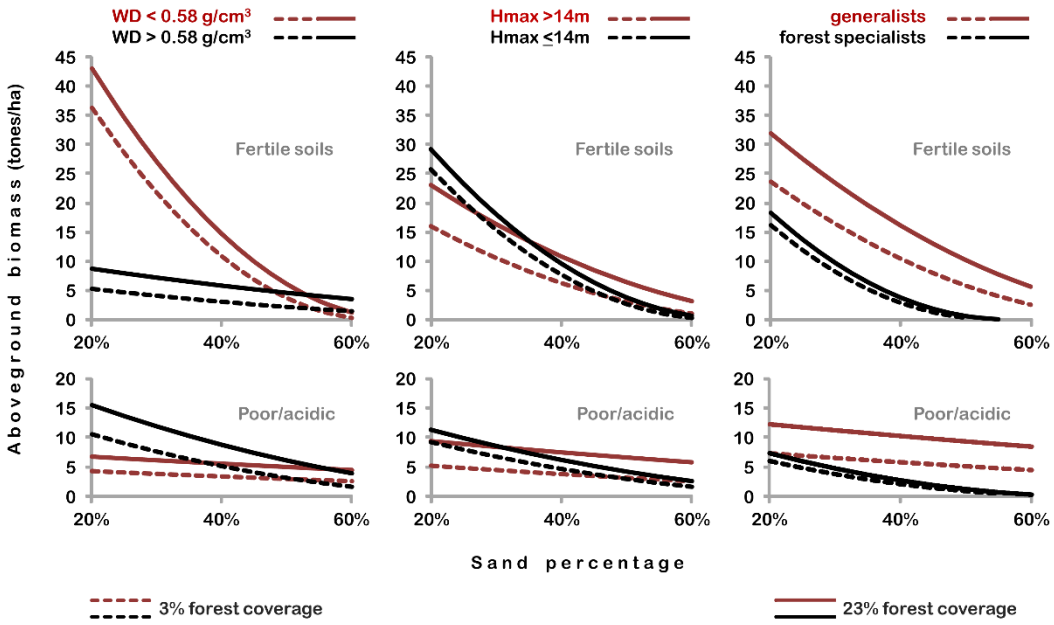

Figure 2.3 AGB as a function of sand percentage with species grouped by wood density, maximum height and habitat selectiveness. Predictions within observed range for two fertility conditions (fertile soils and poor/acidic), and two forest coverage percentages in a 200m buffer (interquartile extremes in our sampling).

4. Discussion

Assessing the varying results from the PRMC restoration program in Brazil, 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 was quite 'open' after five growing seasons, as indicated by an average stem density of 475 trees per hectare with relatively small average tree size (averages: height = 6m, DBH = 11cm). Patterns of community assembly and total AGB were particularly related to the sand content in the soil, and also to surrounding remnant vegetation coverage, both indicative of the previous intensity of agricultural land use. Notably, our results suggest that unfavorable 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). We discuss the role of

environmental drivers in engendering variability in biomass increase and community composition in the light of ecological theory, in the context of how our results can enable successful restoration programs.

4.1. Aboveground Biomass Responses

The average aboveground biomass we observed can be considered relatively poor. Poorter et al. (2016) estimated the average biomass recovery for neotropical secondary forest as 122 ton/ha during 20 years of recovery, with higher biomass yields in the first years, and predictions of biomass uptake above the average for our study region. But most importantly, our study corroborates that important recovery limitations on biomass yields operate at the local scale, given that environmental heterogeneity in soils was correlated with the high variability in biomass we found across and within watersheds. As pointed out by Holl & Zahawi (2014), we found edaphic conditions greatly varying across short distances in a tropical region, and our data also support the short range influence of surrounding habitat patches on recovering sites (de REZENDE et al., 2015; KAUANO et al., 2013; SOUZA et al., 2013): when remaining forest fragments are beyond 200 m from the target site, reductions in community and biomass recovery are apparent. This implies that the targeting of restoration sites requires careful thought, and may need to consist of a staged approach building out from remaining fragments.

The extensive database used by Poorter et al. (2016), indicated strong correlations between AGB increases and water availability, weaker correlations with soil fertility, and no correlation with former land-use and current forest coverage. Holl & Zahawi (2014) detected a minor association between soil nutrient concentrations and biomass variation in recovering tropical forests. However, our model results predict a large difference in biomass between non-sandy fertile soils and non-sandy acidic/poor soils. Holl & Zahawi (2014) also highlights that tree growth both affects and is influenced by soil chemistry. For instance, pH is expected to decrease during forest growth, while organic matter production becomes higher than mineralization with time (HOONAY et al., 2002). On the other hand, edaphic divergence can also be amplified, rather than masked, by regenerating communities. For example, Lebrija-Trejos et al. (2010) observed in Mexican tropical forests that soil matric potential rapidly

accompanied tree density increases. Therefore, long-term assessments, coupled with baseline data, are needed to properly investigate the role of nutrient availability on forest recovery.

Hallett et al. (2014) demonstrated that sandier soils can be favorable for seedling emergence during the rainy season, but during the dry season, sandy soils are associated with much higher seedling mortality due its lower water holding capacity. 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 at al. (2005) found diminishing rainy days correlating to decreasing forest coverage across São Paulo State. At the broader scale, tree mortality and forest die-off intensification has been associated with “hotter drought” (ALLEN et al., 2015). Our findings also suggest that vulnerability may be attenuated at “buffered refugia” if landscape heterogeneity provides climate relicts where trees have cooler-moister conditions. It seems reasonable to assume that hotter drought is intensified by the agricultural matrix in the studied region, and that soil heterogeneity can also amplify or attenuate water shortage. Our results suggest that patches of non-sandy soils are favorable 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 coverage (DE REZENDE et al., 2015; ZAHAWI, et al., 2013; DE LA PEÑA-DOMENE et al., 2014) also 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 coverage and sand percentage, which could indicate climatic buffering. Similarly, we found no significant interaction between forest coverage and soil fertility, showing no evidence of nutrient buffering by lateral diffusion. In this case, it is suggested that the consistent forest coverage effect that we observed is most likely related to biotic connection, e.g. through seed dispersal.

4.2. Tree Community Assemblage

The strong correlations between AGB, species richness, and effective species number exp(H) found in the present study adds weight to the perspective that restoring diversity is important for biomass recovery (Perring et al. 2015a). Nevertheless, unlike biomass, effective species number (eH) and species richness were only significantly affected by the interaction sand:fertility, both are higher in non-sandy fertile soils . However, functional composition, along with tree assemblages, presented some clear responses to environmental variables.

Higher AGB found in favorable environmental conditions (non-sandy, fertile soils and forested surroundings) was not due to the prevalence of hardwood species, which could bring higher coefficients e.g. for wood density, to allometric equations. On the other hand, intrinsic growth rates are highly associated with soft-woods and tall-species among tropical trees (Rüger et al. 2012), which could be a valuable attribute during the early successional stages we surveyed. Softwood species were highly prevalent where ABG was greater, whilst Hmax groups were quite balanced, with, as predicted, a minor dominance of taller species. Biomass share among WD groups also indicated that softer woods are more sensitive to sand percentage, supporting the sand-drought relation, also reflective of lower endurance to drought in soft-wooded species (POORTER & MARKESTEIJN, 2008). However, softwood species were predicted to always be rare at 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, and accordingly, WD and Hmax are expected to be low for fast growing and short lived species given they are light-demanding pioneer tropical trees (WRIGHT et al., 2010). Therefore, in part, our results possibly reflect a temporary pattern, when growth speed is more important to biomass composition than the achievable height or longevity. However, under unfavorable edaphic conditions, lowered contributions from taller and/or soft-wooded species is potentially a persistent pattern, given that the lowered biomass uptake evident under these conditions is still far smaller than expectations for tropical forest succession.

Above ground biomass from moist-forest specialists presented a high sensitivity to sand concentration, and this can be considered particularly challenging for biodiversity conservation, since the pool of species which better represents the restoration target are predicted to disappear in over a fifth of surveyed conditions i.e. where sand percentage was greater than 55%. In addition, the positive effect from forest coverage on tree biomass was only significant for generalist species and small trees. These results suggest that the rarity of moist forest specialists in sandier, and consequently-drier, environments, may be a pattern that persists into the future. It is worth mentioning that smaller species are predominant within the generalist species group, which makes sense in an evolutionary perspective, and so our data are not appropriate to identify distribution differences between these groupings. The lack of an effect of neighbouring forest coverage on moist-forest species presence in target sites may also be due to a regionally impoverished species pool, given local diversity can depend upon regional diversity (RICKLEFS, 1987), and since a large proportion of current Atlantic forest is relatively recent second growth (LIRA et al., 2012). Poor regional diversity, potentially in conjunction with dispersal limitation, implies the surpassing of a biotic threshold for recovery (HOBBS et al., 2009), while the persistence of a weakened presence of endemic old-growth moist forest species on sandy soils would indicate that an abiotic threshold has been surpassed. These ideas require further testing and monitoring.

4.3. Implications For Restoration Planners And Practitioner

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. Opportunely, 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 micro-climate (e.g. windbreaks or buffering woody agriculture) on restoration success. In addition, 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).

Funding is a major concern for forest restoration (HOLL & AIDE, 2011) and financial support from offsetting schemes has proliferated (SUDING 2011, MARON et al., 2012), especially through carbon sequestration initiatives (ALEXANDER, 2011; de GROOT, 2013). However, restoration based offsetting targets involving tropical forests currently have to reflect potential recovery as there are few extant restored systems, due in part to current restoration standards being a recent endeavour (see RODRIGUES et al., 2009). The novel habitats we surveyed demonstrated different paths after very similar implementation, questioning the expectations of certainty associated with offsetting. Our results suggest it is reasonable to presume that without further intervention not all sites will eventually resemble moist forests, nor will they be able to deliver comparable ecosystem services. Our survey also indicates that constraining edaphic and biotical contexts were quite abundant, with severe consequences for ongoing recovery. Therefore, our findings do not support Atlantic Moist Forest recovery as being the mostly likely scenario to follow a tree plantation restoration action in highly modified landscapes.

As a final remark we note that ecological restoration is a human activity in which engagement is indispensable, as advocated by extensive literature (e.g. CHAZDON, 2008; ARONSON et al., 2011; DE GROOT et al., 2013; SUDING, 2015). In this study, we have found that variable recovery results are also related to varying degrees of environmental challenge. In this sense, it is suggested that if social actors are not aware of the strong effect from fine-scale recovery drivers, wrong expectations can threaten the cooperation network.

