Paula María Montoya Pfeiffer

Plant-bee interactions and pollen flux in restored areas of Atlantic Forest

Interações planta-abelha e o fluxo de pólen em áreas restauradas de Mata Atlântica

São Paulo

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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ecologia, na Área de concentração: Ecologia de Ecossistemas Terrestres.

Orientadora: Isabel Alves dos Santos

São Paulo

2018

Ficha cartográfica

Montoya-Pfeiffer, Paula María
Plant-bee interactions and pollen flux in restored areas of Atlantic Forest
91 pages
Thesis (Doctoral) - Institute of Biosciences of the University of São Paulo. Department of Ecology.
1. Apoidea 2. Community Ecology 3. Pollination. I. University of São Paulo. Institute of Biosciences. Department of Ecology.

Comissão julgadora:

Prof

Prof.

Prof

Prof.

Orientadora Prof.

Acknowledgements

I would like to thank my adviser, Prof. Isabel Alves dos Santos, for the friendship and advice she has provided throughout my time as her student and for giving me the opportunity to make part of this program. The members of my dissertation committee Ricardo Ribeiro Rodrigues, Jean Paul Metzger, Claudia Inês da Silva, and the professors Oswaldo Baquero and Peter Kevan, for the valuable suggestions they made to this work.

I thank the staff from the BeeLab for the research support, in particular Paulo Cesar Fernandes for his help in field work. I also want to thank the Online Pollen Catalogs Network (RCPol) for the help with pollen analysis, and the secretary from the department of Ecology Vera Lima for the patient guidance in bureaucratic procedures.

I am grateful to the Administrative Department of Science, Technology and Innovation from Colombia (COLCIENCIAS) and the Coordination for the Improvement of Higher Education Personnel from Brazil (CAPES), for providing the funding which allowed me to undertake this research. I also thank the Organizing Committees of the VII World Conference on Ecological Restoration SER 2017 and the XIX International Botanical Congress for giving me the opportunity to attend conferences and share this work.

Finally, I wish to thank my family and friends, especially Sebastian, Dioneval and Julian for the company and providing me with many ways to escape from my studies. I am most thankful and want to apologize to my mom for not being with her, and all the bees I had to kill, to whom I dedicate this work.

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General Introduction

Habitat fragmentation on agricultural landscapes reduces the population size of many plant species and increases their spatial isolation. As a result, plant genetic variability is diminished due to a blockage in the gene flux that is carried out by pollinators and seed dispersers (Dick et al. 2008; Aavik & Helm 2018). Within the remaining isolated populations, reproduction between close relatives or genetically similar plants (produced by seeds from the same matrix or matrixes with a certain grade of relatedness) can be problematic as a consequence of genetic self-incompatibility systems that impede seed fecundation, even when pollination (i.e. transference of pollen grains to the stigma) is accomplished (McKay et al. 2005). Thus, plant species success becomes critical because of a seed production decline. High genetically varied populations in conserved areas in contrast, have greater adaptive capacity in the face of environmental changes, since they contain genes from distant relatives adapted to different environmental conditions, which enhance the survival chances for their descendants in the long term (Dick et al. 2008; Aavik & Helm 2018).

As a consequence of fragmentation, the conservation and restoration of pollinators is essential for sustaining viable plant populations, because they promote pollen transport and gene flux among individuals in isolated fragments. As it is expected that populations in remnant and restored plant communities perpetuate with the passing of the years, restoration programs on high fragmented agricultural landscapes should be planned with consideration for achieving this purpose (Montalvo et al 1997; Castro, 2007; Castro et al. 2007). However, little has been done in this regard, as most studies on restoration ecology have been centered in solving problems of shorter term priority, specially related with the initial establishment of plant populations (e.g. seed colonization and germination, seedling survival and so on) (Rodrigues et al. 2009; 2011), while applied pollination studies have been focused on meliorating the reproductive success and productivity of crop plant species important for human food security (Kremen et al. 2007; Dixon 2009; Menz et al. 2011).

In this work, we evaluate plant-pollinator interactions in restored tropical forests, aiming to establish first, the pollination requirements of plant species in these forests, and secondly, if the pollinator requirements are being fulfilled and the interactions between plants and pollinators are being recovered throughout restoration practices. This work comprises two chapters structured as articles:

Chapter 1. Are the assemblages of tree pollination modes being recovered by tropical forest restoration? By doing an extensive literature review about the pollination biology of tree species in primary forests, restoration plantings and naturally regenerated forests, we compare and identify patterns on the functional diversity and the assemblages of plant pollination modes in these communities.

Chapter 2. Functional responses and effects from bee communities in restored tropical forests. By sampling bees (i.e. the most important pollinators) and identifying the pollen grains attached to their bodies, we analyze and compare the functional diversity of bee communities and their floral resources, and the structure of plant-bee interactions in primary forests, restoration plantings, disturbed herbaceous areas and sugar cane fields, as well as in response to habitat isolation.

Finally, we discuss the implications of different restoration and landscape design practices on the recovery of plant-pollinator interactions.

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Chapter 1

Are the assemblages of tree pollination modes being recovered by tropical forest restoration?[1]

ABSTRACT

Questions: Do the assemblages of pollination modes in restored (tree plantings) and secondary (naturally regenerated) forests change in comparison with primary forests, and how do these assemblages relate to species turnover at regional scale?

Location: Southeast region of Brazil.

Methods: We classified tree species found in a total of 40 forest sites (18 primary, 11 restored, 11 secondary) according to pollination mode, based on the literature. We calculated and compared functional dissimilarity distances, amounts of species and accumulated abundance of pollination modes, and functional indices of richness and evenness between forest types.

Results: Functional dissimilarity distances were much smaller than species dissimilarity distances within forest types (mean values, < 20%, > 80%, respectively), indicating a small variation in pollination modes between sites. Functional indices of richness and evenness did not differ between forest types. However, significant changes

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[1] Article published in: Montoya-Pfeiffer, P. M., Rodrigues, R. R., Metzger, J. P., da Silva, C. I., Santos Baquero, O., & Alves dos Santos, I. (2018). Are the assemblages of tree pollination modes being recovered by tropical forest restoration? *Applied Vegetation Science*, 21(1): 156-163. Manuscript attached at the end of this document.

were found in the species and abundance proportions of several pollination modes. Primary forests were characterized by the predominance of generalized insect-pollinated species, followed by secondary proportions of bee, wind, and moth pollination; other pollination modes were underrepresented. In restored forests, reductions were found in generalized insect, moth, wind, fly, pollen-consuming insect, and very-small insect pollination, whereas the species pollinated by bees and bats were more than doubled. Smaller changes were found among secondary forests, including reductions in moth, fly, and fig-wasp pollination, whereas there were incremental changes in bee, beetle, big animal, and small insect pollination.

Conclusions: Our results indicated a rather stable assemblage of pollination modes and also high ecological redundancy among trees regardless of the species replacement at the regional scale. Major changes among restored forests are probably in response to larger disturbance effects and/or restoration practices conducted in these sites. In contrast, smaller changes among secondary forests could be in response to smaller disturbance effects and natural selection processes and also seem to suggest that highly resilient degraded areas are more likely to recuperate their functional diversity by natural regeneration alone. In both cases, however, efforts in recovering such patterns should be encouraged to avoid possible negative effects in plant–pollinator interactions.

Keywords: Atlantic forest; Brazil; community structure; ecosystem management; forest fragmentation; functional diversity; human disturbance; meta-analysis; natural regeneration; plant-animal interactions; pollination syndromes; reproductive traits; restoration ecology; semi-deciduous forest.

RESUMO

Perguntas: Os sistemas de polinização em florestas restauradas (plantios de árvores) e secundárias (naturalmente regeneradas) diferem daqueles das comunidades de florestas primárias, e como estes se relacionam com a substituição de espécies em escala regional?

Localização: Região sudeste do Brasil.

Métodos: Classificamos as espécies de árvores encontradas em 40 áreas florestais (18 primárias, 11 restauradas, 11 secundárias) por seu modo de polinização, baseando-nos na informação achada na literatura. Calculamos e comparamos as distâncias de dessemelhança funcional, quantidades de espécies e abundâncias acumuladas dos modos de polinização, e índices funcionais de riqueza e equitatividade entre tipos de florestas.

Resultados: A dissimilaridade funcional foi muito menor que a dissimilaridade em espécies entre locais de amostragem (valores médios, < 20%, > 80%, respectivamente). A riqueza e equitatividade funcional não se diferenciaram entre tipos de florestas. Porém, se encontraram diferenças significativas nas proporções de espécies e abundância de vários modos de polinização. As florestas primárias se caracterizaram pela predominância de espécies generalistas polinizadas por insetos, seguidas por proporções secundárias de espécies polinizadas por abelhas, vento e mariposas; outros modos de polinização estiveram sub-representados. Nas florestas restauradas diminui a polinização por insetos (generalistas), mariposas, vento, insetos consumidores de pólen, e insetos muito pequenos, enquanto que as proporções das plantas polinizadas por abelhas e morcegos duplicaram. As diferenças foram menores nas florestas secundárias, incluindo reduções na polinização por mariposas, moscas, vespas das figueiras, enquanto foram incrementadas as proporções das espécies polinizadas por abelhas, besouros, animais grandes e insetos pequenos.

Conclusões: Nossos resultados indicam uma assembléia de modos de polinização relativamente estável, além de alta redundância ecológica nas comunidades de árvores em escala regional. As maiores diferenças nas florestas restauradas provavelmente responderam a maiores efeitos de degradação e/ou às práticas de restauração ativa conduzidas nestas áreas. Por sua vez, as menores diferenças nas áreas secundárias poderiam ser explicadas pelos menores efeitos de degradação e os processos de seleção natural, sugerindo que as áreas altamente resilientes são mais propensas a recuperar sua diversidade funcional simplesmente mediante regeneração natural. Nos dois casos, porém, os esforços para recuperar os padrões das florestas primárias devem ser estimulados, para evitar possíveis consequências negativas nas interações planta-polinizador.

Palavras chave: floresta atlântica; Brasil; estrutura de comunidades; manutenção de ecossistemas; fragmentação florestal; diversidade funcional; distúrbio antrópico; regeneração natural; interações planta-animal; síndromes de polinização, atributos reprodutivos; ecologia da restauração; floresta semidecidual.

INTRODUCTION

Tropical forests are rapidly being degraded worldwide, affecting biodiversity, ecosystem functioning, and the provision of ecosystem services. Consequently, their recuperation by means of ecological restoration is becoming a pressing necessity to recreate lost habitats for endangered species, while promoting human welfare and economic development (SER 2004). The success and sustainability of restoration programs depend on not only the retrieval of species diversity but also the diversity of functional traits, i.e., morphological, physiological, behavioral, structural, and phenological characteristics, considered relevant to their response to the environment and/or their effect on ecosystem properties and services (Lugo 1992; Silver 1996; Violle et al. 2007; Rodrigues et al. 2009; Cadotte et al. 2011). These include, for example, traits involved in the ability of a plant to colonize, compete, and regenerate, to establish and persist in a restored community (e.g., seed viability, dispersal strategy, light tolerance, and growth rate) or traits associated with ecosystem services like water purification, carbon sequestration, or wood provision (e.g., nutrient fixation, wood density, and growth rate), from which landholders would benefit.

Plant pollination modes, comprising strategies and adaptations for attracting pollinators, have received little attention in the context of restoration ecology (Girao et al. 2007; Ceccon & Varasin 2014; Garcia et al. 2015; Martins & Antoni 2016). Yet, the restoration of floral source diversity and availability in plant communities guarantees the wellbeing of their pollinators (Heithaus 1974; Carvalheiro et al. 2013; Dicks et al. 2015) and subsequently, the maintenance of the functions and services derived from plant species (Ashman et al. 2004; Fontaine et al. 2006; Kremen et al. 2007). The intraspecific genetic diversity in plants, which is indispensable for the preservation and evolution of restored forests, sometimes relies more on pollen vectors than on seed vectors (e.g., in the case of autochoric species) (Helsen et al. 2016; Lexer et al. 2016) or may be dissimilarly affected by both when these exhibit different dispersal patterns, occurring at different distances and directions (Beckie et al. 2016; Miller 2016; Wang et al. 2016). Moreover, pollinators may sometimes indirectly benefit seed dispersal and seedling recruitment by the enhancement of seed and fruit set/size (Bond 1994; Lundgren et al. 2016). Pollinator conservation by ecological restoration has also been shown to improve crop pollination services, which could be translated into additional incentives and revenues for the implementation of restoration programs in agricultural regions (Heithaus 1974; Carvalheiro et al. 2013; Dicks et al. 2015).

Different restoration scenarios may lead to variable species assemblages with possible detrimental effects on the diversity of pollination modes. For instance, highly devastated areas that have lost their capacity to auto recuperate and require tree plantings for restoration would probably generate plant communities diverging more from the original ones. In contrast, less disturbed areas that are still highly resilient and capable of auto regenerating naturally, without the necessity to implement active restoration practices, would probably generate plant communities diverging less from the original ones (Rodrigues et al. 2009; Brancalion et al. 2015). The consequences of these possible scenarios have been explored to a small extent (Chazdon et al. 2003; Girão et al. 2009; Lopes et al. 2009; Kimell et al. 2010; Garcia et al. 2015; Martins & Antoni 2016). Hence, in the present study, we compared the diversity of pollination modes in restoration plantings and naturally regenerated forests with that in primary forests in Brazil. Given that species assemblages vary spatially in response to local environmental and landscape conditions and the geographic distribution of species (Torres et al. 1997, Brancalion et al. 2015), we included plant communities from several locations to understand how the diversity of pollination modes relates to species turnover at a regional scale, as well as to search for patterns that could be used as a model for restoration planning in tropical forests.