5. CONCLUSION

We have shown that sandy soils can severely constrain tropical forest restoration, that favorable chemical conditions are highly effective at promoting biomass in non-sandy soils, and that adjacent forest coverage 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 moist forest specialists was particularly sensitive to sand percentage, and AGB from small trees and generalist species was the most positively affected by forest coverage. Notably, moist-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 fertility has been degraded and/or the percentage of sand has increased. Practitioners and policy makers need to carefully determine what are the most appropriate restoration targets in these landscapes to avoid wasted effort and engagement decline due to the perception of failure. When abiotic conditions resemble pristine environments, 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 to the paper

Toledo, R.M. et al. Soil properties and adjacent forest coverage affect aboveground biomass and functional composition during tropical forest restoration.

Appendix S 1 SPECIES LIST, AND SPECIES GROUPING CLASSIFICATION (maximum height, wood density, wide geographical distribution including savannas / moist forest specialists, and genus included/non-included in the plantation list).

Species	Family	H max. group	WD group	Distribution	Plantation list
Aegiphila integrifolia	Lamiaceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Albizia procera	Fabaceae	> 14m	< 0.58 g/cm³	wide	included
Alchornea sidifolia	Euphorbiaceae	> 14m	< 0.58 g/cm³	moist forest	included
Alchornea triplinervia	Euphorbiaceae	> 14m	< 0.58 g/cm³	wide	included
Aloysia virgata	Verbenaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Anadenanthera colubrina	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Anadenanthera peregrina	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Andira fraxinifolia	Fabaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Annona cacans	Annonaceae	> 14m	< 0.58 g/cm³	moist forest	included
Araucaria angustifolia	Araucariaceae	> 14m	< 0.58 g/cm³	moist forest	non-included
Astronium fraxinifolium	Anacardiaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Baccharis dracunculifolia	Asteraceae	≤ 14m	< 0.58 g/cm³	wide	included
Balfourodendron riedelianum	Rutaceae	> 14m	≥ 0.58 g/cm³	wide	included
Bauhinia forficate	Fabaceae	≤ 14m	< 0.58 g/cm³	wide	included
Boehmeria caudate	Urticaceae	≤ 14m	< 0.58 g/cm³	moist forest	non-included
Cabralea canjerana	Meliaceae	> 14m	< 0.58 g/cm³	moist forest	included
Campomanesia xanthocarpa	Myrtaceae	> 14m	≥ 0.58 g/cm³	wide	included
Casearia lasiophylla	Salicaceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Casearia sylvestris	Salicaceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Cecropia hololeuca	Urticaceae	≤ 14m	< 0.58 g/cm³	moist forest	included
Cecropia pachystachya	Urticaceae	≤ 14m	< 0.58 g/cm³	wide	included
Cedrela fissilis	Meliaceae	> 14m	< 0.58 g/cm³	wide	included
Ceiba speciosa	Malvaceae	> 14m	< 0.58 g/cm³	wide	included
Cestrum corymbosum	Solanaceae	≤ 14m	< 0.58 g/cm³	moist forest	non-included
Cestrum intermedium	Solanaceae	≤ 14m	< 0.58 g/cm³	moist forest	non-included
Chromolaena laevigata	Asteraceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Chrysophyllum gonocarpum	Sapotaceae	> 14m	≥ 0.58 g/cm³	wide	non-included
Citharexylum myrianthum	Verbenaceae	> 14m	< 0.58 g/cm³	moist forest	included
Citronella gongonha	Cardiopteridaceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Clethra scabra	Clethraceae	≤ 14m	< 0.58 g/cm³	moist forest	non-included
Cordia ecalyculata	Boraginaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Cordia myxa	Boraginaceae	≤ 14m	< 0.58 g/cm³	wide	non-included
Croton floribundus	Euphorbiaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Croton urucurana	Euphorbiaceae	≤ 14m	< 0.58 g/cm³	wide	included
Dalbergia brasiliensis	Fabaceae	> 14m	≥ 0.58 g/cm³	moist forest	included
Dasyphyllum brasiliense	Asteraceae	> 14m	≥ 0.58 g/cm³	moist forest	non-included
Dendropanax cuneatus	Araliaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Enterolobium contortisiliquum	Fabaceae	> 14m	< 0.58 g/cm³	wide	included
Erythrina cristagalli	Fabaceae	≤ 14m	< 0.58 g/cm³	wide	included
Erythrina falcate	Fabaceae	> 14m	< 0.58 g/cm³	moist forest	included
Erythrina speciosa	Fabaceae	≤ 14m	< 0.58 g/cm³	moist forest	included
Erythrina velutina	Fabaceae	≤ 14m	< 0.58 g/cm³	wide	included
Erythroxylum deciduum	Erythroxylaceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Ficus luschnathiana	Moraceae	> 14m	< 0.58 g/cm³	moist forest	included

Species	Family	H max. group	WD group	Distribution	Plantation list
Genipa Americana	Rubiaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Guatteria australis	Anacardiaceae	≤ 14m	< 0.58 g/cm³	wide	non-included
Guazuma ulmifolia	Malvaceae	> 14m	< 0.58 g/cm³	wide	included
Handroanthus chrysotrichus	Bignoniaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Handroanthus vellosoi	Bignoniaceae	> 14m	≥ 0.58 g/cm³	moist forest	included
Helietta apiculata	Rutaceae	> 14m	≥ 0.58 g/cm³	moist forest	non-included
Heliocarpus popayanensis	Malvaceae	≤ 14m	< 0.58 g/cm³	wide	included
Inga edulis	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Inga laurina	Fabaceae	> 14m	< 0.58 g/cm³	wide	included
Inga sessilis	Fabaceae	> 14m	< 0.58 g/cm³	moist forest	included
Jaracatia spinosa	Caricaceae	> 14m	< 0.58 g/cm³	wide	included
Lafoensia glyptocarpa	Lythraceae	> 14m	≥ 0.58 g/cm³	wide	included
Lafoensia pacari	Lythraceae	> 14m	≥ 0.58 g/cm³	wide	included
Lithraea molleoides	Anacardiaceae	≤ 14m	< 0.58 g/cm³	wide	included
Lonchocarpus cultratus	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Luehea divaricata	Malvaceae	> 14m	< 0.58 g/cm³	wide	included
Machaerium brasiliense	Fabaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Machaerium hirtum	Fabaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Machaerium nyctitans	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Machaerium stipitatum	Fabaceae	> 14m	< 0.58 g/cm³	wide	included
Machaerium villosum	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Maclura tinctoria	Moraceae	> 14m	≥ 0.58 g/cm³	wide	included
Melia azedarach	Meliaceae	> 14m	< 0.58 g/cm³	wide	non-included
Miconia latecrenata	Melastomataceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Miconia sellowiana	Melastomataceae	> 14m	≥ 0.58 g/cm³	wide	non-included
Mimosa bimucronata	Fabaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Moquiniastrum polymorphum	Asteraceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Morus nigra	Moraceae	≤ 14m	< 0.58 g/cm³	wide	non-included
Myrcia hebepetala	Myrtaceae	> 14m	< 0.58 g/cm³	moist forest	non-included
Myrsine coriacea	Myrsinaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Myrsine umbellate	Myrsinaceae	> 14m	≥ 0.58 g/cm³	wide	included
Nectandra grandiflora	Lauraceae	> 14m	≥ 0.58 g/cm³	moist forest	included
Nectandra lanceolata	Lauraceae	> 14m	< 0.58 g/cm³	moist forest	included
Ocotea puberula	Lauraceae	> 14m	< 0.58 g/cm³	wide	non-included
Peltophorum dubium	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Pera glabrata	Euphorbiaceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Piptadenia gonoacantha	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Poecilanthe parviflora	Fabaceae	> 14m	≥ 0.58 g/cm³	moist forest	non-included
Pseudobombax grandiflorum	Malvaceae	> 14m	< 0.58 g/cm³	moist forest	included
Psidium guajava	Myrtaceae	≤ 14m	≥ 0.58 g/cm³	moist forest	included
Pterocarpus violaceus	Fabaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Sapindus saponaria	Sapindaceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Sapium glandulosum	Euphorbiaceae	> 14m	< 0.58 g/cm³	wide	non-included
Schinus terebinthifolius	Anacardiaceae	≤ 14m	< 0.58 g/cm³	wide	included
Schizolobium parahyba	Fabaceae	> 14m	< 0.58 g/cm³	moist forest	included
Sebastiana brasiliensis	Euphorbiaceae	≤ 14m	≥ 0.58 g/cm³	wide	non-included
Senegalia polyphylla	Fabaceae	> 14m	≥ 0.58 g/cm³	wide	included
Senna multijuga	Fabaceae	≤ 14m	≥ 0.58 g/cm³	wide	included
Senna obtusifolia	Fabaceae	≤ 14m	< 0.58 g/cm³	wide	included
Solanum argenteum	Solanaceae	≤ 14m	< 0.58 g/cm³	wide	included
Solanum lycocarpum	Solanaceae	≤ 14m	< 0.58 g/cm³	wide	included
Solanum mauritianum	Solanaceae	≤ 14m	< 0.58 g/cm³	wide	included
Tapirira guianensis	Anacardiaceae	≤ 14m	< 0.58 g/cm³	wide	included
Tecoma stans	Bignoniaceae	≤ 14m	< 0.58 g/cm³	wide	non-included
Tibouchina mutabilis	Melastomataceae	≤ 14m	≥ 0.58 g/cm³	moist forest	included
Tibouchina stenocarpa	Melastomataceae	≤ 14m	≥ 0.58 g/cm³	wide	included

Species	Family	H max. group	WD group	Distribution	Plantation list
Trema micrantha	Cannabaceae	≤ 14m	< 0.58 g/cm³	wide	included
Triplaris Americana	Polygonaceae	> 14m	< 0.58 g/cm³	wide	included
Vernonanthura phosphorica	Asteraceae	≤ 14m	< 0.58 g/cm³	wide	included
Zanthoxylum rhoifolium	Rutaceae	≤ 14m	< 0.58 g/cm³	wide	non-included

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Appendix S 2. Statistics of soil chemical variables within soil groups.

g1 (poor/acidic)

	lowest	Q25	median	Q75	highest
pH (CaCl2 0.01 M)	3.8	4.0	4.2	4.3	4.9
P (mg/dm³)	1.0	2.0	4.0	6.0	37.0
K (mmolc/dm³)	0.2	0.7	1.0	1.5	7.4
Ca (mmolc/dm³)	1.0	4.0	6.0	12.0	24.0
Mg (mmolc/dm³)	1.0	1.0	2.0	3.0	10.0
H + Al(mmolc/dm³)	16.0	54.0	80.0	109.0	228.0
O.M. (g/dm³)	11.0	20.00	28.0	40.0	86.0
Sand (%)	11.6	43.6	51.5	55.3	67.0

g2 (fertile)

	lowest	Q25	Median	Q75	highest
pH (CaCl2 0.01 M)	4.0	4.5	4.8	5.0	6.5
P (mg/dm³)	3.0	6.0	7.0	13.00	77.0
K (mmolc/dm³)	0.5	1.3	1.9	2.7	9.1
Ca (mmolc/dm³)	9.0	18.0	25.0	36.0	79.0
Mg (mmolc/dm³)	4.0	6.0	8.0	15.0	21.0
H + Al(mmolc/dm³)	13.0	36.0	43.0	64.0	94.0
O.M.(g/dm³)	21.0	29.0	37.0	46.0	59.0
Sand (%)	10.1	44.1	50.1	55.105	66.6

Capitulo 3

Fragmentos jovens e florestas antigas, distintos aportes para a restauração de florestas tropicais

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Resumo:

A restauração de florestas tropicais tem sido requisitada em paisagens altamente degradadas pelo uso agropecuário, como forma de reduzir cenários críticos de ameaça à biodiversidade e à oferta de serviços ecossistêmicos. É bastante reconhecido o papel de remanescentes de florestas nativas como fonte da diversidade que alicerça a sucessão ecológica em área degradadas, o que, em tese, permite que uma floresta tropical se desenvolva a partir de um plantio de árvores. Porém, muitas vezes, apenas florestas secundárias resultantes de regeneração recente são encontradas nas proximidades da área a ser restaurada. Neste trabalho investigamos se a restauração florestal estabelecida no contexto de florestas jovens difere do desenvolvimento da restauração florestal próxima à cobertura florestal mais antiga, em estágio sucessional avançado. Com este intuito, selecionamos 27 plantios de restauração com histórico de implantação semelhante, porém em contextos distintos de paisagem, quanto à quantidade (i.e. 0,2% a 49,9%) e idade (i.e. <30 anos ou ≥30 anos) de cobertura florestal remanescente. Nas restaurações selecionadas foram instaladas quatro parcelas para identificação de todas as plantas lenhosas com altura superior a 50 cm, que foram agrupadas como “jovens regenerantes” (DAP<5cm) e “árvores” (DAP≥5cm). Definimos por imagens de satélite a quantidade e a idade da cobertura florestal adjacente a cada parcela num raio de 200m, variáveis que foram então avaliadas como preditoras de diferentes atributos da comunidade regenerante por meio de modelos lineares mistos. Os resultados indicam que em contextos de maior cobertura florestal a regeneração tende a ser mais densa e rica em espécies nas proximidades de florestas com menos de 30 anos, efeito impulsionado por espécies não dispersas por

vertebrados. Porém, estes aumentos de riqueza e densidade não foram verificados em restaurações adjacentes à florestas mais antigas. Por outro lado, a regeneração próxima a fragmentos novos é caracterizada pela menor presença de espécies de sementes grandes e/ou especialistas em florestas úmidas. Nossos resultados indicam que a idade da cobertura florestal próxima é uma variável importante para a restauração florestal, sugerindo prognósticos e recomendações específicos à restauração de localidades desprovidas de florestas maduras em suas adjacências, cenário frequente em paisagens fortemente antropizadas.

Palavras-chaves: Restauração ativa. Fragmentação. Mata Atlântica. Regeneração. Sucessão secundária.

1. INTRODUÇÃO

O desmatamento de florestas tropicais se proliferou em taxas sem precedentes ao longo do século passado (CHAZDON, 2014), e as áreas desmatadas já predominam na maior parte do domínio das florestas tropicais úmidas desde 2005 (ASNER et alt., 2009). Em nível global, a perda de florestas tropicais (HANSEN et al., 2013). Já no Brasil, embora o desmatamento tenha desacelerado, as taxas ainda são elevadas. Entre 2000 e 2013 a taxa de desmatamento foi reduzida de 37.000 Km²/ano para 23.000 Km²/ano (HANSEN, et al., 2013).

O declínio de cobertura florestal primária também implica no aumento de florestas secundárias regenerantes, e esta tendência é altamente associada ao abandono de uso da terra em áreas com baixa aptidão para agropecuária extensiva (ASNER et al., 2009). Atualmente, na maior parte das regiões tropicais, predominam florestas que são fruto de regeneração secundária (CHAZDON, 2014), como se observa na Mata Atlântica (LIRA et al., 2012). Estudos recentes têm ressaltado a importância da regeneração de florestas em paisagens tropicais (CHAZDON & GUARIGUATA, 2016), porém Gibson et al. (2016) demonstra que florestas em regeneração secundária são incapazes de substituir florestas primárias, uma vez que apresentam biodiversidade substancialmente reduzidas.

Programas de restauração florestal e políticas de proteção de habitat têm sido elaborados para a diminuição de riscos relacionados à redução exacerbada de cobertura florestal, como a perda de biodiversidade e a degradação de serviços ecossistêmicos (SUDING, 2011; BRANCALION et al., 2013). A restauração florestal busca reproduzira sucessão secundária em áreas degradadas por meio de diferentes protocolos, que abrangem desde a restauração passiva, focada na remoção de perturbação antrópica, até a manipulação ativa do processo de recuperação (HOLL & AIDE, 2011). Atualmente, a restauração florestal ativa, com o plantio de árvores, é amplamente difundida (LAMB et al., 2005; RODRIGUES et al., 2009), e esta técnica é recomendada em paisagens tropicais severamente desmatadas (MALHI et al., 2014). A restauração passiva e a proteção de habitat é mais efetiva em áreas de maior cobertura florestal, por exemplo com de mais de 20% (BANKS-LEITE et al., 2014). Neste contexto, a restauração florestal tem sido requisitada para remediar paisagens extremamente deficitárias em cobertura florestal. Porém, a ausência de manchas florestais nas adjacências da área em restauração é reconhecidamente uma condição que inibe a recuperação florestal (MATTHEWS 2009; CHAZDON & GUARIGUATA, 2016).

Em áreas de uso agropecuário consolidado, a diversidade local que favorece a recuperação de florestas tropicais é demasiadamente empobrecida, uma vez que as plantas nativas são eliminadas do banco de sementes pela agricultura e pela pecuária (LOPEZ-TOLEDO & MARTINEZ-RAMOS, 2011). Neste sentido, plantações de árvores com alta riqueza de espécies são recomendadas para iniciar o processo de recuperação (LAMB et al., 2005; RODRIGUES et al., 2009), porém a reintrodução de uma parcela relevante da biodiversidade de florestas tropicais não é factível, reforçando a necessidade de conectividade biológica no processo de recuperação (LAMB et al., 2005). É esperado que o crescimento das árvores plantadas inicie a estruturação da floresta, abrigando um sub-bosque crescentemente diverso, combinando os descendentes das árvores plantadas e imigrantes dispersos por comunidades próximas (BRANCALION et al., 2010; BERTACHI et al., 2015; REID et al., 2015)

A recuperação contínua é contingenciada por limitações de dispersão e de recrutamento (FLINN & VELLEND, 2005). A chuva de sementes autóctonas é

moldada pela comunidade vegetal local, enquanto a chegada de propágulos alóctones depende da composição da paisagem, que modera os fluxos entre manchas de habitat, influenciando o fluxo de espécies (TSCHARNTKE et al., 2012). A chuva de sementes arbóreas é mais expressiva em paisagens de maior cobertura de florestal (HOLL, 2007), em particular as plantas que produzem sementes grandes tendem a ser favorecidas pela presença de florestas maduras (REID et al., 2015; LAMB et al., 2005; COSTA et al., 2012). Ainda com relação às limitações de dispersão, a teoria da nucleação prevê que nos contextos de plantios de árvores nativas o crescimento de árvores sobreviventes também favorece a chegada de propágulos (REIS et al., 2010; ZAHAWI, 2013). Já com relação às limitações de recrutamento, a alta mortalidade seguida do crescimento de poucas árvores inibe a sucessão microclimática, reduzindo o estabelecimento e crescimento de indivíduos de espécies típicas de ambientes florestais (HOOPER et al., 2005).

No presente trabalho estudamos a regeneração de plantas lenhosas em vinte e sete plantios de restauração florestal sob diferentes contextos de paisagem, os quais foram implantados com a mesma técnica de plantio e cultivo de mudas de espécies nativas. Investigamos se a regeneração em restaurações próximas a florestas mais antigas se diferencia da regeneração estabelecida nas proximidades de florestas secundárias nativas mais recentes. As nossas hipóteses principais são:

- A regeneração nas restaurações é mais densa e mais rica em espécies quando os fragmentos adjacentes são representados por florestas antigas, e a magnitude deste efeito é moderada pela área de floresta nas adjacências.
- A proximidade de florestas mais antigas, diferentemente de fragmentos jovens, favorece principalmente as sementes dispersas por vertebrados, as espécies especialistas, as de sementes grandes.

2. MÉTODOS

O Projeto de Recuperação de Matas Ciliares (PRMC), coordenado pela Secretaria de Meio Ambiente do Estado de São Paulo representou um marco para as políticas públicas brasileiras de restauração florestal. Esta iniciativa sem

precedentes, em termos de abrangência, incluiu a implantação de mais de 500 áreas demonstrativas de restauração florestal em propriedades rurais voluntárias, distribuídas no eixo Leste a Oeste do Estado de São Paulo. Estas áreas demonstrativas foram implantados por grupos de trabalho regionais que também aprimoraram políticas e fomentaram o engajamento de atores sociais (WUETRICH, 2007; CHAZDON, 2008).

O presente estudo foi realizado em restaurações da porção Leste, localizados dentro dos limites da província geomorfológica e botânica do planalto Atlântico (SCUDELLER et al., 2001), e no contexto da ecorregião das florestas atlânticas da Serra do Mar (OLSON et al., 2001). Apesar da grande variação altimétrica verificada entre as restaurações (i.e. de 550m a 1550m) e do distanciamento relativamente grande entre as microbacias em que se inserem (i.e. até 150Km), a precipitação anual média varia apenas entre 1.400 e 1.900mm, sendo que a duração de meses com precipitação média inferior a 50 mm varia entre 3 e 5 meses (HIJMANS et al., 2005). Os plantios estudados se encontram em microbacias que pertencem aos municípios paulistas de: Cunha, Guaratinguetá, Joanópolis, Nazaré Paulista, Paraibuna e Socorro (Figura 3.1). A expansão agropecuária nesta região do Estado de São Paulo ocorreu no século XIX, promovendo grandes desmatamentos (DEAN, 1991). Atualmente a cobertura do solo é bastante variada, incluindo pastagens, silvicultura, agricultura, manchas urbanas, florestas nativas e reservatórios de água.