METHODS

The present study was based on data from 40 floristic surveys conducted in tree communities within the domain of tropical semi-deciduous forests in the Atlantic forest biome in Brazil (Veloso et al. 1991). These surveys were selected because they used a similar methodology (phytosociological data obtained from trees above 4.5 cm diameter at breast height) and the species importance values (used herein as a proxy for abundance) were available. 18 surveys were conducted in relatively well-conserved primary forest fragments, although some of them were slightly affected by selective logging and livestock grazing (named herein as “remnants”). 11 surveys were conducted in degraded sites restored with tree plantings of various native and exotic species (named herein as “restored”). The remaining 11 surveys were conducted in less degraded areas restored by natural regeneration alone (named herein as “secondary”). The maximum distance between sites was 986 km and the minimum was 100 m (19°26′–23°33′S and 41°13′–50°27′W). The elevation varied between 100 and 1025 masl. The climate of the region was classified as Cwa, Cwb, or Cfa in the Köppen system (1948), with a dry winter from June to September, a rainy summer from December to March, a mean annual temperature of 18°C–22°C, and annual precipitation of 1100–1730 mm. The references are summarized in Appendix 1.1.

The species registered in these surveys were classified into the following pollination modes: “bird”; “bat”; “wasp”; “fly”; “moth”; “beetle”; “small insect” (trips, rove beetles, etc.); “bee”; “mammal” (non-flying); and “wind.” Mixed pollination modes are indicated by the conjunction of two or more of the former, but the most common modes received different names: “insect” (various types); “pollen consumer” (various types of insects excluding nectar consumers like lepidopterans); “big animal” (large bees, birds, lepidopterans, and bats); “long tongue” (bees, lepidopterans, and birds); and “vertebrate” (hummingbirds and bats). These pollination modes were established after conducting an extensive literature review on the pollinators of each species. The species without any information were classified into the category of another in the same genus or family showing similar floral morphology (see Appendix 1.2). We decided not to use the traditional pollination syndromes of Fægri and van der Pijl (1979) that are based on floral-trait combinations alone, given their inability in predicting the pollinators of several species

(Mayfield et al. 2001; Ollerton et al. 2009; Rosas-Guerrero et al. 2014). Likewise, taking into account the recommendations of many authors (Waser et al. 1996; Ollerton et al. 2009, 2015; Rosas-Guerrero et al. 2014), we considered not only the most efficient pollinators but also the secondary or less effective ones because pollinator efficiency can vary in space and time (Waser et al. 1996; Price et al. 2005; Ollerton et al. 2015) and because secondary pollinators represent important selecting forces in the expression and evolution of many flower phenotypes (Sargent and Otto 2006; Strauss and Whittall 2006). In addition, pollination modes represent an ecological function of resource provision from which both primary and secondary pollinators benefit.

Comparisons between sites and forest types (remnants, restored, and secondary) were conducted using Morisita–Horn dissimilarity distances, as suggested by Wolda (1981), for dealing with different sample sizes. Species dissimilarity distances were calculated on a matrix containing the species abundances by site (i.e., importance value*sample area/100). Functional dissimilarity distances were calculated on two matrices: one containing the species quantities from each pollination mode by site (functional dissimilarity for species) and the other containing the accumulated abundances of pollination modes by site (functional dissimilarity for abundances). Spatial autocorrelations were tested by performing Mantel tests with dissimilarity and geographical distances between sites (significance level = 0.05). Overall differences in the assemblages of species and pollination modes among forest types were tested using multivariate analyses of variance (MANOVA, significance level = 0.05). The functional diversity of each site was estimated using the indices of functional richness and evenness provided by Villéger et al. (2008) and Schleuter et al. (2010). Particular differences in functional indices and pollination modes were tested separately using generalized linear models (GLM). Beta models were fitted to functional indices, Poisson and negative binomial models to species quantities, and Gaussian models to accumulated abundances. Binomial-Gamma hurdle models were fitted to rare pollination modes with zero-inflated data (> 30% zero values). Forest type was included as the explanatory variable with a significance level of 0.05. Sample area was added as an offset variable in Poisson and binomial models and as an explanatory variable in beta and gamma models to control for unequal sampling. Model fitting was measured by R^2 values, the ratio deviance: degrees of freedom, residual analysis, and AUC values. All analyses were performed using R, packages FD, vegan, lme4, betareg, and ggplot2 (R Foundation for Statistical Computing 2011).

RESULTS

From a total of 974 tree species registered in the floristic surveys, 660 species were found in remnants, 305 in restored forests, and 452 in secondary forests. The species were spatially structured (Mantel test, r = 0.42, $p < 0.01$) and varied greatly between sites (mean dissimilarity distances were higher than 0.8, see Fig. 1) and forest types (MANOVA, F = 2.57, $p < 0.01$).

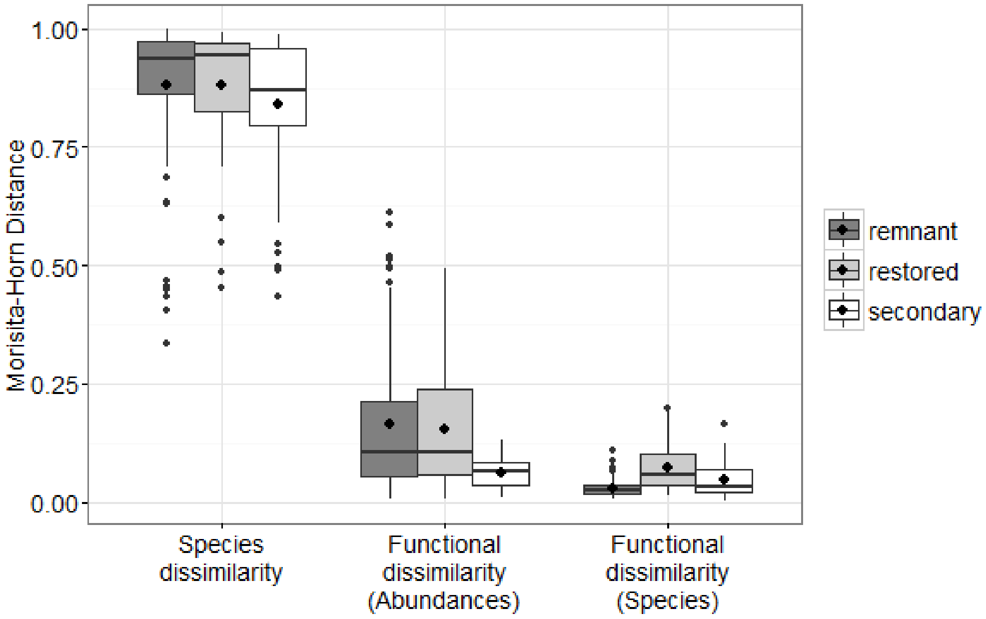

Figure 1.1. Box-plot of species and functional dissimilarities in remnants (primary forest), restored (tree plantings) and secondary (naturally regenerated) tropical semi-deciduous forests. Central boxes span the first quartile to the third quartile (the inter-quartile range or IQR). Segments and points inside the boxes show the median and the mean values respectively, and "whiskers" below and above the boxes show the location of the smallest and the largest values no further than 1.5*IQR from the first and the third quartiles. Small points indicate data beyond the whiskers or "outliers". Species dissimilarity indicates the differences in the tree species composition among

sites, whereas functional dissimilarity indicates the differences in the abundances and the number of species from different pollination modes among sites. No statistical differences were found among forest types, but the figure indicates much higher dissimilarities in the species composition than in the assemblages of pollination modes in all forest types.

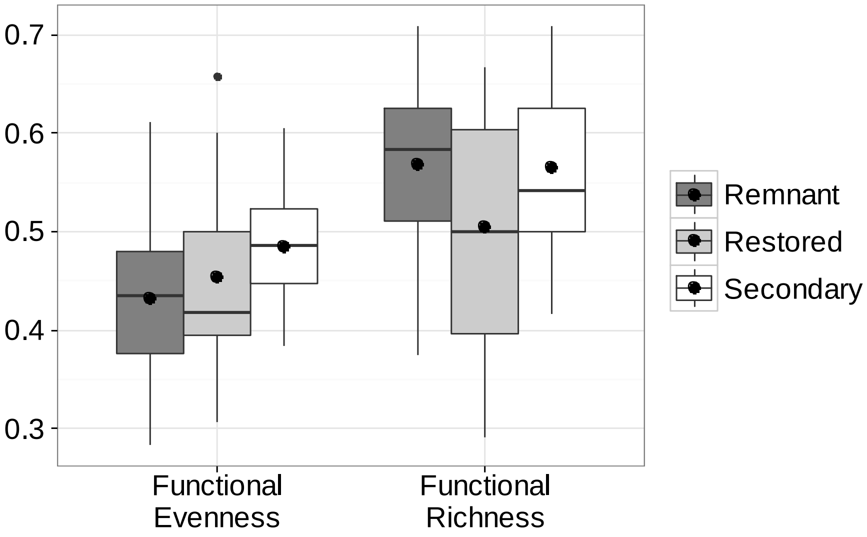

Figure 2. Box-plot of the functional indices of richness and evenness of pollination modes in remnants (primary forests), restored (tree plantings) and secondary (naturally regenerated) tropical semi-deciduous forests. Central boxes span the first quartile to the third quartile (the inter-quartile range or IQR). Segments and points inside the boxes show the median and the mean values respectively, and “whiskers” below and above the boxes show the location of the smallest and the largest values no further than 1.5*IQR from the first and the third quartiles. The small point indicates a datum beyond the whisker or “outlier”. No statistical differences were found among forest types.

Remnant forests were particularly characterized by the predominance of insect-pollinated trees, represented by nearly half the species and individuals in every site (Fig. 3) and by 48 families, among which Lauraceae, Leguminosae (mimosoid species), Sapindaceae, Sapotaceae, and Rutaceae were some of the most important. This pollination mode was followed by bee pollination, mainly represented by species from the families Leguminosae (sf. Caesalpinoidae, Papilionoidae), Bignoniaceae, Solanaceae, and Melastomataceae; wind pollination, with various common Moraceae, Euphorbiaceae, and Urticaceae species; moth pollination in many Apocynaceae (genera *Aspidosperma, Himatanthus,* and *Tabernaemontana*), Meliaceae (*Guarea* and *Cabralea*), Ebenaceae (*Diospyros*), Proteaceae (*Euplassa* and *Roupala*), and Rubiaceae (*Posoqueria, Randia,* and *Tocoyena*) species; and pollen-consumer pollination in Mytaceae. Other pollination modes were found in mean proportions smaller than 0.04.

In restored forests, the prevalent abundance of insect-pollinated trees was maintained, although a significant reduction of about 6% was found in the amount of species (Fig. 3). From a total of 48 families of insect-pollinated species in remnants, only 28 were found in restored forests. Some families with the largest reductions in species included Lauraceae (7/36 spp.), Rubiaceae (1/15 spp.), and Sapotaceae (2/14 spp.). Wind-pollinated species and abundance were reduced by more than one third probably because only three of 15 wind-pollinated euphorbs found in remnants were also found in restored forests. Moth pollinated species diminished by a half, and their abundance by more than a half (11/31 spp.). The Apocynaceae family, which had the most number of moth-pollinated species, was represented here by only five species, compared with 15 species found in remnants. Other families of moth-pollinated species that were absent in restored forests included Rubiaceae (e.g., *Posoqueria* spp.), Ebenaceae (e.g., *Diospyros* spp.), and Proteaceae (e.g., *Roupala montana*). The species and abundances for pollen-consuming insects decreased, mainly because of reductions in Myrtaceae species (7/43 spp.). Flowers specialized in very small insects significantly decreased, probably as a result of the absence of Monimiaceae species (2/8 spp., genera *Mollinedia* and *Siparuna*). The abundance of fly-pollinated species reduced as well, in response to the scarcity of individuals of *Metrodorea nigra*, which was an important species among remnants. These reductions in pollination modes were replaced by much higher abundances and species pollinated by bees (mainly Caesalpinoidae, Papilionoidae, and Bignoniaceae species) and bats (mostly Malvaceae sf. Bombacoideae species). The mean number of bird-pollinated species increased, although not significantly, because of the presence of the introduced species *Erythrina speciosa* in many restored forests.

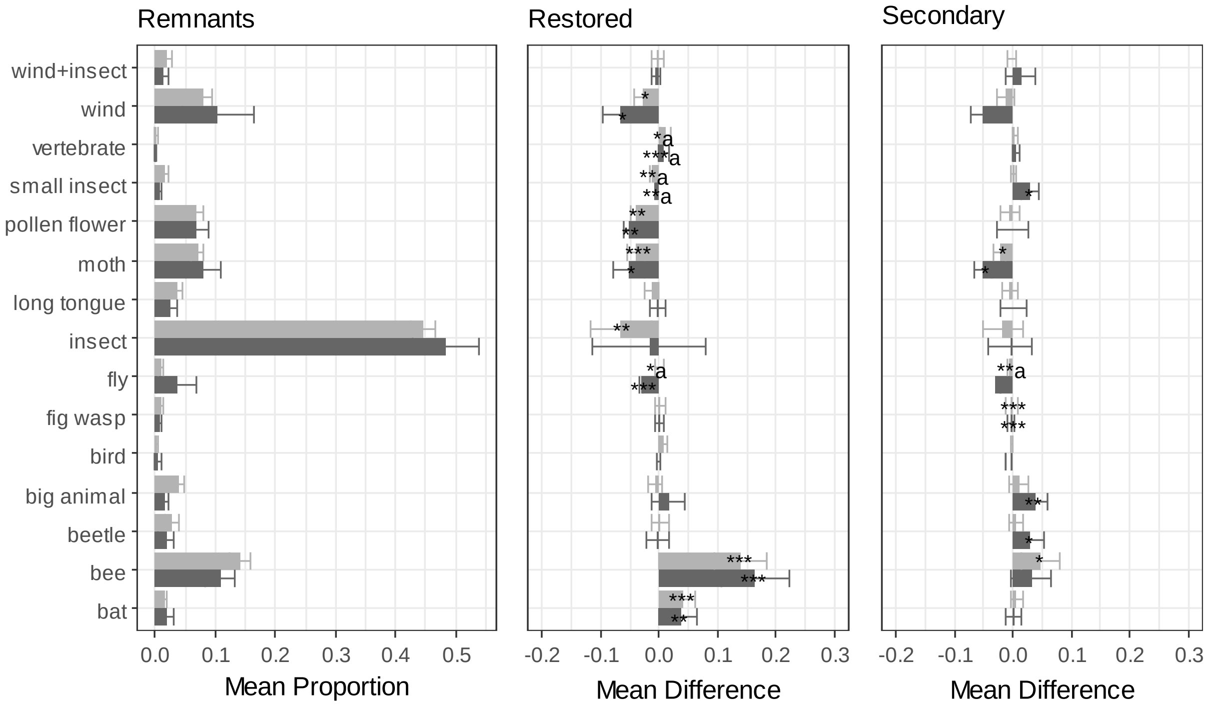

Figure 3. Mean values and confidence intervals (95%) of species (light-gray) and abundance (dark-gray) proportions of pollination modes at remnants (primary forest) and the differences found among restored (tree plantings) and secondary (naturally regenerated) tropical semi-deciduous forests are shown in the figure. The figure shows greater changes among restored forests than secondary forests, compared with primary forests. Asterisks (*) denote significant differences in generalized linear models: *0.05, **0.01, ***0.001. “a” indicates changes in the presence-absence of pollination modes using zero-inflated binomial models.

Secondary forests also differed from remnants but changed to a lesser extent than restored forests (Fig. 3). Bee-pollinated species significantly increased. Moth-pollinated species significantly reduced to one half, and important reductions were found in the abundances of Apocynaceae (e.g., genera *Aspidosperma* and *Tabernaemontana*) and Meliaceae species (particularly *Cabralea canjerana*). The occurrence of fly pollination decreased owing to the absence of *Metrodorea nigra*. Abundances were smaller in fig-wasp pollination (*Ficus* spp.) and wind pollination (various Euphorbiaceae species such as *Actinostemon* spp., *Sebastiana commersoniana*, and *Tetrorchidium rubrivenium*) but greater in beetle (*Xylopia sericea* and other Annonaceae species), small insect (higher frequency of *Siparuna guianensis* trees), and big animal pollination (*Inga* spp.).

DISCUSSION

We observed several patterns that are helpful in understanding the processes governing the assemblage of pollination modes among species, as well as in the decision-making processes aimed at restoring functional diverse ecosystems.

First, species dissimilarity was much higher than functional dissimilarity among forest locations (Fig. 1). High species dissimilarity could be explained by the great distances between some of our study areas; however, the restricted geographic distribution of many species responding to specific environmental requirements (i.e., topography, soil types, and pluviometric regimes), in conjunction with possible stochastic events, can also contribute to a high species turnover between communities on a minor scale (Torres et al. 1997; Brancalion et al. 2015). Small degrading effects in our remnants relating to fragmentation, border effects, or other human pressures could be additional causes of variation in species composition. However, the significant differences between the three forest types demonstrated that the major causes of differentiation reside in the processes of total deforestation, land use practices, and subsequent restoration.

In contrast, the smaller functional dissimilarity indicates a rather stable functional assemblage of pollination modes and also a high ecological redundancy among communities (Petchey et al. 2007; Pillar et al. 2013), regardless of the species replacement. The lack of spatial autocorrelation confirms this result because the variations in pollination modes were not related to the differences in species composition (and its spatial autocorrelation) among locations. Comparable studies support our findings and suggest that, among communities, differentiation for particular traits can be relatively small because of habitat-filtering forces selecting species with similar adaptations from the regional pool, as opposed to within communities, where the interactions between coexisting species are supposed to augment functional diversity by niche segregation (Pavoine and Dolédec 2005; de Bello et al. 2009).

Second, pollination systems were characterized by the high predominance of generalist insect pollination and the secondary incidences of bee, wind, moth, and pollen-consuming insect pollination, whereas many other specialized and mixed modes were underrepresented. This fairly low functional diversity of tree communities could possibly be ascribed to an environmental filtering mechanism where several selecting forces, perhaps including both pollinator and nonpollinator agents (i.e., herbivores, pathogens, and abiotic stressors), may be interacting (Sargent and Otto 2006; Strauss and Whittall 2006). Underrepresented modes such as beetle, bat, and bird pollination seem to be more common in understory plants (Bawa 1990; Frankie et al. 1990; Schatz 1990; Sazima et al. 1999; Buzato et al. 2000; Fleming and Muchhala 2008; Diogo et al. 2016), for example, in many herbaceous monocots (Costaceae and Heliconiaceae by hummingbirds and bats and Cyclantaceae by beetles) and epiphytes (Araceae by beetles and bromeliads by hummingbirds and bats). Such great trait divergence among plant growth forms is expected and seems to be a pattern for various functional traits (de Bello et al. 2009). In the context of ecological restoration, this issue is of high concern and highlights the importance of encouraging projects aimed at reintroducing plants with different habits into restored and secondary forests (e.g., Duarte and Gandolfi 2013; Le Bourlegat et al. 2013) to fully recover functional diversity.

Third, restored forests showed more accentuated and variable changes on the assemblages of pollination modes than secondary forests, as was expected. One of the possible causes could be the artificial selection of species for plantings, which is generally performed to recover functional traits more relevant during the initial establishment of seedlings (e.g., light requirements) and/or which depends on the cost and availability of seedlings in nurseries; hence, it sometimes includes both native and exotic species (Brancalion et al. 2015). As a result, many functional traits essential for the stability of the ecosystem in the long term (e.g., reproductive traits) could remain neglected. Other causes could be the major disturbance impacts associated with these areas, causing alterations, for example, in soil seed banks, soil properties, and the loss of connectivity with the surrounding forests that facilitates propagule arrival. The smaller changes found among secondary forests, in turn, seem to be reflected in the minor disturbance impacts and the lack of human intervention in these areas. In the present study, we could not test how specific restoration practices, ages of restoration, and other local environmental variables explain variations in pollination modes within forest types because of the small number of sites and a lack of detailed information. However, our results suggest that highly resilient degraded sites could easily recuperate their functional diversity by natural regeneration alone, whereas at more disturbed sites, selecting better species for plantings and monitoring natural regenerants is recommended to better reassemble functional diversity.

Despite the changes found in several pollination modes, the functional richness among restored and secondary forests did not significantly differ from remnants, although we found lower values among several restored sites. Similarly, the functional evenness did not significantly differ among forest types, probably because the predominance of the most important pollination modes, as well as the underrepresentation of the less common ones, was still maintained. This lack of variation seems to be concordant with the suggestion of Schleuter et al. (2010) that states that functional diversity indices are not so reliable when using categorical data because they were specially developed for numerical traits. In this case, the variation in functional diversity indices alone would probably not be able to detect significant changes in particular functional attributes that may have important implications for biodiversity conservation.

Some of the changes we found in pollination modes are reinforced by previous studies, such as the negative effect of forest fragmentation on moth pollination found by Girão et al. (2009) and the greater representation of beetle-pollinated species (i.e., *X. aromatica*) in secondary areas found by Martins and Antoni (2016). However, divergent results appear when comparing our findings with those of studies that include different plant growth forms and strata. For example, Chazdon et al. (2003) and Lopes et al. (2009) have found major proportions of generalized insect pollination among secondary wet forests in Costa Rica and Brazil, but in the present study, we found it was predominant even among primary forests. Other specialized modes, such as bird, bat, and non-flying mammal pollination, have been reported to be intensely reduced by human disturbances in other tropical wet forests (Girão et al. 2009; Lopes et al. 2009; Kimell et al. 2010; Chazdon et al. 2003). In the present study, such pollination modes were underrepresented in general among tree species and did not significantly change in secondary areas.

Conflicting results may also occur as a consequence of ambiguous methods for plant classification. In previous studies conducted in semi-deciduous (Kinoshita at al. 2006; Yamamoto et al. 2007) and other tropical forests (Kress and Beach 1994; van Dulmen 2001; Girão et al. 2007; Araujo et al. 2009; Diogo et al. 2016), there was a predominance of bee pollination instead of generalized insect pollination because the authors used the traditional pollination syndromes (i.e., Fægri and van der Pijl 1979) or just included the most efficient pollinators during plant species classification. We do not deny that bees are the preponderant pollinators of tropical wild species (i.e., according to these studies, bees pollinate more than 50% of species), but this does not necessarily mean that bee-pollinated plants are particularly adapted to bee pollination or that these plants prevent visits from other types of pollinators (e.g., Mayfield et al. 2001). Similarly, Kimell et al. (2010) have found an overrepresentation of moth pollination in two secondary fragments because of the high dominance of *Inga ingoides* and *Albizia saman* trees. In the present study, we found an increase in the abundance of various *Inga* species among secondary forests, but we classified them as big-animal pollinated trees because they are secondarily pollinated by birds, bats, and butterflies (Koptur 1983; Amorim et al. 2013).

Conclusions

In conclusion, we found that the assemblages of pollination modes in these tropical forests describe a pattern which is maintained at regional scale, and can be recovered throughout natural regeneration after low disturbance, but could remain altered after high disturbance and subsequent restoration practices. Several effects resulting from alterations in these assemblages may be expected. Reductions among specialized pollination modes (principally moth, fly, and small insect) are likely to cause major competition between animal vectors. Pollinators have been seen to change their foraging behavior to more generalized visitation patterns in less diverse plant communities (Heithaus 1974). Under the former conditions, plant pollination would be negatively affected by smaller visitation frequency and the arrival of alien pollen to the stigmas. At the community level, less stable and robust interaction networks would be anticipated as well as mismatches in flowering periods (Miller-Rushing et al. 2010). Increases in the species and abundance proportions of pollination modes (particularly bees and bats in our case) are expected to be advantageous for their pollinators because of major resource availability (Carvalheiro et al. 2013; Dicks et al. 2015). Plant species having such pollination modes would be enhanced by means of facilitation and by greater attraction of their pollinators (Ghazoul 2006). Still, plant species could be negatively affected as well because of major competition for pollination (Mitchell et al. 2009).

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Chapter 2

Functional responses and effects from bee communities in restored tropical forests

ABSTRACT

Wild pollinators are necessary not only to enhance the production of many crop species but also for ensuring the reproduction continuity of plants among remnant and restored ecosystems. Therefore, restoration activities should lead to their recovery by improving their connectivity and habitat requirements. We assessed the functional responses and effects from bee communities in middle aged restoration plantings (restored corridors) and compared them with communities in conserved and degraded fragments of primary forest, disturbed herbaceous areas in wetlands (secondary corridors), and sugarcane fields, as well as in response to habitat isolation.

We characterized bee species and the pollen grains transported on their bodies using functional traits (bees: body size, nesting location, sociality and foraging strategy; plants: habit, successional class, geographic origin and pollination mode), evaluated changes between habitat types in bee abundances and pollen frequencies, and created interaction networks between functional groups of bees and plants, aiming to test differences in network topology and identify modules in the overall community.

We found that the bee communities and their plant interactions were not still fully recovered in restoration plantings, although these areas were better than secondary corridors in enhancing the recuperation of pollinators, as they played an important role in floral resource provisioning. The effect of habitat isolation was negative in general and highlighted the importance of preserving remnant fragments in providing pollinators to restored areas. Larger bee species with more restricted nesting and floral requirements seamed to be the most affected, while the smaller bees that nest below ground and are more related to herbaceous ruderal plants, were practically unaffected by habitat changes or isolation. The structure of interaction networks was little affected, but the composition and diversity of functional groups significantly changed, showing more negative consequences on the woody species that represent the basis for restored and remnant ecosystems, as they were more strongly associated to the most vulnerable bee species.

Keywords: biodiversity conservation; community assemblage; connectivity; ecosystem degradation; functional diversity; habitat restoration; interaction networks; land-use change; modularity; pollen transport; pollination.

RESUMO

Os polinizadores silvestres são necessários não somente para melhorar a produção das plantas cultivadas, mas também para garantir a continuidade na reprodução das espécies vegetais nos ecossistemas remanescentes e restaurados. Desta forma as atividades de restauração ecológica devem ser planejadas considerando também a recuperação dos polinizadores, através da melhoria da conectividade da paisagem e da presença de seus requerimentos de habitat. Neste trabalho avaliamos as respostas e os efeitos funcionais das comunidades de abelhas em plantios de restauração de meia-idade (corredores em restauração), e comparamos com comunidades em fragmentos remanescentes de floresta primária, áreas alagadas e degradadas dominadas por herbáceas (corredores secundários), e cultivos de cana-de-açúcar, assim como em resposta ao isolamento de habitat.

Caracterizamos as espécies de abelhas e dos grãos de pólen transportados no seu corpo mediante atributos funcionais (abelhas: tamanho do corpo, local de nidificação, socialidade e estratégia de forrageamento; plantas: hábito, classe sucessional, origem geográfica e modo de polinização), avaliamos as variações na abundância de abelhas e a freqüência de pólen entre os tipos de habitat, e construímos redes de interação entre grupos funcionais de abelhas e plantas, objetivando avaliar as diferenças na topologia das redes e identificar módulos de interação na comunidade em geral.