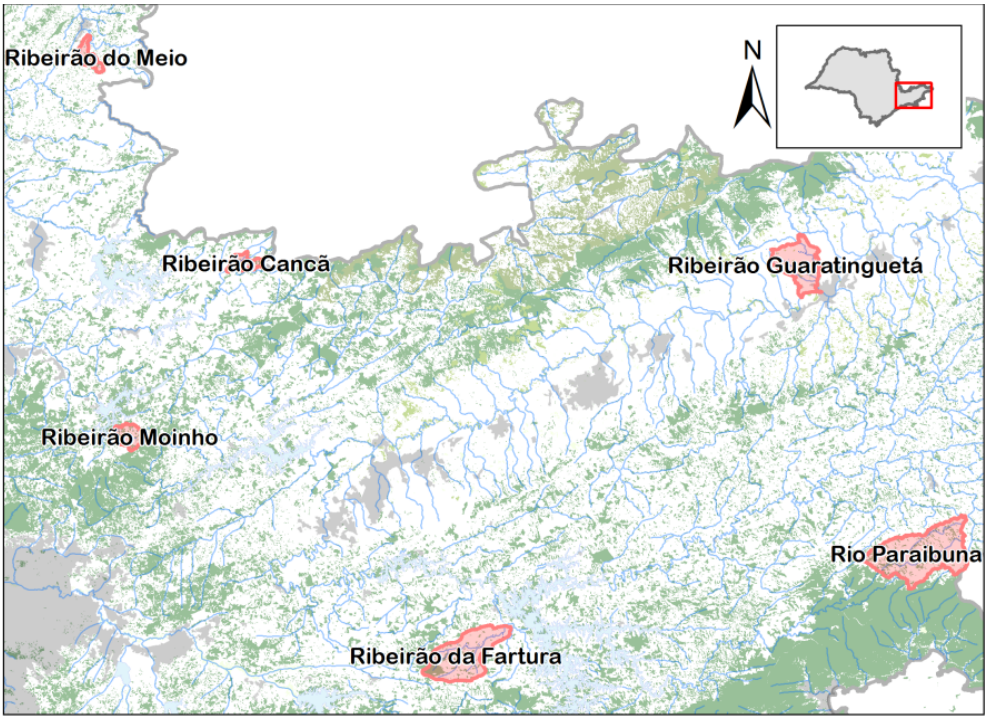

Figura 3.1. Localização das microbacias em que se inserem os plantios de restauração florestal amostrados.

Nós promovemos uma triagem entre os 146 plantios executados pelo PRMC, que primeiramente eliminou restaurações que adotavam outros protocolos que não o plantio sistemático de mudas com alta riqueza de espécies. Ainda utilizando as informações fornecidas pela SMA-SP, foram eliminados todos as restaurações que não fossem estabelecidas sobre campos antrópicos. Em seguida, foram privilegiados os plantios que não apresentassem valores discrepantes (fora da zona interquartil) para as seguintes variáveis: área, relação perímetro/área, altimetria, precipitação e declividade média. Nesta etapa foram utilizadas modelos de altimetria SRTM e modelos climáticos fornecidos pela base WorldClim (HIJMANS, 2005).

Com base nesse conjunto de características, nós selecionamos um grupo de plantios prioritários com distância mínima de um quilômetro entre si. Por fim, foram eliminados as restaurações que não apresentavam qualquer cobertura florestal em seu entorno, considerando uma faixa de 200m. Para esta análise foram utilizadas ortofotos de 2005 (pré-implantação), Com isto a seleção foi concluída com 27 restaurações florestais que foram amostradas pelo presente estudo, sete anos após a implantação.

Em cada restauro florestal selecionado foram instalados quatro parcelas amostrais de 200m^2 posicionadas aleatoriamente. Nestas parcelas todos os indivíduos lenhosos com diâmetro a altura do peito (DAP) maior que cinco centímetros foram contados e identificados em nível de espécie. Para indivíduos de múltiplos fustes a inclusão se deu pela conversão de diâmetros em área, cuja somatória deveria ser superior a 19,2 cm². Ao centro de cada parcela foi instalada outra parcela de 100m^2 na qual foram contados e identificados todos os indivíduos lenhosos com altura superior a 0,50m e DAP< 5cm. Para os indivíduos que não puderam ser identificados em campo, foi coletado material para identificação no ESA Herbarium (Departamento de Biologia, ESALQ-USP). A padronização de nomenclatura seguiu a base de dados “Flora do Brasil 2020”, que adota o sistema APG IV.

Bases de dados botânicos e informações disponíveis na literatura foram utilizadas para classificar as espécies identificadas quanto: à síndrome de dispersão (dispersas por vertebrados / não dispersas por vertebrados), peso das sementes (gramas por semente) e seletividade de habitat (“especialistas” de florestas tropicais / generalistas). A classificação de síndromes de dispersão e peso de sementes foi realizada com a consulta ao SID (Seed Information Database – Kew – Royal Botanic Gardens), Espécies não abrangidas por esta base foram consultadas em Lorenzi (1992) e Lorenzi (1998). Para a identificação das espécies “especialistas” em florestas tropicais úmidas, a distribuição de cada espécie amostrada foi levantada no Global Biodiversity Information Facility Database (GBIF, 2016), e então foi sobreposta com o mapa de ecorregiões terrestres (OLSONET et al., 2001), as espécies que apresentavam registros em hábitat natural não classificado como florestas úmidas foram consideradas como “generalistas”, as demais apresentaram registros na Mata Atlântica, e foram consideradas como “especialistas”.

Foi considerado como paisagem periférica relevante para a restauração a faixa de 200 metros ao redor de cada restauro, de acordo com estudos que apontam que o efeito de vizinhança de florestas tropicais em áreas com restauração ou com regeneração espontânea (KAUANO et al., 2013; SOUZA et al., 2014; REZENDE et al., 2015). Esta faixa foi mapeada para quantificação de cobertura florestal com fotointerpretação de ortofotos de 2005 utilizadas pelo PRMC,

cedidas em resolução de 0.8 metros. Os fragmentos florestais mapeados nesta etapa foram então avaliados quanto à idade da mancha florestal. Para tanto, foi elaborada uma série temporal de imagens NDVI (Normalized Difference Vegetation Index) a partir de imagens do satélite Landsat5 de 1985, 2000 e 2014. O método se baseia numa equação simples NDVI=(NIR-R)/(NIR+R), onde “NIR” representa os valores medidos pelo sensor infravermelho próximo e “R” representa o vermelho visível (ROUSE, 1973). Com a série de NDVIs foi possível verificar quais fragmentos apresentavam valores semelhante a campos antrópicos em alguma das imagens, e outros que apresentavam altos valores consistentes ao longo da séries. Com isto, todas as parcelas foram classificadas em duas classes: as vizinhas a fragmentos densamente vegetados ao longo de toda a série histórica de 30 anos, ou adjacentes a “cobertura florestal antiga”; e as parcelas adjacentes a “cobertura florestal jovem”, parcelas que se avizinhavam apenas a fragmentos que vegetação apresentaram densidade semelhante a de campos antrópicos ao menos em uma das imagens da série histórica.

A análise de dados foi realizada com o programa R.3.2.0. (R Foundation for Statistical Computing, Vienna, AT), os testes estatísticos foram conduzidos por meio de modelos lineares mistos (nlme package, version 3.1-128, R-Core team) em nível de parcelas, considerando-se que estas amostras eram aninhadas por restauração. Foram desenvolvidos seis modelos, que avaliaram os efeitos da paisagem e da comunidade arbórea local sobre a regeneração lenhosa. Estes modelos tiveram como variáveis resposta: (a) Densidade, (b) Riqueza de espécies, (c) Densidade de plantas dispersas por vertebrados, (d) Densidade de plantas não dispersas por vertebrados, (e) Média ponderada pelas abundâncias do peso da semente na comunidade (CWM) e (f) Densidade relativa de espécies especialistas.

Todos os modelos assumiram como variáveis fixas a porcentagem de cobertura florestal e a presença ou ausência de fragmentos antigos num raio de 200 metros a partir da coordenada central da unidade de restauração. A cada modelo também foi adicionada mais uma variável fixa, que representa a medida análoga à variável resposta, porém obtida na comunidade arbórea (DAP>5cm), ou seja: (a) Densidade de árvores, (b) Riqueza de espécies entre as árvores, (c)

Densidade de árvores dispersas por vertebrados, (d) Densidade de espécies não dispersas por vertebrados, (e) CWM- peso de sementes entre as árvores e (f) densidade relativa de espécies especialistas.

Para melhor ajuste, e para satisfazer as premissas do modelo, os CWMs peso de sementes (entre indivíduos DAP≤5cm e entre indivíduos DAP≥5cm) sofreram transformações logarítmicas, e as densidades relativas de espécies especialistas foram transformadas pela raiz quadrada. Duas parcelas que não apresentaram nenhum indivíduo DAP≥5 precisaram ser desconsideradas nestes dois modelos. A correlação entre o CWM de peso de sementes e a densidade relativa de espécies especialistas foi averiguada com o teste de correlação de postos de Spearman.

3. RESULTADOS

No total de parcelas foram contabilizados 1033 indivíduos DAP≥5cm e 3199 indivíduos DAP<5cm (jovens regenerantes). A identificação em nível de espécie foi possível para 927 árvores, totalizando 94 espécies, ao passo que 153 espécies foram verificadas entre os 2833 jovens regenerantes identificados. Considerando todos os indivíduos, foram identificadas 168 espécies ao total. Considerando os indivíduos de ambos os portes, foram identificadas um total de 168 espécies. Avaliou-se que 52,4% dos indivíduos arbóreos são compostos por somente dez espécies, enquanto que as espécies mais abundantes entre os jovens regenerantes representam 54,7% dos indivíduos (dados apresentados no material suplementar)

Das 108 parcelas amostradas, 40 apresentaram vizinhança restrita a fragmentos jovens (regeneração com idades inferiores a 29 anos). Neste grupo a cobertura florestal média foi de 15,3%, variando de 0,02% a 49,9%, já entre as 68 parcelas próximas a fragmentos antigos (com idade superior a 30 anos) a cobertura florestal variou de 0,5% a 41,6%, com média de 18,4% (material suplementar). A participação de jovens regenerantes dispersos por vertebrados foi semelhante entre os dois grupos de restaurações: 55,6% no contexto de cobertura florestal nova e 60% no contexto de cobertura florestal antiga). Notavelmente, nas parcelas em contexto de cobertura florestal antiga o CWM para peso de

sementes apresenta valores semelhantes entre árvores (0,180g por semente) e regenerantes jovens (0,185g por semente), porém nas parcelas próximas a fragmentos novos o CWM para peso de sementes apresentou diferenças expressivas entre árvores e jovens regenerantes (0,238g e 0,077g, respectivamente). Apenas 9,3% das árvores e 7,5% dos jovens regenerantes são de espécies incluídas na categoria de especialistas em restaurações próximas a fragmentos mais novos, enquanto 17,1% das árvores e 13,2% dos jovens regenerantes se incluem no mesmo grupo de espécies nas restaurações próximas a florestas antigas. Verificamos entre os jovens regenerantes correlação positiva fraca entre o CWM do peso de sementes e a densidade relativa de espécies especialistas (Spearman $\rho = 0,190$, $p=0.051$).