Encontramos que as comunidades de abelhas e suas interações com as plantas não estavam totalmente recuperadas nos plantios de restauração, porém, estas áreas representaram um papel muito melhor que os corredores secundários, no que se refere ao aprovisionamento de recursos florais para as abelhas. O efeito do isolamento de habitat, que foi negativo de maneira geral, destaca a importância de preservar os remanescentes de floresta primária para o fornecimento de polinizadores para as áreas em restauração. As abelhas de maior porte e com mais restrições de nidificação e forrageamento foram as mais afetadas, enquanto que as abelhas menores que nidificam no solo e estão mais relacionadas com plantas herbáceas ruderais, não foram muito afetadas pelas mudanças ou isolamento do habitat. A estrutura das redes de interação variou pouco, mas a composição e diversidade de grupos funcionais mudaram significativamente. As plantas lenhosas que são base dos ecossistemas florestais remanescentes e restaurados foram as mais afetadas, pois estão mais fortemente ligadas as espécies de abelhas mais vulneráveis.

Palavras chave: conservação da biodiversidade; degradação ecossistémica; diversidade funcional; estrutura de comunidades; modularidade; mudanças no uso da terra; polinização; redes de interações; restauração de habitat; transporte de pólen.

INTRODUCTION

The conservation and restoration of wild pollinator communities are necessary not only to enhance the production of many crop species important on human food security (Kremen et al. 2007), but also for ensuring the reproductive continuity and resilience of wild plant species among remnant and restored ecosystems. For this reason, restoration activities should lead to the recovery of pollinators and their functionality, specifically, through the spatial integration of habitat areas to facilitate their movement and dispersal within the landscape, as well as by fulfilling all the habitat requirements for their survival (Dixon 2009; Menz et al. 2011). According to the pollinator necessities and the level of environmental degradation in the region, restoration activities may vary from small and passive interventions like maintaining vegetated areas as linear landscape elements (e.g. ditches, hedgerows) or “stepping stone” patches between habitat areas, for guiding their movement through the inhospitable matrix (e.g. Dicks et al. 2010; Van Rossum & Triest 2012; Kormann et al. 2016), to more complex and active actions that include the increase of habitat areas or the reintroduction of specific requirements (e.g. nesting materials, floral resources) (Falcy & Estades 2007; Dixon 2009; Menz et al. 2011). The way how pollinators and their functional processes respond to these possible actions should be evaluated and considered for guiding the decisions to be made during restoration planning.

The responses of pollinators can be assessed by their “response traits”, i.e. morphological, physiological and behavioral characteristics among species that mediate their tolerance to environmental changes (Violle et al. 2007). In the case of bees, which are the main pollinators of flowering plants (Kremen et al. 2007), traits related with dispersal capacity, sociality, nesting and foraging are indicated as the principal predictors of species occurrence and abundance in disturbed (Williams et al. 2010; de Palma et al. 2015; Coutinho et al. 2018) and restored habitats (Kremen & M'Gonigle 2015; Öckinger et al. 2017). The effects on the pollination function are generally studied by following a network approach, where it is possible to visualize the structure of the dynamics between plants and pollinator species, so that the consequences of species additions or losses in the face of restoration and other environmental changes can be predicted (Forup et al. 2008; Williams 2011; Kaiser-Bumbury et al. 2017). However, a challenge still remains in understanding how these ecological networks could be scaled to a functional trait level instead of focusing on the taxonomical diversity, so as to enable the identification of general patterns that work for species with similar phenotypes, and could better serve as a basis for biodiversity and ecosystem management, at the same time that other evolutionary and phylogenetic processes can be explored (Suding et al. 2008; Menz et al. 2011; Raimundo et al. 2018).

In this work, we assessed the trait responses of bee communities in middle-aged (9-15 year-old) restoration plantings aimed to recreate highly diverse sustainable forests in a sugarcane producing region in Brazil (Rodrigues et al. 2011). We compared them with “reference” communities in remnant fragments of undisturbed and disturbed primary forest, as well as with communities in more disturbed herbaceous areas in wetlands -which may also play a role in providing habitat and connectivity-, and the sugarcane matrix. We hypothesized that bee trait assemblages in restoration plantings would differ less from reference communities than those in the more disturbed areas, being the species with higher restrictions on mobility, nesting and foraging the most affected (Kremen & M'Gonigle 2015; Öckinger et al. 2017). Additionally, we compared communities sampled at different distances from reference fragments with the expectation to find a negative effect of habitat isolation on the functional responses of pollinators (Öckinger et al. 2017).

In a second part of this paper, we analyzed the bee community effect on pollination by examining the pollen grains transported by bees, and assigning traits relevant to restoration ecology and pollination on the identified plant species (i.e. habit, geographic origin, successional class and pollination mode). We expect climax, native and woody plants to be more affected by losses on bee functional diversity, due to their correlation with specialized bee pollination modes (Chazdon et al. 2003; Ghazoul 2006; Montoya-Pfeiffer et al. 2018). Afterwards, we created interaction networks between functional groups of bees and plants, aiming to establish first, if the network structure in restoration plantings differ from that in reference forests and disturbed areas, and responded to habitat isolation, and secondly, if more strengthen links (i.e. modules) between certain functional groups of bees and plants exist. For the first objective, we predict smaller network complexity and robustness in restoration plantings than in reference forests but higher than in disturbed habitats, as well as a negative effect of habitat isolation, in consequence to functional diversity losses on bee communities (Forup et al. 2008; Williams 2011; Kaiser-Bumbury et al. 2017; Öckinger et al. 2017). For the second objective, our prediction is to find tightly linked functional groups, because bee species with similar functional traits could select for plant species with also similar traits as a result of coevolutionary processes (Olesen et al. 2007).

METHODOLOGY

Study area

We conducted fieldwork in sugarcane farms located within the domain of the Atlantic forest in southeast Brazil (municipality of Araras, Sao Paulo state) (22°25'46.95"S, 47°20'36.80"W) (Veloso et al. 1991). The area is greatly devastated with about 7% of its original vegetation and dominated by a matrix of sugarcane fields (Fig. 2.1). The small forest fragments that still remain are highly degraded and characterized by a discontinuous canopy covered by superabundant native lianas, and borders heavily colonized by invasive non-native grasses (hereafter degraded fragments). Some fragments are connected by highly diverse (i.e. ~80 spp.) tree restoration plantings that were initiated between the years of 2001-2005, with the intention to protect the water bodies from the area while increasing forest cover and connectance between fragments (hereafter restored corridors) (Naves 2013; Rodrigues et al. 2011). Other fragments remain linked by anthropogenic wet lands created after siltation of water courses, which are now dominated by herbaceous vegetation with very low potential of autogenic restoration (hereafter secondary corridors). Two still remaining bigger fragments showing less degradation (i.e. continuous forest canopy without aggressive lianas, presence of epiphytes, understory shaded and natural regeneration taking place) were taken as reference ecosystems in our data analysis (hereafter conserved fragments) (Naves 2013; Rodrigues et al. 2011).

Sampling design and data collection

We established sampling sites in reference fragments (4), disturbed fragments (5), restored corridors (15), secondary corridors (12) and sugarcane fields (16). Sampling sites in restored and secondary corridors, and sugarcane fields were placed at distances from fragments ranging from 100 to 2500m and separated from each other by at least 100m. Given the close proximity of various fragments that may affect the occurrence and behavior of bee species in several sites, we calculated the total fragment cover area within 1000m-radius buffers and used this measurement as an explanatory variable for analyzing the effect of fragment isolation. Fragment cover areas were calculated by using digitalized maps of land use performed in QGis 2.18.0, GNU-GPL, Boston, MA.

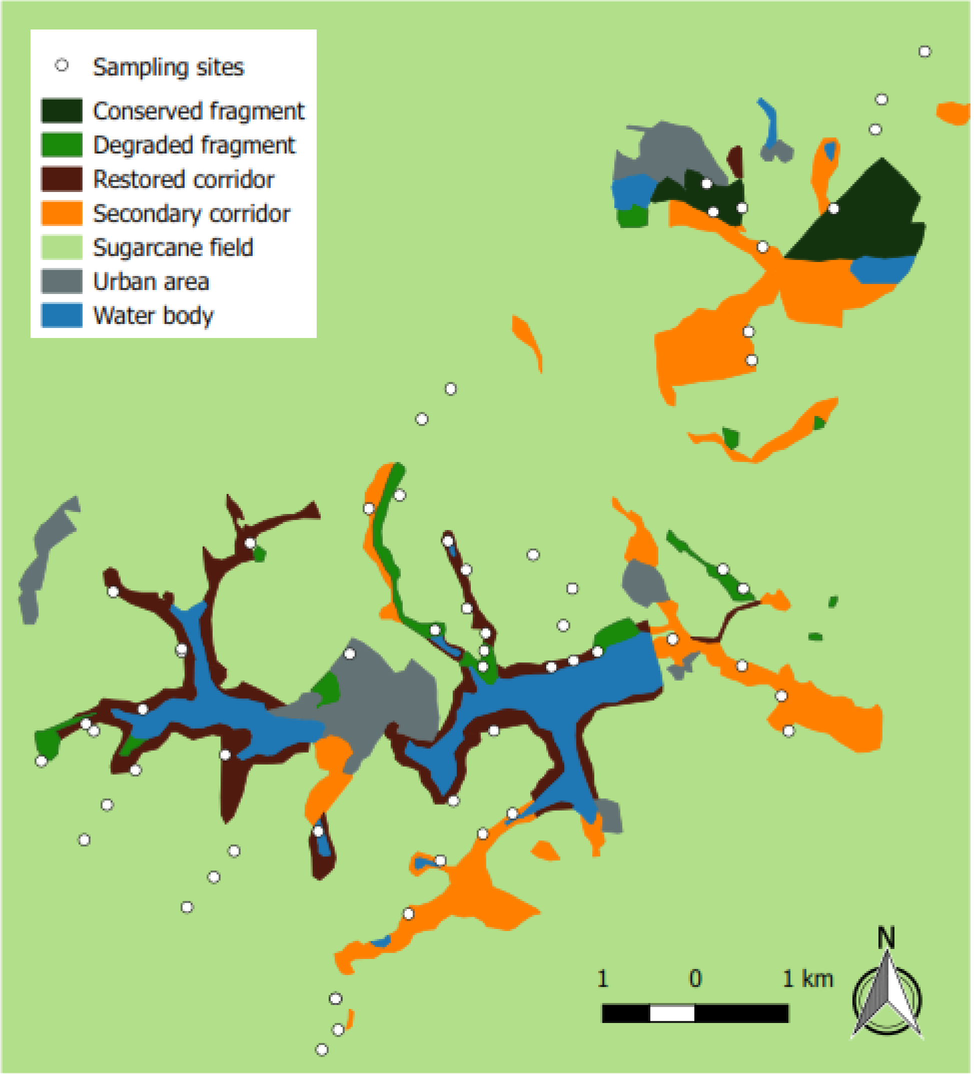

Figure 2.1. Map of the study area indicating vegetation cover types and sampling sites.

Bees were sampled over three 24h-periods per site, during the flowering pick times in October-January 2015-2017, by using pantraps (six of each color, white, yellow and blue) (Leong & Thorp 1999) and bait traps for euglossine bees (three of each bait, eugenol and eucalyptol, Dodson et al. 1969; Campos et al. 1989). Trap sets in corridors and fragments were placed at 10m inside, 0m, and 10m outside from the border line to control from border effects. Trapped bees were taken to the lab for identification to genus or species level (see the list in Appendix 2.1). Pollen grains on bee bodies were removed by washing with ethanol, then prepared through acetolysis (Erdtman 1943) and mounted on slides for identification to the highest level of taxonomic resolution possible (list in Appendix 2.2).

Traits

Following previous works on bee functional diversity (Williams et al. 2010; Kremen & M'Gonigle 2015; Öckinger et al. 2017; Coutinho et al. 2018), we classified bee species using four qualitative functional traits: body size, nesting location, sociality and foraging strategy. Bee species were classified based on intertegular distance measures as small-sized (≤ 2.2 mm), medium-sized (2.5 - 4.0 mm) or big-sized (≥ 4.3 mm). Nesting location was classified as below-ground or above-ground; sociality was classified as solitary, semisocial or social; and foraging strategy as polylectic or oligolectic. We selected four traits for assessing the effects on the functional diversity of plant species: habit (herb, liana, woody), successional class (initial, climax), geographic origin (native, exotic) and pollination mode (generalist, bee specialist, other). Information on bee and plant traits was compiled from the literature by reviewing published works on each species or inferring trait data based on phylogeny. Species with uncompleted information were dropped from the analysis. We pooled all bee and plant species in functional groups according to the interactions found between traits (see Fig. 2.2 and 2.4), and calculated the richness and the Shannon's diversity of functional groups on each site (hereafter functional richness and diversity), and the differences in functional group composition between reference fragments and other habitats with Morisita-Horn distances (hereafter functional similarity). Correlations between traits were assessed via chi-square tests in order to determine whether trait responses should be analyzed by separately or jointly in associations (Williams et al. 2010; de Palma et al. 2015)

Interaction networks

We constructed quantitative interaction networks by site with functional groups of bees and plants, and calculated the following topological metrics as suggested by Blüthgen (2010): weighted nestedness, interaction diversity, interaction evenness and network specialization. Basing on the algorithm from Dormann & Strauss (2014), we calculated modularity *Q* and identified modules of functional groups only in the general network, given that the networks from each site were small sized and therefore lacked sufficient statistical power to detect significance in modularity.

Data analysis

Before starting data analysis, we evaluated sampling completeness of bees (85 species, 727 individuals) and plant interactions (221 species, 78320 interactions) by using the richness estimators Chao (bees = 70%; plants = 72%) and Jacknife 1 (bees = 74%; plants = 73%), and tested spatial autocorrelation on bee and plant species compositions, using Mantel tests with Bray-Curtis dissimilarity and geographic distances between sites, finding no autocorrelation on neither of the two (bees: r = 0.06, p = 0.08; plants: r = 0.1, p = 0.09) (significance level = 0.05). Additionally, we assessed the sample size effect of bee abundance on pollen variables (i.e. overall pollen frequency and functional richness, diversity and similarity), as well as the effect of plant species' local abundance (data obtained from the floristic survey conducted by Naves 2013) on pollen type frequencies in samples.

We analyzed bee community responses and effects on pollination using generalized and linear models. Overall bee abundance and pollen frequency, functional richness, diversity and similarity of bees and plants, and interaction network indices were included as response variables, whereas habitat type (conserved fragments, disturbed fragments, restored corridors, secondary corridors and sugarcane fields), fragment cover area and their interaction were taken as fixed effects within the models. Bee / plant functional group was included as a new interacting fixed effect in models, taking bee abundance / pollen frequency as the response variable, respectively. Other effects such as trap type (pan or bait trap), sampling date and trap-set location (inside, border-line, outside) were excluded from the analysis by pooling all samples from the same site. Best models were selected based on significant differences in AIC values (ANOVA tests, significance level = 0.05), and residuals were visually inspected to assess model fit. All analyses were performed in R v.3.5.0 software (R Development Core Team, 2018).

RESULTS

Bee communities and their plant interactions in general tended to demonstrate negative responses to habitat changes. However, the responses in restored corridors showed an intermediate trend with mean proportional differences to conserved fragments greater than disturbed fragments (0.49 ± 0.37 and 0.30 ± 0.30 respectively) but smaller than secondary corridors (0.51 ± 0.63) and sugarcane fields (0.54 ± 0.31) (Table 2.1, Figs. 2.3 and 2.5). From a total of 57 response variables tested, 13 showed significant differences from conserved fragments in restored corridors, while 2 were found in disturbed fragments, 16 in secondary corridors and 23 in sugarcane fields. The effect of fragment cover area was positive in general and appeared to be stronger in restored corridors (four significant correlations in restored corridors to zero in secondary corridors and one in sugarcane fields).

Bee community responses to restoration and habitat degradation

Overall bee abundance varied in response to habitat type, with significant diferences in secondary corridors and sugarcane fields but not in restored corridors and degraded fragments (Table 2.1) (explained deviance D^2 = 0.22, p = 0.003). Fragment cover area was positively correlated with bee abundance in restored corridors (D^2 = 0.21, p = 0.03), but had no significant effect in other habitat type. Functional richness decreased significantly only in sugarcane fields (D^2 = 0.13, p = 0.19) and was not affected by fragment cover area. Functional diversity was neither related to habitat type nor fragment cover area. Functional group composition was significantly different from conserved habitats in sugarcane fields but not in other habitat type ($R^2 = 0.13$, $p < 0.001$), and did not vary in response to fragment cover area.

Functional traits were not randomly distributed within the overall bee community (Fig 2.2). Small bees were found to be predominant (47%), as well as below-ground nesters (60%), semi-socials (46%) and polylectics (89%). Below-ground nesters were greatly associated to small bees (91%, $X^2 = 240.8$, $p < 0.001$).), while above-ground nesters were better represented among medium-sized (54%) and big-sized bees (69%) ($X^2 = 109.7$, $p < 0.001$). Solitary bees were principally found among medium sized bees (56%, $X^2 = 29.3$, $p < 0.001$) social bees were only registered among small (79%) and medium sized bees (21%, $X^2 = 100.5$, $p < 0.001$), semisocials tended to be more common among big sized bees (66%, $X^2 = 9.4$, p 0.008) and above ground nesters (26%, $X^2 = 19.5$, $p < 0.001$), and cleptoparasites were more abundant among big sized bees (80%, $X^2 = 100.9$, $p < 0.001$). Oligolecty was almost exclusively found within a group of solitary, below ground nesting and medium sized bees (97%, $X^2 = 186.2$, $p < 0.001$).

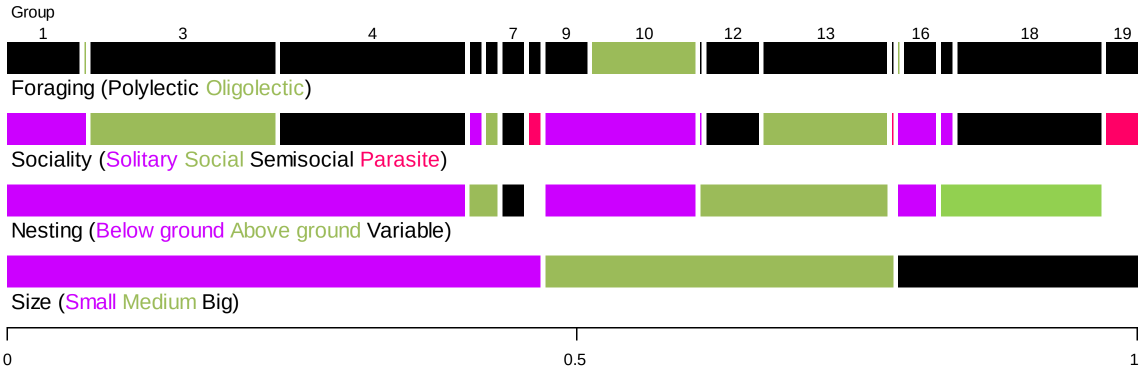

Figure 2.2. Double decker plot for bee traits, showing de distribution of abundance proportions (horizontally) and combinations between traits (vertically). The group numbers on the upper side of the graph represent different combinations between traits.

Table 2.1. Effects of habitat types and isolation (fragment cover area) on bee communities, pollen loads and network structure.

Bee community variables

	Overall Abundance				Functional Richness				Functional Diversity				Functional Similarity			
	Coef*.	SE	Z	P	Coef.	SE	Z	P	Coef.	SE	t	P	Coef.	SE	t	P
Conserved fragment	28.25	8.45	11.17	<0.01	7.00	1.32	10.30	<0.01	1.57	0.23	6.90	<0.01	0.30	0.04	16.96	<0.01
Disturbed fragment	-0.50	0.20	-1.71	0.09	-0.23	0.21	-0.96	0.34	-0.10	0.31	-0.57	0.57	0.09	0.05	1.19	0.23
Restored corridor	-0.42	0.20	-1.59	0.11	-0.19	0.18	-0.97	0.33	-0.12	0.26	-0.79	0.43	-0.01	0.05	-0.11	0.91
:Fragment cover area	**1.04**	**0.02**	**2.10**	**0.03**	1.00	0.02	0.31	0.76	0.01	0.02	0.15	0.89	<0.01	<0.01	1.61	0.11
Secondary corridor	**-0.59**	**0.15**	**-2.52**	**0.01**	-0.20	0.18	-1.01	0.32	-0.05	0.26	-0.32	0.75	-0.04	0.05	-0.57	0.57
:Fragment cover area	1.00	0.01	0.63	0.52	1.01	0.01	1.45	0.15	0.02	0.01	2.05	0.07	<0.01	<0.01	1.48	0.15
Sugarcane field	**-0.69**	**0.11**	**-3.39**	**<0.01**	**-0.39**	**0.14**	**-2.22**	**0.03**	-0.22	0.25	-1.41	0.16	**-0.12**	**0.05**	**-2.72**	**0.01**
:Fragment cover area	1.02	0.02	1.09	0.27	-1.00	0.01	-0.24	0.81	-0.01	0.01	-0.38	0.71	<0.01	<0.01	-0.48	0.64

Pollen load variables

	Overall Frequency				Functional Richness				Functional Diversity				Functional Similarity			
	Coef.	SE	Z	P	Coef.	SE	Z	P	Coef.	SE	t	P	Coef.	SE	t	P
Conserved fragment	212.50	89.81	12.68	<0.01	17.00	2.22	21.72	<0.01	2.40	0.23	10.40	<0.01	0.65	0.05	7.27	<0.01
Disturbed fragment	-0.55	0.26	-1.40	0.16	-0.13	0.16	-0.77	0.44	-0.07	0.31	-0.51	0.61	-0.09	0.06	-0.52	0.60
Restored corridor	**-0.60**	**0.19**	**-1.93**	**0.05**	**-0.32**	**0.10**	**-2.54**	**0.01**	-0.16	0.26	-1.50	0.14	**-0.42**	**0.05**	**-2.78**	**0.01**
:Fragment cover area	**1.05**	**0.02**	**2.21**	**0.03**	1.02	0.01	1.91	0.06	**0.02**	**0.01**	**3.07**	**0.01**	**0.01**	**0.00**	**2.89**	**0.01**
Secondary corridor	**-0.67**	**0.16**	**-2.25**	**0.02**	**-0.27**	**0.11**	**-2.01**	**0.04**	-0.09	0.27	-0.85	0.40	**-0.46**	**0.05**	**-2.96**	**<0.01**
:Fragment cover area	-0.99	0.01	-0.36	0.72	1.00	0.01	0.58	0.57	0.01	0.01	0.87	0.41	<0.01	<0.01	1.89	0.06
Sugarcane field	**-0.68**	**0.15**	**-2.41**	**0.02**	**-0.48**	**0.08**	**-4.18**	**<0.01**	**-0.21**	**0.26**	**-2.69**	**0.01**	**-0.88**	**0.05**	**5.77**	**<0.01**
:Fragment cover area	**1.06**	**0.03**	**2.16**	**0.03**	1.01	0.01	0.62	0.53	0.01	0.02	0.76	0.46	<0.01	<0.01	0.76	0.45

Network variables

	Weighted nestedness				Interaction Diversity				Interaction Evenness				Specialization H_2’			
	Coef.	SE	t	P	Coef.	SE	t	P	Coef.	SE	t	P	Coef.	SE	t	P
Reference fragment	0.62	0.13	4.82	<0.01	3.44	0.34	10.09	<0.01	0.74	0.06	13.24	<0.01	0.16	0.07	2.28	0.03
Disturbed fragment	-0.27	0.17	-1.01	0.32	-0.10	0.46	-0.72	0.47	-0.01	0.08	-0.06	0.95	0.19	0.09	0.31	0.76
Restored corridor	-0.23	0.15	-0.96	0.34	-0.20	0.38	-1.78	0.08	-0.09	0.06	-1.17	0.25	0.57	0.08	1.18	0.25
:Fragment cover area	<0.01	0.01	0.34	0.74	0.04	0.02	1.53	0.14	0.01	0.01	1.43	0.17	<0.01	0.01	0.37	0.72
Secondary corridor	-0.43	0.15	-1.84	0.07	-0.12	0.39	-1.06	0.29	0.01	0.06	0.08	0.94	0.19	0.08	0.36	0.72
:Fragment cover area	<0.01	0.01	0.17	0.87	0.01	0.01	1.31	0.21	<0.01	<0.01	-0.55	0.59	<0.01	<0.01	0.55	0.59
Sugarcane field	-0.27	0.15	-1.18	0.24	**-0.26**	**0.38**	**-2.38**	**0.02**	0.02	0.06	0.24	0.81	0.44	0.08	0.84	0.40
:Fragment cover area	<0.01	0.01	-0.27	0.79	0.01	0.01	0.84	0.42	<0.01	<0.01	0.30	0.77	<0.01	<0.01	0.56	0.59

*Coefficients in restored corridors, secondary corridors and sugarcane fields are presented as mean proportional differences from conserved fragments. Negative values indicate decreases in relation to reference values. Positive values in fragment cover area coefficients indicate detrimental effects of habitat isolation. Significant effects are indicated in bold numbers (significance level = 0.05).

The bee trait associations mentioned above served to explain the responses of bee functional groups to the predictor variables. The general tendency of functional group abundance was to decrease all habitat types, although with some exceptions (D^2 = 0.73) (Fig. 2.3, full model results in Appendix 2.3). Groups 1, 3, 4 and 9, representing species with small or medium size, below-ground nests, variable levels of social behavior and polylectic diet (i.e. mainly Exomalopsine, Eucerine and Halictid bees) were found to be between the most abundant groups in the study area, without being affected by habitat types or with a tendency to increase in some disturbed habitats. Conversely, groups 12, 18 and 19, including species with big or medium size, above ground nests, semisocial or parasitic behavior and polylectic diet (i.e. principally euglossine bees), were found to be predominant in conserved fragments and the most diminished in restored corridors, secondary corridors and sugarcane fields. Group 10 representing oligolectic bees (i.e. mainly Euphorine and Eucerine bees), was also found to respond negatively to habitat types. Fragment cover area had an overall positive effect on bee group abundance (coef. 1.02, SE=0.005, D^2= 0.006, p<0.001), which did not change significantly between functional groups and habitat types (Appendix 2.3).