Nossos dados não evidenciam associação entre a densidade de regenerantes jovens com a densidade de árvores, tão pouco com a quantidade ou idade da cobertura florestal adjacente. Porém, foi verificado o efeito significativo da interação entre a idade da cobertura florestal e a densidade da cobertura florestal (Tabela 3.1), uma vez que a densidade crescente da regeneração dos plantios foi verificada somente em contexto de cobertura florestal adjacente nova (Figura 3.1a). Esta interação também foi significativa para a riqueza de espécies, uma vez que o incremento da riqueza de espécies em paisagens mais florestadas também se restringe às restaurações localizadas em contexto florestal recente (Tabela 3.1 e Figura 3.2). No entanto, neste caso foi verificada correlação entre a riqueza de espécies regenerantes e a riqueza de espécies arbóreas (Tabela 3.1).

Em relação a densidade de indivíduos de espécies dispersas por vertebrados não foi verificada correlação significativa com os preditores avaliados (Tabela 3.1). Já a densidade de jovens regenerantes de espécies não dispersas por vertebrados apresentou efeito significativo da interação entre idade e quantidade de cobertura florestal Adjacente. Neste caso a cobertura florestal se mostrou positivamente associada com a densidade de espécies não-dispersas por vertebrados em restaurações localizadas sob contexto de cobertura florestal nova, o oposto foi verificado para restaurações em paisagens de cobertura florestal antiga (Tabela 3.1 e Figura 3.3).

Tabela 3.1. Efeito da taxa de cobertura florestal, da idade da cobertura florestal e da comunidade arbórea (DAP>5cm), sobre (a) densidade total de regenerantes por parcela, (b) riqueza de espécies de regenerantes, (c) densidade de regenerantes dispersos por vertebrados, e (d) não dispersos por vertebrados.

resposta (DAP<5cm)	variáveis fixas	denDF	F-value	p-value	
a. densidade	a.taxa de cobertura florestal	78	0,0009	0,9757	
	b.idade do fragmento	25	0,0000	0,9995	
	c. abundância (DAP≥5cm)	78	0,9136	0,3421	
	d. interação a:b - cobertura e idade	78	5,8157	0,0182	*
b. riqueza de espécies	a.taxa de cobertura florestal	78	0,8510	0,3591	
	b.idade do fragmento	25	0,1114	0,7413	
	e. riqueza de espécies (DAP≥5cm)	78	11,7142	0,0010	**
	d. interação a:b - cobertura e idade	78	7,3706	0,0082	**
c. densidade de dispersos por vertebrados	a.taxa de cobertura florestal	78	3,8598	0,0530	.
	b.idade do fragmento	25	0,0617	0,8059	
	g. abundância de dispesas por vertebrados (DAP≥5cm)	78	0,0619	0,8042	
	d. interação a:b - cobertura e idade	78	0,9525	0,3321	
d. densidade de não dispersos por vertebrados	a.taxa de cobertura florestal	78	0,6228	0,4324	
	b.idade do fragmento	25	0,0884	0,7687	
	f. abundância de não dispesas por vertebrados (DAP≥5cm)	78	3,4926	0,0654	.
	d. interação a:b - cobertura e idade	78	7,0478	0,0096	**

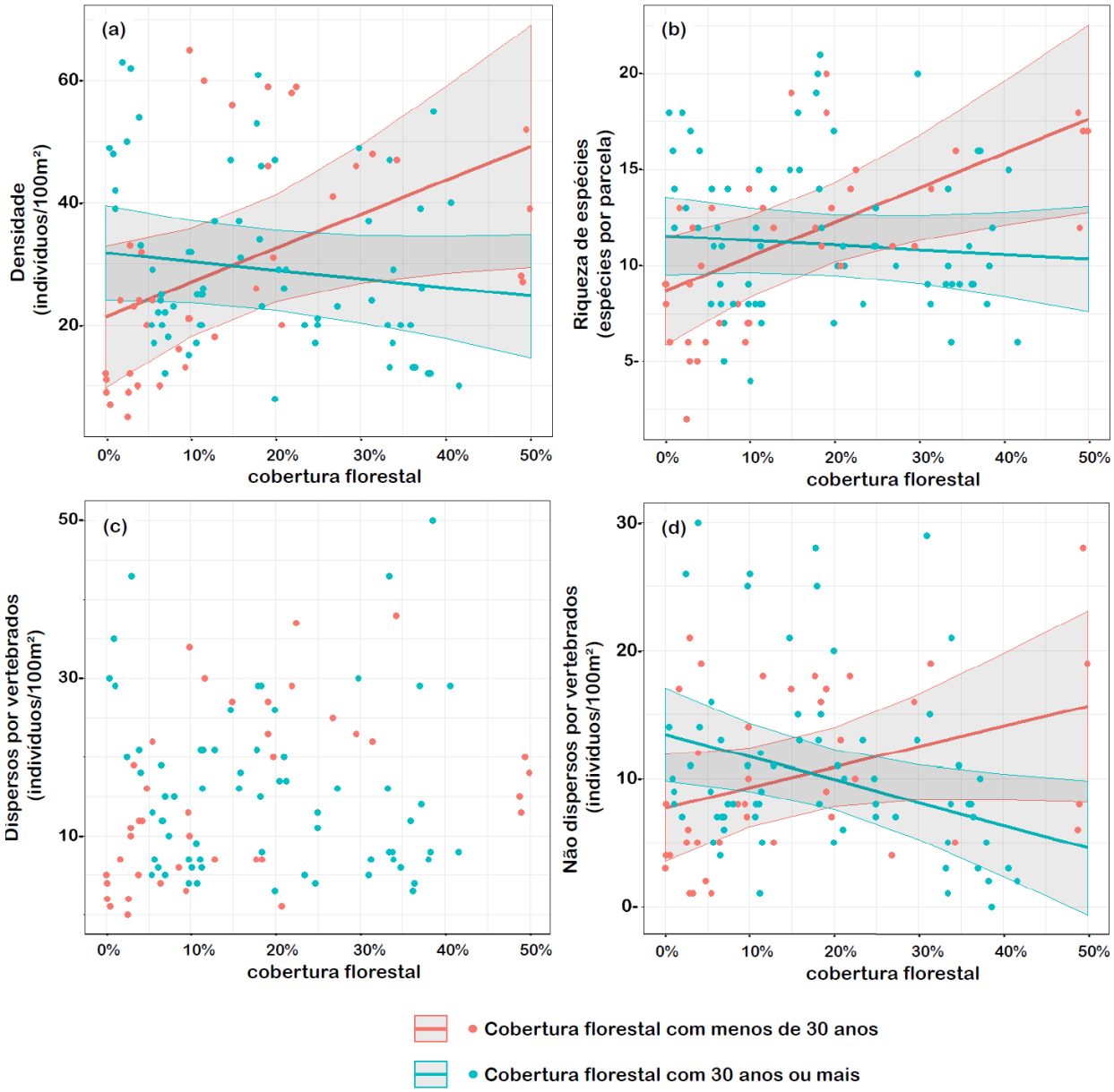

Figura 3.2. Características de regenerantes em função da cobertura florestal e idade (a) densidade total de regenerantes por parcela, (b) riqueza de espécies de regenerantes, (c) densidade de regenerantes dispersos por vertebrados, e (d) não dispersos por vertebrados;. As linhas mostram predições dos modelos (cf. Tabela 1) e intervalo de confiança de 95%, exceto para densidade de indivíduos dispersos por vertebrados, que não apresentou qualquer correlação significativa. As projeções foram realizadas fixando-se a variável que representa a comunidade arbórea pela mediana observada entre as árvores ((a) densidade = 7,5 árvores por parcela, (b) riqueza = 5 espécies e (c) densidade de não dispersos por vertebrados = 3 árvores)

O peso médio de sementes ponderado pela abundância relativa (CWM) entre jovens regenerantes não foi afetado significativamente pela taxa de cobertura florestal, mas se mostrou fortemente correlacionado com o CWM de peso de sementes da comunidade arbórea e com a idade da cobertura florestal, apresentando maior presença de sementes maiores e mais pesadas provenientes de cobertura florestal mais antiga (Tabela 3.2 e Figura 3.3). Já a

densidade relativa de espécies jovens regenerantes especialistas se mostrou fortemente correlacionada com a idade da cobertura florestal adjacente e, significativamente correlacionada com a densidade relativa de árvores especialistas.

Tabela 3.2 Efeito da taxa de cobertura florestal, da idade da cobertura florestal e da comunidade arbórea (DAP>5cm), em nível de parcelas, sobre (e) Peso da semente (CWM)`e (f) Densidade relativa de especialistas em florestas úmidas

resposta (DAP<5cm)	variáveis fixas	denDF	F-value	p-value	
e. CWM peso de sementes	a.taxa de cobertura florestal	76	26.612	0.1070	
	b.idade do fragmento	25	43.770	0.0467	*
	c.CWM peso de sementes (DAP≥5cm)	76	123.720	0.0007	***
	d. interação a:b - cobertura e idade	76	0.3478	0.5571	
f. desidade relativa de especialistas em florestas umidas	a.taxa de cobertura florestal	76	215.523	0.1462	
	b.idade do fragmento	25	858.238	0.0071	**
	h. dens. Rel. de especialistas (DAP≥5cm)	76	457.556	0.0356	*
	d. interação a:b - cobertura e idade	76	0.81774	0.3687	

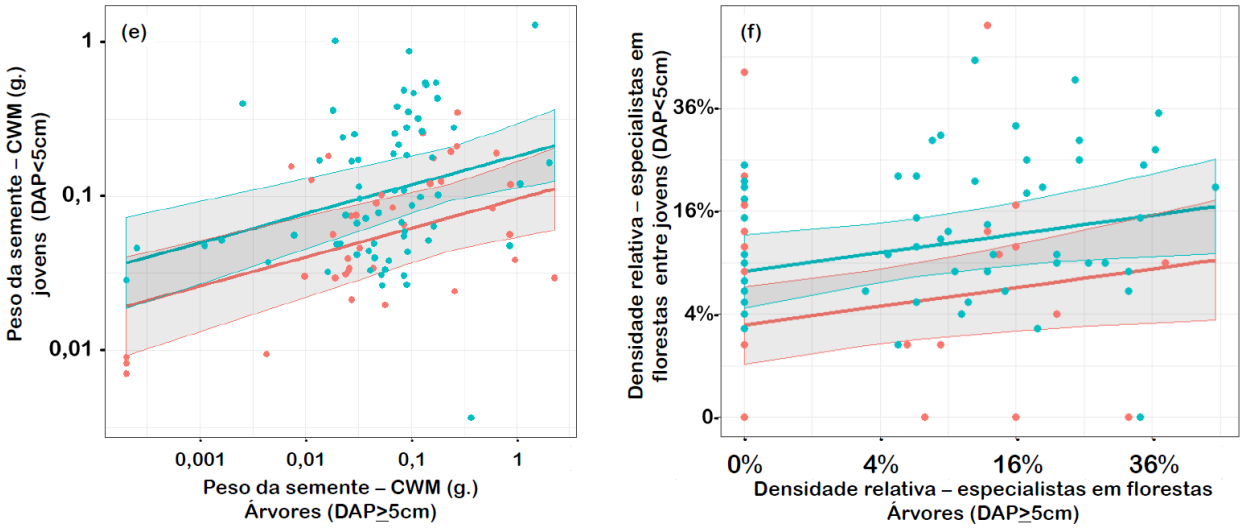

Figura 3.3. (e) Peso da semente (CWM) entre indivíduos jovens em função do peso da semente entre árvores e da idade da cobertura florestal, em nível de parcela. (f) Densidade relativa de especialistas em florestas úmidas entre indivíduos jovens em função da densidade relativa de especialistas em florestas úmidas entre árvores, em nível de parcelas. Ambos os gráficos apresentam dados observados (pontos), predições dos modelos (linhas) e respectivos intervalos de confiança de 95%. As projeções consideram cobertura florestal fixa de 13,7% (mediana entre as parcelas amostradas).