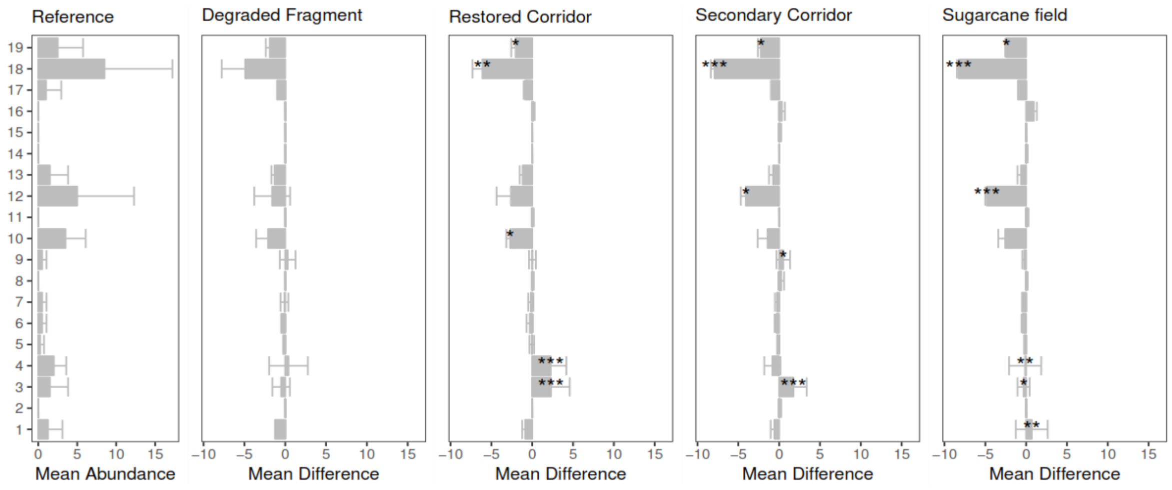

Figure 2.3. Mean values and CIs (95%) for the abundances of bee functional groups at reference (conserved fragments) and the mean differences found among degraded fragments, restored corridors (tree plantings), secondary corridors (naturally regenerated) and sugarcane fields. Group

numbers represent different combinations between functional traits (see Fig. 2.2) Asterisks (*) denote significant differences in GLM: *0.05, **0.01, ***0.001.

Effects on pollen transport and interaction networks

All pollen variables were found to be correlated with bee abundance on each site (Pearson correlations, p-values < 0.05), while the mean pollen frequency of individual plant species was related to their individual abundance in the study area (Pearson $r = 0.33$, $n = 55$, $p = 0.02$).

Overall pollen frequency tended to decreased in all habitat types, with significant effects in restored corridors, secondary corridors and sugarcane fields ($D^2 = 0.12$, $p = 0.08$) (Table 2.1), and increased by the effect of fragment cover area in restored corridors ($D^2 = 0.23$, $p = 0.02$) and sugarcane fields ($D^2 = 0.14$, $p = 0.03$). Functional richness was reduced in restored corridors, secondary corridors and sugarcane fields ($D^2 = 0.26$, $p < 0.001$) without being affected by fragment cover area. Functional diversity was only significantly reduced in sugarcane fields ($R^2 = 0.14$, $p = 0.02$), and had a positive effect of fragment cover area in restored corridors ($R^2 = 0.37$, $p = 0.01$). Functional composition differ from conserved fragments in restored corridors, secondary corridors and sugarcane fields ($R^2 = 0.24$ $p < 0.001$), but the difference was reduced in restored corridors by the effect of fragment cover area ($R^2 = 0.11$, $p = 0.01$).

Regarding functional traits, woody plants were found to be predominant (59%), as well as initials (92%), natives (67%) and generalists (48%) (Fig. 2.4). Climax and cultivated plants were scarce in general, exotic species tend to be better represented among herbs (47%, $X^2 = 13.4$, p 0.001), generalist species tend to be more common among herbs (71%) and lianas (69%, $X^2 = 16.8$, $p < 0.001$) and bee specialists were better represented among woody plants (56%, $X^2 = 55.6$, $p < 0.001$).

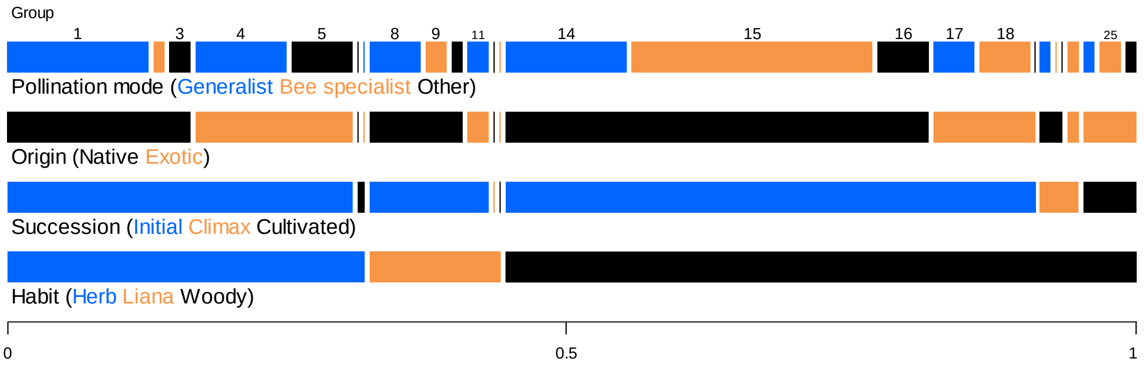

Figure 2.4. Double decker plot for plant traits, showing the distribution of abundance proportions (horizontally) and combinations (vertically) between traits. The group numbers on the upper side of the graph represent different combinations between traits.

The frequency of the majority of functional pollen groups tended to decrease in all habitat types (D^2 = 0.66, Fig. 2.5). Sugarcane fields registered the highest reductions (nine groups with significant effects), followed by secondary corridors (six groups), restored corridors (five groups) and degraded fragments (two groups). Groups 15 and 16 were found within the most affected ones, representing initial-native-woody plants with specialist pollination modes, as well as groups 1 and 5, including native or exotic initial herbs with generalist or specialist ("other") pollination modes. Other groups with minor changes were the woody plant groups 14, 17, 20, 23 and 26, with variable trait arrangements, the initial liana groups 9 and 11, and the initial herb groups 2 and 4. Fragment cover area had an overall positive effect on pollen group frequency in restored corridors (coef. 1.02) secondary corridors (coef. 0.98) and sugarcane fields (coef. 0.98) (D^2=0.006, $p < 0.001$), but did not significantly change between pollen groups (Appendix 2.4).

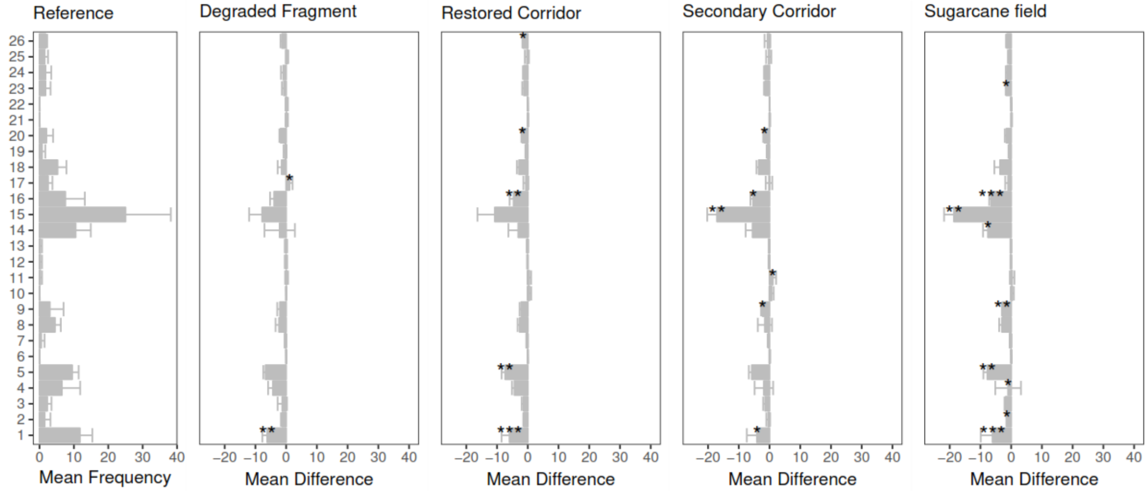

Figure 2.5 Mean values and CIs (95%) for the abundances of plant functional groups at conserved fragments and the mean differences found among degraded fragments, restored corridors (tree plantings), secondary corridors (naturally regenerated) and sugarcane fields. Group numbers represent different combinations between functional traits (see Fig. 2.4) Asterisks (*) denote significant differences in GLM: *0.05, **0.01, ***0.001.

The topology of interaction networks little differed between habitats and was practically unaffected by fragment cover area (Table 2.1). Network nestedness was high in conserved fragments and tended to decrease in all habitat types, interaction diversity showed a similar pattern with a significant reduction in sugarcane fields ($R^2 = 0.08$, $p = 0.1$), interaction evenness was high and conserved among habitat types (differences < 0.02), and network specialization was small in conserved fragments and tended to increase in other habitats.

Interactions between bee and plant functional groups were distributed in three modules (modularity = 0.14, z = 15.49, $p < 0.001$) (Fig 2.6). The biggest module principally included medium and big sized bees (58%), above-ground nesters (77%), variable social level and polylectics (99%), which were mainly associated to plant groups including woody species (92%), initials (90%), natives (87%) and variable pollination modes. A second module corresponded to small and medium sized bees that were mainly below-ground nesters (95%), had different social level and polylectic strategy (71%), in association with mainly initial herbs (92%) from variable geographic origin and generalist pollination (74%). The third and smallest module comprised groups with more homogeneously distributed interactions within the network.

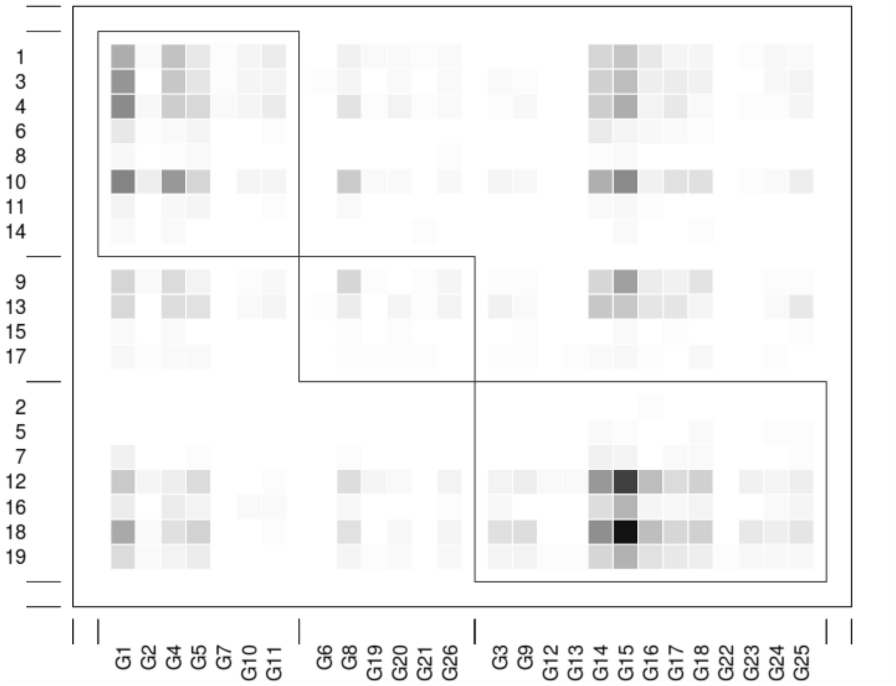

Figure 2.6. Modules identified for the interactions between bee groups (left axis) and plant groups (bottom axis). Darker squares indicate more observed interactions and the boxes delineate the tree modules. Group numbers represent different combinations between functional traits (see Figs. 2.2 and 2.4).

DISCUSSION

Bee community responses to restoration and habitat degradation

Bee communities in general showed negative responses to habitat changes, characterized by reductions in abundance, functional richness, similarity to conserved fragments, and variations among several functional groups. However, our results suggested that restored corridors better enhanced the recovery of bee communities, given their smaller differences to conserved fragments. Secondary corridors, even with larger differences still demonstrated to be able to attract bees and therefore should represent important elements in providing habitat and landscape connectivity on bee communities (Dicks et al. 2010; Van Rossum & Triest 2012; Kormann et al. 2016). Similarly, the small differences found between degraded and conserved fragments, and the overall positive effect of fragment cover area on bee responses (i.e. negative effect of habitat isolation), highlight the need for forest remnant conservation to supply bee populations on restored sites (Öckinger et al. 2017).

Overall bee trait responses seemed to be primarily driven by an interaction between nesting location and body size. Larger bees nesting above ground were found to predominate in the more conserved habitats, but replaced by smaller bees that nest below ground in the more degraded habitats. Such relation between nesting location and habitat degradation is well documented (Kremen et al. 2007; Williams et al. 2010; Kremen and M'Gonigle 2015; da Encarnação Coutinho et al. 2018; but see Öckinger et al. 2017), and explained by the major dependency of above ground nesting bees on forest resources like preexisting cavities on trees and other different plant substrates. In this work, the nesting resource availability might be restricted to fragments, as the younger trees in restored corridors and other degraded areas still do not have cavities and substrates enough for them (Morato & Martins 2006).

On the contrary, the relation between body size and habitat changes was expected to be the opposite (Forup et al. 2008; Williams et al. 2010; Menz et al. 2011; de Palma et al. 2015; Öckinger et al. 2017), given the positive correlation of bee body size with flight range and dispersal capability (Greenleaf et al. 2007), which should make smaller species more vulnerable to landscape barriers (Forup et al. 2008; Menz et al. 2011). Other correlated factors, such as the larger amounts of resources required by larger bees and their higher specialization, in addition to the interaction with nesting location, seemed to be better predictors of body size responses to habitat changes (Larsen et al. 2005; Kremen and M'Gonigle 2015).

Sociality appeared to be benefited by disturbance as a result of the association found between social behavior, below-ground nesting and small body size. However, various studies registered a high vulnerability on social bees to habitat fragmentation and degradation (Winfree et al. 2009; Williams et al. 2010; Coutinho et al. 2018), specially attributed to their need for big preexisting cavities and available floral resources during their longer yearly activity periods. In this work, the social bees that nest above ground and/or are medium or big sized, such as many stingless bees and bumblebees, were absent and presumably locally extinct even on conserved fragments -with the exception of the exotic species *Apis mellifera* in group 13 whose abundance may be greatly influenced by the presence of apiaries in the zone-, hence corroborating the hypothesis of being the primary affected species by isolation and habitat loss. Conversely, solitary and semisocial bees did not show an overall clear pattern and responded according to combinations with other functional traits, whereas the occurrence of cleptoparasite bees seemed to be controlled by their hosts' abundances (Williams et al. 2010), as it was indicated in this study by a similar variation pattern between the cleptoparasite species *Exaerete smaragdina* (group 19) and its host *Eulaema nigrita* (group 18) (see Fig.2.3).

Foraging strategy seemed to be not an important trait predictor for bee abundance, given the typical great prevalence of polylectic species in the Brazilian tropics (Schlindwein 2004) (Fig. 2.2). Nevertheless, the few oligolectic bees aggregated in group 10 were found to show a decreasing trend in all habitat types, probably due to their high sensibility to habitat disturbances because of their more specific requirements (Williams et al. 2010; de Palma et al. 2015; Öckinger et al. 2017; Coutinho et al. 2018).

Effects on pollen transport and interaction networks

All the response variables from pollen loads were primary determined by the bee abundance in samples and, as a consequence, presented patterns similar to bee responses: reductions in all habitat types that were smaller in degraded fragments, intermediate in restored and secondary corridors and larger in sugarcane fields, with a general negative effect of habitat isolation. Pollen load responses however, showed to be stronger (14 significant correlations) than bee community responses (five significant correlations) (Table 2.1), suggesting that small changes on bee communities could cause more relevant consequences on their function of pollen transport and pollination (Larsen et al. 2005; Suding et al. 2008).

Conversely, the topology of functional networks little changed in response to habitat or fragment cover area, probably because the reductions on bee abundance were not enough to cause significant effects on the strength and complexity of the interactions at this functional level. Nevertheless, the small reductions in nestedness and interaction diversity, and the increases in specialization, denote a trend to higher mutual dependencies and loss of redundancy among the interacting species, which could lead to negative implications on the robustness and resilience of these restored and degraded ecosystems (Forup et al. 2008; Bluthgen 2010; Williams 2011; Kaiser-Bumbury et al. 2017).

The functional networks also revealed to be modular, showing non-random patterns of interaction among both, bees and plants (Olesen et al. 2007; Dormann & Strauss 2014). This result helps us to explain the variations between habitats in plant group frequencies, as well as to identify target interactions for the improvement of restoration processes. We found two general main modules: a first module included bee groups that were unaffected by habitat degradation (i.e. bees with small size, below ground nesting location, different social levels and polylectic strategy), in association with mainly ruderal plants that are also not affected or even benefited by antropogenic disturbance (i.e. mainly initial herbs with native or exotic origin and generalist pollination), hence representing a fraction of the community that little contributes to the restoration process and may not require conservation priority. However, the pollen frequencies from the principal plant groups in this module (groups 1, 2, 4, and 5, Fig. 2.5) were reduced in degraded habitats in response to decreases in oligolectic bees (group 10, Fig. 2.3). It is not clear why oligolectic bees decreased in abundance, given their association with such unobstructed floral resources. Probably their limiting factors are more related to other aspects that were not considered in this work (p.e. parasitism, soil requirements, reproductive rates, population sizes) and may deserve further analysis. For the rest of bee species in this module, such association with ruderal plants represents an additional adaptive trait that enables them to colonize and disperse through disturbed habitats without relying on remnant vegetation fragments.

The second module was mainly compounded by the most vulnerable bee species (i.e. medium to large bees that nest above ground, with variable social behavior and polylectic strategy), in interaction with plants that constitute the principal component of restoration plantings and forest remnants (i.e. woody plants from initial succession stages, native origin and different pollination modes), both responding in the same way to habitat changes and isolation as a result of their association (bee groups 12, 18, 19 in Fig. 2.3, plant groups 14, 15, 16 in Fig. 2.5). The great individual abundance of plants from this module in restored corridors supports our initial hypothesis, which states that the more vulnerable bee species rely on primary forest fragments not because of limitation on floral resources, but on nesting resources. Additionally, this module revealed that pollination of the most important tree species in restored and conserved areas strongly depends on larger bees, whose longer flight ranges facilitate the outcrossing with individuals at further distances, contributing in this way to maximize their genetic diversity (Dick et al. 2008). Hence, the conservation of the bee species from this module should be prioritized in restoration programs, for example, throughout the reintroduction of nesting materials and/or populated nests in cases of local extinct species (Cortopassi-Laurino et al. 2006; Dicks et al. 2010; Menz et al. 2011).

It is worthy to remark that bee species in general were strongly related with plants abundant in the study area. The preference for abundant plants is common among bees (Waser 1986; Ghazoul 2006) and could lead to negative effects on the reproductive success of rare plants if their pollinators are monopolized by the more attractive abundant species (e.g. Ghazoul 2006; Bartomeus et al. 2007). In some cases though, abundant plants have demonstrated to have no effect or even facilitate the pollination of rare plants by attracting more visitors (e.g. Ghazoul 2006; Bartomeus et al. 2007). Given the difficulty to predict the consequences of bee preference for abundant plants, we recommend restoration practitioners to make an effort to resemble the original plant densities in plantings, with special consideration on isolated species (e.g. climax species in this work), which could require increases in population size to achieve adequate rates of pollen dispersal (Menz et al. 2011).

Conclusions

Here we demonstrated that the functional diversity of bee communities was still not fully recovered in restored habitats especially because of probable deficiencies in nesting resource provisioning, although these areas showed to be important in floral resources. The recuperation of bee communities might be achieved in restored corridors as the time goes by and the trees get bigger and older, bringing this way new nesting sites and other plant substrates for bee species. Secondary corridors were also found to play a role of complementary habitat support in spite of their high degradation stage, in the same way as other studies indicate that antropogenic landscape elements are important for directing the dispersal of pollinators to better quality patches throughout a hostile matrix (e.g. Dicks et al. 2010; Van Rossum & Triest 2012; Kormann et al. 2016). Among sugarcane fields, however, several bee species with different sizes and flight capabilities were also present even at far distances from fragments (>1000 km), hence supporting the idea that in order to enhance the dispersal and colonization of bees in restored areas, the implementation of corridors directly connected to source fragments might not be required since bees can disperse throughout the matrix, but other cheaper possibilities as for example the creation or preservation of stepping-stone vegetation areas between habitat patches could result more adequate (Menz et al. 2011; Forup et al. 2008).

Regarding pollination, we found that although the structure of the interactions between bees and plants was not very affected, the diversity and composition of floral resources significantly changed, with more negative consequences on the woody species that represent the basis of restored and remnant ecosystems, giver their stronger association with the more vulnerable bee species. Environmental degradation is driving the communities of interacting bees and plants to a state of equilibrium were both are well adapted to each other and therefore, do not depend on conserved habitats for their maintenance. Consequently, new plant communities as restoration plantings should not rely on the pollinators present on degraded areas, but on those in the surrounding primary forest patches for ensuring their reproductive success. In cases of highly degraded remnants, additional actions such as reintroducing extinct pollinators or increasing plant/bee population sizes might be required.

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General Conclusions

On the first chapter, we demonstrate how different restoration practices can lead to variable functional assemblages in plant communities that could alter the equilibrium of ecological functions like pollination. Changes on the proportions of several pollination modes could affect pollinators by decreasing or increasing floral resource availability, but also, may have negative or positive consequences on plant pollination throughout competition or facilitation processes, respectively. Such changes on pollination modes were found to be stronger under higher levels of historical disturbance in the region, and human manipulation in active restoration practices.

The information obtained from the first chapter allows us to estimate the pollinator diversity requirements of tree communities, and the resource availability for pollinators in these tropical forests. Specifically in the case of bees, we found that the demand for their function as pollinators in restored forests is even higher than that in primary forests, since many bee pollinated tree species are widely and preferably used in restoration plantings due to their great colonizing ability, or because of the many other ecosystem functions and services that they provide.

On the second chapter we observed that bee communities were getting benefited by such over-representation of bee floral resources in restoration plantings. Many bee species were found to visit more frequently the tree species in these areas than other plants in primary forests (i.e. climax species) and other more disturbed sites (i.e. ruderals). In spite of this preference, the pollination function in restored communities was probably still not assured, since the bee abundance and functional diversity of bee communities was not fully recovered, maybe because of other habitat requirements that remain undersupplied (e.g. nesting resources).

Nevertheless, we found that there was a high functional diversity on bee communities in restored areas and their associated habitats in the landscape, that were able to survive under conditions of very high habitat degradation and fragmentation. However, only a small part of these communities, which was also found to be the most vulnerable one, was the principal in charge of the pollination of the most important plant species in primary and restored forests. We hope these groups of bee species, as well as other susceptible plant groups that were indicated throughout this work, get prioritized and considered in future decisions on conservation and restoration planning of tropical forests.

General Abstract

The conservation and restoration of pollinators is essential for sustaining viable plant populations in fragmented landscapes because they promote genetic diversity among isolated individuals. As it is expected that populations in remnant and restored forests perpetuate with the passing of the years, restoration programs on highly fragmented agricultural landscapes should be planned with consideration for achieving this purpose. In this work, we evaluated plant-pollinator interactions in restored tropical forests, aiming to establish first, the pollination requirements of plant species in these communities, and secondly, if the pollinator requirements are being fulfilled and the interactions between plants and pollinators are being recovered throughout restoration practices.

This work comprises two chapters: On the first one (*“Are the assemblages of tree pollination modes being recovered by tropical forest restoration?”*) we did an extensive literature review about the pollination biology of tree species in primary forests, restoration plantings and naturally regenerated forests, to compare and identify patterns on the functional diversity and the assemblages of plant pollination modes. On the second chapter (*“Functional responses and effects from bee communities in restored tropical forests”*) we sampled bees (i.e. the most important pollinators) and identified the pollen grains attached to their bodies in primary forests, restoration plantings, disturbed herbaceous areas and sugar cane fields; afterwards we analyzed and compared the functional diversity of bee communities and their floral resources, and the structure of plant-bee interactions, as well as in response to habitat isolation.

We found that different restoration practices leaded to changes on patterns of abundance and species proportions of several plant pollination modes, which were stronger in locations under active restoration activities than in naturally regenerated forests. Specifically in the case of bees, we found that the demand for their function as pollinators in restoration plantings was even higher than that in primary forests, since many bee pollinated tree species were being widely and preferably used due to their great colonizing ability, or because of the many other ecosystem functions and services that they provide. We observed that bee communities were getting benefited by such over-representation of bee floral resources, since many species visited more frequently the tree species in restoration plantings than any other habitat. In spite of such preference, the bee abundance and functional diversity of bee communities was not fully recovered in restoration areas, maybe because of other habitat requirements that still remained undersupplied (e.g. nesting resources). Although the functional diversity on bee communities was high in general, only a small part, which was also the most vulnerable (i.e. larger bees that nest above-ground, have different levels of sociality and are polylectics), was the principal in charge of the pollination of the most important plant species in primary and restored forests (i.e. native woody plants, from initial successional stages and with different pollination modes).

Throughout this work we analyzed and discussed the implications of these results for the recovery of plant-pollinator interactions and on future decisions in restoration and conservation planning.

Keywords: biodiversity conservation; community assemblage; ecosystem management; forest fragmentation; functional diversity; pollination syndromes; semi-deciduous forest.

Resumo Geral

A conservação e restauração dos polinizadores são essenciais para a manutenção das populações vegetais nas paisagens fragmentadas, pois eles proporcionam diversidade genética entre os indivíduos espacialmente isolados. Dado que se espera que as populações nas florestas remanescentes e restauradas se perpetuem com o passar dos anos, os programas de restauração devem ser planejados também considerando alcançar este objetivo. Neste trabalho avaliamos as interações planta-polinizador em florestas tropicais em restauração, objetivando estabelecer primeiro, os requerimentos de polinização nestas comunidades e segundo, se os requerimentos de habitat dos polinizadores estão sendo satisfeitos e as interações entre plantas e polinizadores estão se recuperando através das práticas de restauração.

O trabalho compreende dois capítulos: No primeiro (*"Os sistemas de polinização de espécies arbóreas estão se recuperando por meio da restauração de florestas tropicais?"*) realizamos uma revisão exaustiva na literatura sobre a biologia da polinização das espécies de árvores em florestas primárias, plantios de restauração e florestas naturalmente regeneradas, para depois comparar e identificar os padrões na diversidade funcional e nas assembléias de modos de polinização. No segundo capítulo (*"Respostas e efeitos funcionais das comunidades de abelhas em florestas tropicais restauradas"*) coletamos abelhas (i.e. os principais polinizadores) e identificamos os grãos de pólen aderidos no seu corpo, em florestas primárias, plantios de restauração, áreas herbáceas degradadas e cultivos de cana-de-açúcar; depois analisamos e comparamos a diversidade funcional das comunidades de abelhas e seus recursos florais, a estrutura das redes de interação e também em resposta ao isolamento do habitat.