4. Discussão

Apesar das grandes diferenças verificadas entre as restaurações, os resultados totais indicam avanços processo de recuperação, uma vez que identificamos um número expressivo de espécies lenhosas (i.e. 168 espécies), e a densidade média de indivíduos lenhosos foi maior que o dobro da densidade dos plantios (i.e 3340 indivíduos por hectare, dos quais 448 apresentaram DAP $\geq$ 5 cm). Porém, a densidade e a riqueza variaram bastante entre parcelas (Figura 3.3).

Os modelos avaliados indicam que a interação entre idade da cobertura florestal e a quantidade de floresta adjacente afeta a densidade e a riqueza de espécies do estrato regenerante, uma vez que coberturas florestais maiores levaram à maior discrepância entre restaurações em contextos de coberturas florestais de diferentes idades, padrão favorecido por espécies não dispersas por vertebrados. Também verificamos que a composição da comunidade regenerante responde às caraterísticas da comunidade arbórea sob a qual se escabece sob dois aspectos: o peso de sementes e a especialização às florestas úmidas, variáveis que também foram afetadas pela idade da cobertura florestal. Contudo também observamos que a formação do estrato regenerante é um processo complexo, no qual os preditores avaliados não apresentaram o efeito esperado em muitos dos casos.

Em especial, a densidade de indivíduos dispersos por vertebrados e o efeito da quantidade de florestas mais antigas não apresentaram qualquer padrão na escala estudada. Os dados analisados indicam que a vizinhança de florestas novas é mais eficaz no incremento de densidade de riqueza de espécies e de densidade de indivíduos regenerantes no início do processo de restauração. Entretanto, a distribuição do peso das sementes e a participação das espécies “especialistas” sugerem que a composição da regeneração em ações próximas às florestas jovens é funcionalmente estreitada em relação à regeneração verificada em restaurações contextualizadas em cobertura florestal antiga.

Nossa primeira hipótese é frontalmente refutada pelos resultados: a regeneração não apresentou incremento na densidade, ou na riqueza de espécies, quando as florestas adjacentes são representadas por florestas mais antigas, e potencialmente mais avançadas quanto à sucessão florestal. Em grande parte,

a constatação de que, separadamente, a quantidade e a idade da cobertura florestal não foram bons preditores de densidade e riqueza de espécies, reflete a ausência de padrão observado para espécies dispersas por vertebrados (tabela 1, figura 3c), que representam a maior parte dos regenerantes.

Sobre o limitado desempenho da idade da cobertura florestal adjacente como preditora de densidade e riqueza de espécies, cabe considerar que florestas maduras tendem a regredir na sucessão de espécies por efeito da fragmentação (TABARELI et al., 2007). Desta forma, parte dos fragmentos aqui classificados como antigos, podem apresentar comunidades semelhantes às pioneiras, por estarem expostas à elevada fragmentação por um período prolongado. Cabe também ressaltar que avaliamos o produto da fase inicial da restauração, em áreas que eram campos antrópicos apenas oito anos antes da amostragem. Com isto, é possível que padrões não evidenciados na nossa amostragem sejam detectáveis futuramente. Já com relação ao desempenho limitado da quantidade de florestas adjacentes como preditora, Reid et al. (2015) sugere que a chuva de sementes também é influenciada por árvores isoladas e outras fontes não florestais. E de fato, verificamos indivíduos arbóreos isolados em todas as faixas adjacentes mapeadas para as parcelas. Este estudo realizado na Costa Rica, não evidenciou efeito da cobertura florestal (raios de 100 e 500 metros) sobre a chuvas de sementes em restaurações florestais. Nos domínios da Mata Atlântica, Pereira et al. (2013) não verificaram efeito direto da cobertura florestal (raios de 500 m e 1000 m) sobre a densidade e a riqueza de espécies em restaurações florestais e sugerem que fatores não controlados, como a defaunação e degradação das manchas florestais podem ter interferido substancialmente a regeneração. Assim, é possível que efeitos pronunciados da cobertura florestal fossem evidenciados, caso a classificação da cobertura florestal do presente trabalho fosse realizada com dados de vegetação, e se tivéssemos estudado paisagens em que os campos antrópicos fossem desprovidas de espécies lenhosas.

A segunda hipótese, centrada na composição da comunidade regenerante foi parcialmente corroborada pelos nossos resultados, uma vez que não verificamos nenhuma associação entre a densidade de indivíduos dispersos por vertebrados e os preditores avaliados. Por outro lado, a teoria ecológica prevê que a

diversidade local expressa sua dependência à diversidade regional (RICKLEFS, 1987) e ao pool de espécies da paisagem (TSCHARNRTKEET et al., 2012). De fato, a proximidade de florestas mais antigas favoreceu “especialistas”, que são as espécies que melhor representam as florestas maduras, que por sua vez é o habitat referencial objetivado pelos projetos de restauração. Também é previsto que os estágios iniciais da sucessão florestal são fortemente associados à dominância de espécies de sementes pequenas, as quais produzem grandes quantidades de sementes; enquanto grandes sementes promovem plântulas robustas e competitivas em condições sombreadas típicas de florestas maduras (FOSTER & JANSON, 1985; LOHBECK et al., 2015). Em acordo com estas predições, as restaurações estudadas evidenciaram que as espécies com sementes de maior massa, em geral relacionadas à dispersores de maior porte e mais ameaçados pela defaunação (GALLETI et al., 2013), foram mais presentes no contexto de florestas potencialmente mais maduras.

Vale ressaltar que a densidade de regenerantes não apresentou associação com a densidade de árvores, como era esperado, já que a variação de abundância de árvores afetaria a moderação de processos como: a chegada de propágulos pela matriz, a chuva de sementes local, o estabelecimento de herbáceas invasoras e o recrutamento de plântulas (HOOPER et al., 2005; BRANCALION et al., 2010; REIS et al., 2010; BERTACHI et al., 2016). Ainda assim, os dados sugerem que há transferência de atributos da comunidade arbórea para a comunidade regenerante não apenas pela associação entre riqueza de espécies, mas também quanto à composição da comunidade, como apontado pelo CMW e pela densidade relativa de espécies especialistas. É bastante razoável assumirmos que a composição da regeneração que ocorre em plantios de restauração terá como fontes de diversidade a matriz antropizada (LOPEZ-TOLEDO & MARTINEZ-RAMOS, 2011), as manchas de habitat natural ou semi-natural nas proximidades (REIS et al., 2010) e as próprias espécies plantadas (BRANCALION et al., 2010). No caso das restaurações que amostramos, ao seu oitavo ano, a influência da comunidade arbórea estabelecida no plantio, ou logo após, ainda se mostrou forte. Indivíduos ingressantes vindos de comunidades adjacentes não desacoplar a comunidade regenerante da comunidade arbórea

estabelecida, e isto sugere prolongada persistência das espécies inicialmente estabelecidas.

Segundo Suding (2011), a comparação entre restaurações com históricos de implantação semelhantes pode evidenciar a presença de obstáculos a recuperação, como os relacionados à paisagem e ao contexto histórico em que se inserem. Estes dados podem ser fundamentais para tomada de decisões sobre o grau de intervenção necessário e a avaliação de se as metas estabelecidas para a recuperação de uma área são factíveis. Neste sentido, os nossos resultados reforçam que as políticas de restauração devem considerar o papel fundamental que a cobertura vegetal adjacente tem para restauração, uma vez que as comunidades periféricas ao restauro afetam a regeneração, levando à composições alternativas. Porém a previsão do efeito de vizinhança de florestas sobre a restauração é complexa, conforme destacado por Reid et al. (2015), assim, a identificação de um limiar de cobertura florestal, abaixo do qual a regeneração seria severamente afetada, ainda se apresenta como um grande desafio a ser superado. Porém, dificuldade em se prever os efeitos da quantidade de florestas adjacentes tende a se ampliar no futuro, particularmente quando a avaliação de contexto de paisagem for baseada em sensoriamento remoto, assim como o presente trabalho, uma vez que estudos baseados em imagens de satélite têm evidenciado a ampliação localizada de cobertura florestal em paisagens antrópicas (e.g. LIRA et al., 2012, REZENDE et al., 2015, RUDEL et al., 2016), enquanto estudos baseados em dados biológicos destacam a redução de biodiversidade nos remanescentes florestais (eg. TABARELI 2008, PARDINI et al., 2012).

Nossos resultados também reforçam que o sucesso parcial na restauração de florestas tropicais é uma perspectiva que tende a ser recorrente, em especial quando os fragmentos adjacentes são formados por regeneração recente, como evidenciamos com a formação de comunidades onde plantas de sementes grandes e/ou mais espécies especializadas são mais raras quando não ocorrem florestas antigas nas adjacências da restauração em curso. Isto indica que o desafio de reproduzir a biodiversidade em níveis pré-desmatamento é ainda maior sob estas condições. No entanto, esta limitação pode ser minimizada na escolha das espécies a serem plantadas, que como observamos podem ser

persistentes na dinâmica da comunidade em restauração, reforçando a crescentemente valorizada importância dos plantios em de alta diversidade (RODRIGUES et al., 2009), e da concentração de esforços em grupos mais sensíveis à degradação e à fragmentação.

5. CONCLUSÃO

Nossos resultados reforçam que a restauração é expressivamente afetada pela cobertura florestal adjacente, portanto, sua proteção deve ser considerada como um passo fundamental em programas de restauração. A proximidade com florestas mais jovens favorece um recobrimento mais rápido, impulsionado por espécies não dispersas por vertebrados, característica potencialmente oportuna quando o objetivo é voltado à ampliação de cobertura florestal, mas não prioriza a biodiversidade e serviços advindos dela. Neste caso, o incremento da diversidade dependerá substancialmente da seleção inicial de espécies plantadas, de forma a minimizar as tendências impostas pela paisagem. Por sua vez, a proximidade com florestas mais maduras tende a favorecer uma recuperação mais lenta em termos da densidade indivíduos lenhosos, mas é potencialmente mais abrangente ao incluir as espécies especialistas em habitat florestal e as de sementes maiores, resultando em uma trajetória mais promissora aos objetivos de programas de restauração que priorizam a proteção à biodiversidade.

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Material Suplementar

MS 1. Espécies amostradas, a classificação quanto a ocorrência restrita a florestas tropicais úmidas, peso médio das sementes, classificação quanto à síndrome de dispersão, número de indivíduos identificados com DAP≥5cm e número de indivíduos identificados com DAP<5cm.

Família	Espécie	Habitat	mg./semente	Dispersão	DAP≥5cm	DAP<5cm
Anacardiaceae	*Astronium fraxinifolium*	generalistas	31,7	non-vertebrate	1	2
Anacardiaceae	*Astronium graveolens*	generalistas	29	non-vertebrate	0	1
Anacardiaceae	*Lithrea molleoides*	generalistas	47,6	vertebrate	1	1
Anacardiaceae	*Schinus terebinthifolia*	generalistas	18,1	vertebrate	49	155
Anacardiaceae	*Tapirira guianensis*	generalistas	26	vertebrate	1	1
Annonaceae	*Annona cacans*	especialistas	186,2	vertebrate	2	7
Annonaceae	*Guatteria australis*	generalistas	1,6	vertebrate	2	1
Apocynaceae	*Aspidosperma olivaceum*	especialistas	200	non-vertebrate	0	1
Apocynaceae	*Tabernaemontana catharinensis*	generalistas	147,1	vertebrate	0	9
Araliaceae	*Dendropanax cuneatus*	generalistas	5,9	vertebrate	1	0
Araucariaceae	*Araucaria angustifolia*	especialistas	6666,7	vertebrate	3	5
Arecaceae	*Euterpe edulis*	especialistas	1298,7	vertebrate	0	11
Arecaceae	*Syagrus romanzoffiana*	generalistas	7142,9	vertebrate	0	6
Asteraceae	*Baccharis dracunculifolia*	generalistas	0,2	non-vertebrate	48	248
Asteraceae	*Chromolaena laevigata*	generalistas	0,3	non-vertebrate	27	42
Asteraceae	*Dasyphyllum spinescens*	generalistas	0,5	non-vertebrate	0	3
Asteraceae	*Dasyphyllum brasiliense*	especialistas	0,5	non-vertebrate	5	0
Asteraceae	*Gochnatia polymorpha*	generalistas	0,5	non-vertebrate	1	5
Asteraceae	*Vernonanthura phosphorica*	generalistas	1,6	non-vertebrate	19	203
Bignoniaceae	*Cybistax antisyphilitica*	generalistas	36,01	non-vertebrate	0	1
Bignoniaceae	*Handroanthus chrysotrichus*	generalistas	11,6	non-vertebrate	1	1

Família	Espécie	Habitat	mg./semente	Dispersão	DAP≥5cm	DAP<5cm
Bignoniaceae	*Jacaranda mimosifolia*	generalistas	11,7	non-vertebrate	0	1
Bignoniaceae	*Handroanthus ochraceus*	generalistas	13,9	non-vertebrate	0	3
Bignoniaceae	*Handroanthus serratifolius*	generalistas	125	non-vertebrate	0	2
Bignoniaceae	*Tecoma stans*	generalistas	6,9	non-vertebrate	1	1
Bixaceae	*Bixa orellana*	generalistas	25	vertebrate	0	1
Boraginaceae	*Cordia ecalyculata*	generalistas	185,2	vertebrate	4	0
Boraginaceae	*Cordia myxa*	generalistas	492,6	vertebrate	15	13
Boraginaceae	*Cordia superba*	generalistas	303	vertebrate	0	4
Calophyllaceae	*Calophyllum brasiliense*	generalistas	6250	vertebrate	0	1
Cannabaceae	*Trema micrantha*	generalistas	7	vertebrate	8	3
Cardiopteridaceae	*Citronella gongonha*	generalistas	90,9	vertebrate	3	16
Caricaceae	*Jaracatia spinosa*	generalistas	34,8	vertebrate	1	0
Celastraceae	*Maytenus aquifolia*	especialistas	294,1	vertebrate	0	1
Celastraceae	*Maytenus gonoclada*	generalistas	13,5	vertebrate	0	3
Clethraceae	*Clethra scabra*	generalistas	0,25	non-vertebrate	2	2
Ebenaceae	*Diospyros inconstans*	generalistas	421,9	vertebrate	0	2
Ericaceae	*Gaylussacia brasiliensis*	generalistas	sem dado	vertebrate	0	7
Erythroxylaceae	*Erythroxylum deciduum*	generalistas	100	vertebrate	0	2
Euphorbiaceae	*Alchornea glandulosa*	generalistas	51,3	vertebrate	0	1
Euphorbiaceae	*Alchornea sidifolia*	especialistas	52	vertebrate	3	23
Euphorbiaceae	*Alchornea triplinervia*	generalistas	54,1	vertebrate	2	11
Euphorbiaceae	*Croton floribundus*	generalistas	40,2	non-vertebrate	47	89
Euphorbiaceae	*Croton urucurana*	generalistas	8,3	non-vertebrate	83	99
Euphorbiaceae	*Pera glabrata*	generalistas	19,6	vertebrate	2	3
Euphorbiaceae	*Sapium glandulatum*	generalistas	34	vertebrate	12	39
Euphorbiaceae	*Sebastiana brasiliensis*	generalistas	17,2	non-vertebrate	9	22

Família	Espécie	Habitat	mg./semente	Dispersão	DAP≥5cm	DAP<5cm
Fabaceae	*Albizia procera*	generalistas	36	non-vertebrate	3	0
Fabaceae	*Anadenanthera colubrina*	generalistas	142	non-vertebrate	8	10
Fabaceae	*Anadenanthera peregrina*	generalistas	116,3	non-vertebrate	3	0
Fabaceae	*Andira fraxinifolia*	generalistas	14285	vertebrate	4	1
Fabaceae	*Bauhinia forficata*	generalistas	206,5	non-vertebrate	31	40
Fabaceae	*Libidibia ferrea*	generalistas	120,5	non-vertebrate	0	2
Fabaceae	*Copaifera langsdorffii*	generalistas	581,4	vertebrate	0	2
Fabaceae	*Dalbergia brasiliensis*	especialistas	43,5	non-vertebrate	5	3
Fabaceae	*Dalbergia frutescens*	generalistas	162,7	non-vertebrate	0	5
Fabaceae	*Endlicheria paniculata*	generalistas	1298,7	vertebrate	0	1
Fabaceae	*Enterolobium contortisiliquum*	generalistas	253	vertebrate	18	4
Fabaceae	*Erythrina cristagalli*	generalistas	372,8	non-vertebrate	3	2
Fabaceae	*Erythrina falcata*	generalistas	166,6	vertebrate	3	0
Fabaceae	*Erythrina speciosa*	especialistas	175,4	non-vertebrate	4	2
Fabaceae	*Hymenaea courbaril*	generalistas	3678	vertebrate	0	4
Fabaceae	*Inga edulis*	generalistas	539	vertebrate	5	1
Fabaceae	*Inga laurina*	generalistas	200	vertebrate	9	19
Fabaceae	*Inga sessilis*	especialistas	1030	vertebrate	10	7
Fabaceae	*Leucochloron incuriale*	especialistas	12,7	non-vertebrate	0	2
Fabaceae	*Lonchocarpus cultratus*	generalistas	sem dado	non-vertebrate	1	14
Fabaceae	*Dahlstedtia muehlbergiana*	generalistas	943,4	non-vertebrate	0	35
Fabaceae	*Machaerium brasiliense*	generalistas	137	non-vertebrate	1	0
Fabaceae	*Machaerium hirtum*	generalistas	250	non-vertebrate	0	1
Fabaceae	*Machaerium nyctitans*	generalistas	192,3	non-vertebrate	57	50
Fabaceae	*Machaerium stipitatum*	generalistas	158,7	non-vertebrate	16	35
Fabaceae	*Machaerium villosum*	generalistas	476,2	non-vertebrate	6	4

Família	Espécie	Habitat	mg./semente	Dispersão	DAP≥5cm	DAP<5cm
Fabaceae	*Mangifera indica*	generalistas	16466	vertebrate	0	1
Fabaceae	*Mimosa bimucronata*	generalistas	9,5	non-vertebrate	18	37
Fabaceae	*Mimosa scabrella*	especialistas	9,8	non-vertebrate	0	2
Fabaceae	*Myroxylon peruiferum*	generalistas	285	non-vertebrate	0	2
Fabaceae	*Ormosia arborea*	generalistas	1250	vertebrate	0	1
Fabaceae	*Peltophorum dubium*	generalistas	197,4	non-vertebrate	3	18
Fabaceae	*Piptadenia gonoacantha*	generalistas	42,3	non-vertebrate	3	1
Fabaceae	*Platycyamus regnellii*	generalistas	555,6	non-vertebrate	0	1
Fabaceae	*Poecilanthe parviflora*	especialistas	588,23	non-vertebrate	0	2
Fabaceae	*Schizolobium parahyba*	especialistas	954,4	non-vertebrate	2	0
Fabaceae	*Senegalia polyphylla*	generalistas	104,2	non-vertebrate	14	14
Fabaceae	*Senna multijuga*	generalistas	7,1	non-vertebrate	3	8
Lamiaceae	*Aegiphila integrifolia*	generalistas	3	vertebrate	4	3
Lauraceae	*Nectandra grandiflora*	especialistas	769,2	vertebrate	1	3
Lauraceae	*Nectandra lanceolata*	especialistas	1020,4	vertebrate	6	28
Lauraceae	*Nectandra oppositifolia*	especialistas	769,2	vertebrate	0	2
Lauraceae	*Ocotea puberula*	generalistas	333,3	vertebrate	1	0
Lecythidaceae	*Cariniana estrellensis*	generalistas	83,3	non-vertebrate	0	1
Loganiaceae	*Strychnos brasiliensis*	generalistas	sem dado	vertebrate	0	7
Lythraceae	*Lafoensia glyptocarpa*	generalistas	24,4	non-vertebrate	1	0
Lythraceae	*Lafoensia pacari*	generalistas	25,6	non-vertebrate	1	7
Magnoliaceae	*Magnolia champaca*	generalistas	198	vertebrate	0	1
Magnoliaceae	*Magnolia ovata*	generalistas	250	vertebrate	0	3
Malvaceae	*Abutilon regnelli*	generalistas	sem dado	non-vertebrate	0	3
Malvaceae	*Apeiba tibourbou*	generalistas	11	vertebrate	0	2
Malvaceae	*Ceiba speciosa*	generalistas	57,7	non-vertebrate	12	5

Família	Espécie	Habitat	mg./semente	Dispersão	DAP≥5cm	DAP<5cm
Malvaceae	*Guazuma ulmifolia*	generalistas	47	vertebrate	23	16
Malvaceae	*Heliocarpus popayanensis*	generalistas	163	non-vertebrate	3	2
Malvaceae	*Luehea divaricata*	generalistas	3,8	non-vertebrate	17	23
Malvaceae	*Pseudobombax grandiflorum*	especialistas	54,2	non-vertebrate	4	2
Melastomataceae	*Miconia latecrenata*	generalistas	sem dado	vertebrate	2	45
Melastomataceae	*Miconia pusilliflora*	especialistas	sem dado	vertebrate	0	13
Melastomataceae	*Miconia sellowiana*	generalistas	sem dado	vertebrate	5	18
Melastomataceae	*Pleroma heteromalla*	generalistas	sem dado	non-vertebrate	0	26
Melastomataceae	*Pleroma mutabilis*	especialistas	0,3	non-vertebrate	1	8
Melastomataceae	*Pleroma stenocarpa*	generalistas	sem dado	non-vertebrate	2	3
Meliaceae	*Cabralea canjerana*	especialistas	980	vertebrate	1	8
Meliaceae	*Cedrela fissilis*	generalistas	47,6	non-vertebrate	4	6
Meliaceae	*Guarea guidonia*	generalistas	127	vertebrate	0	1
Meliaceae	*Guarea macrophylla*	generalistas	127	vertebrate	0	2
Meliaceae	*Melia azedarach*	generalistas	401	vertebrate	0	4
Meliaceae	*Trichilia pallida*	generalistas	43	vertebrate	0	1
Moraceae	*Ficus adhatodifolia*	generalistas	sem dado	vertebrate	0	1
Moraceae	*Ficus luschnathiana*	especialistas	0,2	vertebrate	3	1
Moraceae	*Maclura tinctoria*	generalistas	2,604	vertebrate	2	4
Moraceae	*Morus nigra*	generalistas	4,2	vertebrate	3	3
Moraceae	*Sorocea bonplandii*	generalistas	416,7	vertebrate	0	1
Myrsinaceae	*Myrsine coriacea*	generalistas	20,2	vertebrate	39	194
Myrsinaceae	*Myrsine gardneriana*	generalistas	sem dado	vertebrate	0	11
Myrsinaceae	*Myrsine umbellata*	generalistas	66,6	vertebrate	21	232
Myrtaceae	*Campomanesia xanthocarpa*	generalistas	76,9	vertebrate	1	0
Myrtaceae	*Eugenia pyriformis*	generalistas	854,7	vertebrate	0	10

Família	Espécie	Habitat	mg./semente	Dispersão	DAP≥5cm	DAP<5cm
Myrtaceae	*Eugenia uniflora*	generalistas	258,3	vertebrate	0	12
Myrtaceae	*Myrcia hebepetala*	especialistas	150	vertebrate	2	2
Myrtaceae	*Myrcia splendens*	generalistas	173	vertebrate	0	29
Myrtaceae	*Psidium cattleianum*	generalistas	15,38	vertebrate	0	43
Myrtaceae	*Psidium guajava*	especialistas	9	vertebrate	6	62
Myrtaceae	*Psidium guineense*	generalistas	53,1	vertebrate	0	2
Phytolaccaceae	*Gallesia integrifolia*	generalistas	65,8	non-vertebrate	0	1
Polygonaceae	*Triplaris americana*	generalistas	sem dado	non-vertebrate	3	10
Rhamnaceae	*Hovenia dulcis*	generalistas	25,6	vertebrate	0	1
Rosaceae	*Eriobotrya japonica*	generalistas	1447	vertebrate	0	18
Rosaceae	*Prunus myrtifolia*	generalistas	sem dado	vertebrate	0	14
Rubiaceae	*Coutarea hexandra*	generalistas	4	non-vertebrate	0	1
Rubiaceae	*Psychotria vellosiana*	especialistas	sem dado	vertebrate	0	1
Rubiaceae	*Psychotria nuda*	especialistas	497	vertebrate	0	9
Rubiaceae	*Psychotria vellosiana*	generalistas	6	vertebrate	0	1
Rutaceae	*Balfourodendron riedelianum*	generalistas	406,5	non-vertebrate	1	3
Rutaceae	*Esenbeckia febrifuga*	generalistas	35,7	non-vertebrate	0	6
Rutaceae	*Zanthoxylum rhoifolium*	generalistas	12	vertebrate	4	10
Rutaceae	*Zanthoxylum riedelianum*	generalistas	25	vertebrate	0	3
Salicaceae	*Casearia lasiophylla*	generalistas	50	vertebrate	4	18
Salicaceae	*Casearia sylvestris*	generalistas	3	vertebrate	17	126
Salicaceae	*Xylosma ciliatifolia*	generalistas	6,7	vertebrate	0	3
Salicaceae	*Xylosma pseudosalzmanii*	generalistas	sem dado	vertebrate	0	2
Sapindaceae	*Allophylus edulis*	generalistas	33,5	vertebrate	0	6
Sapindaceae	*Cupania vernalis*	generalistas	387,6	vertebrate	0	24
Sapindaceae	*Matayba elaeagnoides*	generalistas	307,7	vertebrate	0	4

Família	Espécie	Habitat	mg./semente	Dispersão	DAP≥5cm	DAP<5cm
Sapindaceae	*Matayba juglandifolia*	generalistas	sem dado	vertebrate	0	1
Sapindaceae	*Sapindus saponaria*	generalistas	767	vertebrate	1	0
Sapotaceae	*Chrysophyllum gonocarpum*	generalistas	5670	vertebrate	3	0
Sapotaceae	*Siparuna guianensis*	generalistas	20	vertebrate	0	9
Solanaceae	*Cestrum corymbosum*	especialistas	sem dado	vertebrate	1	24
Solanaceae	*Cestrum intermedium*	especialistas	sem dado	vertebrate	2	8
Solanaceae	*Solanum swartzianum*	generalistas	sem dado	vertebrate	3	10
Solanaceae	*Solanum campaniforme*	generalistas	1,3	vertebrate	0	3
Solanaceae	*Solanum lycocarpum*	generalistas	15,2	vertebrate	1	0
Solanaceae	*Solanum mauritianum*	generalistas	1,1	vertebrate	26	40
Solanaceae	*Solanum pseudoquina*	generalistas	76,9	vertebrate	0	3
Solanaceae	*Solanum variabile*	generalistas	10	vertebrate	0	144
Urticaceae	*Boehmeria caudata*	especialistas	0,1	non-vertebrate	5	22
Urticaceae	*Cecropia hololeuca*	especialistas	1,1	vertebrate	23	48
Urticaceae	*Cecropia pachystachya*	generalistas	0,9	vertebrate	5	1
Verbenaceae	*Aloysia virgata*	generalistas	0,2	vertebrate	1	5
Verbenaceae	*Citharexylum myrianthum*	especialistas	52,6	vertebrate	79	24

MS 2. Variação da regeneração (indivíduos DAP<5cm) entre sítios de restauração. Valores médios de: taxa de cobertura florestal, densidade de regenerantes, riqueza de espécies, densidade de espécies não dispersas por vertebrados, densidade de espécies dispersas por vertebrados, CWM peso de sementes (mg.) e densidade relativa de especialistas em florestas tropicais úmidas.

Idade da cobertura florestal	Sítio de restauração	Cobertura Florestal	Densidade ($100m^2$)	Riqueza de espécies	Dens. ($100m^2$) não dispersos por vertebrados	Dens. ($100m^2$) dispersos por vertebrados	CWM peso de sementes (mg.)	Dens. relativa "especialistas"
< 30 anos		**15,27%**	**29,63**	**11,18**	**10,35**	**14,68**	**84,20**	**5,57%**
	Cunha1	13,88%	60,00	16,50	16,50	29,50	42,88	2,92%
	Cunha2	30,50%	45,50	13,00	11,00	27,00	89,06	4,40%
	Cunha4	9,40%	17,75	7,00	8,25	8,00	8,49	0,00%
	Cunha6	49,28%	36,50	16,00	15,25	16,50	141,48	1,37%
	Cunha7	20,80%	48,50	15,00	11,00	27,25	67,15	2,58%
	Cunha8	3,98%	28,00	11,00	10,50	15,75	25,88	8,93%
	Guaratinguetá2	0,25%	9,75	8,00	4,75	3,00	208,76	10,26%
	N.Paulista5	3,33%	20,00	9,00	8,00	11,50	57,32	27,50%
	Paraibuna2	3,88%	8,50	5,00	5,25	2,75	31,12	2,94%
	Socorro3	17,40%	21,75	11,25	13,00	5,50	169,92	8,05%
≥ 30 anos		**18,39%**	**29,62**	**11,69**	**10,75**	**16,24**	**195,97**	**13,16%**
	Cunha3	7,38%	31,50	10,75	20,25	11,00	31,96	6,35%
	Cunha4	27,25%	15,50	9,00	6,50	8,25	153,38	9,68%
	Cunha5	28,05%	43,25	15,75	11,75	27,50	290,17	9,25%
	Cunha9	20,98%	52,25	20,00	18,50	27,25	58,27	8,61%
	Cunha10	30,08%	37,75	11,75	3,50	32,25	194,35	9,93%
	Guaratinguetá1	19,73%	22,50	12,75	8,75	7,00	271,37	14,44%
	Guaratinguetá3	1,58%	55,50	17,25	10,50	39,50	40,98	18,92%
	Joanópolis1	14,45%	32,00	15,25	11,75	14,75	318,59	28,13%

Idade da cobertura florestal	Sítio de restauração	Cobertura Florestal	Densidade ($100m^2$)	Riqueza de espécies	Dens. ($100m^2$) não dispersos por vertebrados	Dens. ($100m^2$) dispersos por vertebrados	CWM peso de sementes (mg.)	Dens. relativa "especialistas"
	Joanópolis2	7,60%	18,50	7,00	9,25	9,00	48,69	17,57%
	Joanópolis3	26,53%	16,25	9,25	8,75	6,50	125,66	6,15%
	N.Paulista1	25,85%	22,50	10,75	7,25	14,25	172,42	20,00%
	N.Paulista2	35,83%	16,50	9,50	8,50	6,25	311,08	6,06%
	N.Paulista3	17,10%	23,25	9,75	9,25	13,50	116,17	25,81%
	N.Paulista4	32,50%	26,75	8,00	18,25	6,75	193,69	11,21%
	Paraibuna1	9,30%	24,50	8,25	4,50	19,00	46,92	21,43%
	Socorro1	6,30%	18,75	11,00	7,25	8,50	662,45	9,33%
	Socorro2	2,15%	46,25	12,75	18,25	24,75	295,31	4,32%
Média global		**17,23%**	**29,62**	**11,50**	**10,60**	**15,66**	**154,57**	**10,35%**