Encontramos que diferentes práticas de restauração geraram maiores mudanças nas proporções de vários modos de polinização, em lugares submetidos a atividades de restauração ativa do que nas florestas regeneradas naturalmente. Especificamente no caso das abelhas, encontramos que a demanda pela sua função como polinizadores nos plantios de restauração era ainda maior do que nas florestas primárias, pois muitas espécies de árvores polinizadas por abelhas estavam sendo preferivelmente plantadas graças a sua maior habilidade como colonizadoras, ou devido à outras funções e serviços ecossistêmicos que elas provem. Observamos que as abelhas estavam se beneficiando dessa super-representação de recursos florais, dado que várias espécies visitaram mais freqüentemente as árvores presentes nos plantios de restauração do que em outras áreas. Apesar dessa preferência, a abundância de indivíduos e a diversidade funcional nas comunidades de abelhas ainda não estavam totalmente recuperadas nas áreas em restauração, provavelmente porque alguns dos seus requerimentos de habitat estão ainda pouco fornecidos (e.g. recursos de nidificação). Mesmo que a diversidade funcional nas comunidades de abelhas tenha sido alta de maneira geral, somente uma pequena parte dela, que também foi a mais vulnerável (i.e. abelhas de maior porte que nidificam por cima do solo, tem diferentes níveis de sociabilidade e são polilécticas), foi a principal encarregada do transporte de pólen das plantas mais importantes das florestas primárias e restauradas (i.e. plantas lenhosas, nativas, de succession inicial e com diferentes modos de polinização).

Ao longo deste trabalho analisamos e discutimos as implicações destes resultados para a recuperação das interações planta-polinizador e nas futuras decisões no planejamento da restauração e conservação ecológica.

Palavras chave: floresta semidecidual; manutenção de ecossistemas; fragmentação florestal; diversidade funcional; síndromes de polinização, conservação da biodiversidade; estrutura de comunidades

Appendices

APPENDIX 1.1. LOCATION AND DESCRIPTION OF THE STUDIED SITES.

Location		**coordinates**	**Description**	**Ref***
Remnants				
1	São João Sugar Factory, Araras (SP)	22°22'44.80"S, 47°18'28.43"W	100 ha protected fragment within a sugar cane matrix. Sample size 0.3 ha, 69 spp.	(12)
2	Cafundó Natural Reserve, Itapemirim (ES)	20°43'S, 41°13'W	517 ha forest reserve, occasional selective logging. Sample size 2.4 ha, 232 spp.	(1)
3	Fazenda Atibaia, Sao Jose do Barreiro (SP)	22°38'34"S, 44°39'22"W	14 ha fragment close to a natural reserve, occasional selective logging. Sample size 540 ind, 113 spp.	(5)
4	Fazenda São Domingos, Areias (SP)	22°38'34"S 44°43'24"W	300 ha fragment close to a natural reserve, occasional selective logging. Sample size 540 ind, 125 spp.	(5)
5	Fazenda Atibaia, Sao Jose do Barreiro (SP)	22°38'19"S, 44°39'39"W	14 ha fragment close to a natural reserve, occasional selective logging. Sample size 540 ind, 132 spp.	(5)
6	dos Caetetus Ecological Station, Gália (SP)	22°22'S, 49°40'W	2178.84 ha protected area. Sample size 0.6 ha, 62 spp.	(3)
7	Santa Genebra Natural Reserve, Campinas (SP)	22°49'45"S, 47°06'33"W	251.77 ha forest reserve, sampled area 100 m far from border, selective logging, not recently perturbed. Sample size 0.35 ha, 37 spp.	(6)
8	Santa Genebra Natural Reserve, Campinas (SP)	22°49'45"S, 47°06'33"W	251.77 ha forest reserve, sampled area 50 m far from border, selective logging, recently perturbed. Sample size 0.35 ha, 68 spp.	(6)
9	Santa Genebra Natural Reserve, Campinas (SP)	22°49'45"S, 47°06'33"W	251.77 ha forest reserve, sampled area 10 m far from border, selective logging, not recently perturbed. Sample size 0.35 ha, 90 spp.	(6)
10	Fazenda Santa Irene, Itatinga (SP)	23°17'S, 48°33'W	15 ha fragment influenced by Cerrado vegetation. Sample size 0.42 ha, 95 spp.	(7)
11	Cachoeira River, Itarapina (SP)	22°23'S, 47°53'W	Riparian forest with high inclination. Sample size 12.8 ha, 59 spp.	(8)
12	Mata do Paraíso Natural Reserve, Vicosa (MG)	20°48'07"S 42°51'31"W	195 ha forest reserve, occasional selective logging. Sample size 0.3 ha, 78 spp.	(14)
13	Passa Cinco River, Ipeúna (SP)	22°24'02"S, 47°43'32"W	60 ha riparian forest. Sample size 0.8 ha, 66 spp.	(19)
14	Sao Roque Municipal Park, Sao Roque (SP)	23°31'26"S, 47°06'45"W	130 ha forest reserve sampled area close to border. Sample size 0.31 ha, 77 spp.	(9)
15	Sao Roque Municipal Park, Sao Roque (SP)	23°31'26"S, 47°06'45"W	130 ha forest reserve sampled area at interior forest. Sample size 0.31 ha, 65 spp.	(9)
16	Sao Roque Municipal	23°31'26"S,	130 ha forest reserve sampled area at interior	(9)

	Park, Sao Roque (SP)	47°06'45"W	forest. Sample size 0.31 ha, 68 spp.	
17	Sebastião Aleixo da Silva Ecological Station, Bauru (SP)	22°19'S, 49°04'W	200 ha forest reserve, selective logging and occasional livestock grazing. Sample size 0.8 ha, 55 spp.	(22)
18	Sebastião Aleixo da Silva Ecological Station, Bauru (SP)	22°19'S, 49°04'W	200 ha forest reserve, selective logging and intense livestock grazing. Sample size 0.8 ha, 69 spp.	(22)
Restored forests				
19	São João Sugar Factory, Araras (SP)	22°26'22.13"S, 47°21'43.33"W	8 ha, 50 m-width riparian forest stripe, restored 8 years ago after sugar cane cultivation. 3m x 2m spacing plantations using pioneers, secondary initials and climax species without any pre-established spatial arrangement. Sample size 0.3 ha, 69 spp.	(12)
20	São João Sugar Factory, Araras (SP)	22°25'46.95"S, 47°20'36.80"W	12 ha, 150 m riparian forest stripe, planted 12 years ago after sugar cane cultivation. 3m x 2m spacing plantations using pioneers, secondary initials and climax species without any pre-established spatial arrangement. Sample size 0.3 ha, 51 spp.	(12)
21	Bandeirantes highway, Santa Bárbara D'Oeste (SP)	22°46'S, 47°26'W	146.3 ha forest stripe at a highway margin, restored 8 years ago after sugar cane cultivation and pasture. 3m x 2m spacing plantations in quadrangular modules, interspersing species from initial and late successional states. Sample size 0.54 ha, 65 spp.	(15)
22	Ester Sugar Factory, Cosmopolis (SP)	22°40'S, 47°12'W	25 ha riparian forest, planted 55 years ago after sugar cane cultivation and pasture. Plantations included 71 native and exotic species without any pre-established spatial arrangement. Sample size 0.75 ha, 93 spp.	(15)
23	Ribeirao Cachoerinha, Iracemapolis (SP)	22°34'S, 47°30'W	30-50 m width riparian forest stripe, restored 23 years ago after sugar cane cultivation. 3m x 3m and 4m x4m spacing plantations, interspersing species from initial and late successional states. Sample size 0.72 ha, 92 spp.	(15)
24	Edmundo Navarro de Andrade Forest reserve, Rio Claro (SP)	22°25'S, 47°31'W	1.3 ha *Eucalyptus* stand planted 93 years ago. Plantations included native species with spacing of 3m x 2m. Sample size 0.12 ha, 26 spp.	(15)
25	Fazenda Cananeia, Candido Motta (SP)	22°46'S, 50°27'W	640 ha riparian forest restored 18 years ago after agriculture. Plantations include native and introduced species continuously planted until the study date and interspersed with cultivars when light conditions were proper. Sample size 1ha, 23 spp.	(16)
26	Fazenda Cananeia, Candido Motta (SP)	22°46'S, 50°27'W	640 ha riparian forest planted 28 years ago after agriculture. Plantations include native and introduced species continuously planted until the study date and interspersed with cultivars when light conditions were proper. Sample size 1ha, 37 spp.	(16)
27	Viçosa Federal	20°46'28.37"S,	40 year-old forest restored after *Eucalyptus*	(10)

	University, Viçosa (MG)	42°52'37.26"W	cultivation, surrounded by exotic timberlands. Plantations included 56 native and exotic species, with spacing of 4m x 4m. Sample size 1ha, 110 spp.	
28	Pacotuba National Forest, Cachoeiro de Itapemirim ES	20°44'22"S, 41°17'38"W	10 year-old small forest planted after pasture, surrounded by secondary and conserved forest. Plantations included native and exotic species, with spacing of 3m x 4m. Sample size 0.4 ha, 38 spp.	(18)
29	Sao Luiz Dam, Santa Bárbara D'Oeste (SP)	22°45'S, 47°24'W	12 km-length riparian forest stripe, restored 13 years ago after agriculture. Plantations included mainly native local species, with spacing of 3m x 2m. Sample size 1 ha, 55 spp.	(11)
Secondary forests				
30	Viçosa Federal University, Viçosa (MG)	20°46'S, 42°52'W	50 ha forest regenerated 28 years ago after coffee cultivation and pasture, surrounded by conserved forest. Sample size 0.25 ha, 75 spp.	(2)
31	Viçosa Federal University, Viçosa (MG)	20°46'S, 42°52'W	50 ha forest recovered for 50 years after coffee cultivation and pasture, surrounded by conserved forest. Sample size 0.25 ha. 58 spp.	(2)
32	Fazenda Santa Cecília do Ingá, Volta Redonda (RJ)		90 ha forest recovered for 50 years after coffee cultivation. Sample size 0.1 ha, 30 spp.	(4)
33	Dona Rita Hydroelectric Reservoir, Itambé do Mato Dentro (MG)	19°26'S, 43°14'W	9.8 ha fragment recovered for 15 years after logging for charcoal production. Sample size 0.45 ha, 152 spp.	(13)
34	Dona Rita Hydroelectric Reservoir, Itambé do Mato Dentro (MG)	19°26'S, 43°14'W	9.8 ha fragment recovered for 40 years after logging for charcoal production. Sample size 0.38 ha, 145 spp.	(13)
35	Mata do Paraíso Forest Reserve, Viçosa (MG)	20°48'07"S, 42°51'31"W	small forest recovered for 40 years after pasture, surrounded by conserved forest, Sample size 0.3 ha, 55 spp.	(14)
36	Piranga (MG)	20°41'34.3"S, 43°19'38.2"W	139.14 ha forest fragment recovered for 40 years after burning and logging. Sample size 22 ha, 169 spp.	(17)
37	Sao Paulo University, Sao Paulo (SP)	23°33'S, 46°43'W	10.2 ha forest fragment in urban area, recovered for about 100 years after agriculture and pasture, occasional selective logging. Sample size 0.25 ha, 72 spp.	(20)
38	Santa Genebra Natural Reserve, Campinas (SP)	22°49'45"S, 47°06'33"W	10 ha forest recovered for 17 years after burning, surrounded by conserved forest. Sample size 0.45ha, 48 spp.	(21)
39	Sebastião Aleixo da Silva Ecological Station, Bauru (SP)	22°19'S, 49°04'W	forest recovered for 40 years after agriculture and pasture, surrounded by conserved forest, recently perturbed by occasional livestock grazing. Sample size 0.8 ha, 75 spp.	(22)
40	Sebastião Aleixo da Silva Ecological Station, Bauru (SP)	22°19'S, 49°04'W	forest recovered for 40 years after agriculture and pasture, surrounded by conserved forest, recently perturbed by intense livestock grazing. Sample size 0.8 ha, 59 spp.	(22)

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Appendix 1.2. Tree species with pollination modes and number of sites present on each forest type.

Specialized pollination modes were classified as ‘bird’, ‘bat’, ‘wasp’, ‘fly’, ‘moth’, ‘beetle’, ‘small insect’ (trips, rove beetles, etc.), ‘bee’ and ‘wind’. Mixed pollination modes corresponding to combinations of two or more functional groups included ‘insect’ (various types), ‘pollen consumer’ (various types of insects excluding nectar consumers such as lepidopterans), ‘big animal’ (large bees, birds, lepidopterans and bats), ‘long tongue’ (bees, lepidopterans, birds) and ‘vertebrate’ (hummingbirds and bats).

Family	**Species**	**Pollination mode**	**Remnant (n=18)**	**Restored (n=11)**	**Secondary (n=11)**
Achariaceae	*Carpotroche brasiliensis*	pollen consumer	2	1	4
Anacardiaceae	*Astronium concinnum*	pollen consumer	1		
	Astronium fraxinifolium	pollen consumer		1	2
	Astronium graveolens	pollen consumer	11	5	7
	Lithraea molleoides	insect	1	1	
	Mangifera indica	insect		5	
	Myracrodruon urundeuva	insect		3	
	Rhus succedanea	insect		1	
	Schinus molle	insect		1	
	Schinus therebinthifolius	insect	1	9	
	Spondias macrocarpa	insect		1	
	Spondias mombin	insect		1	
	Spondias venulosa	insect	1		
	Tapirira guianensis	insect	4	1	3
	Thyrsodium spruceanum	insect			2
Annonaceae	*Anaxagorea dolichocarpa*	beetle	1		
	Anaxagorea phaeocarpa	beetle			2
	Annona acutiflora	beetle	1		
	Annona cacans	beetle	7	1	3
	annona glabra	beetle	3		
	Annona muricata	beetle		3	
	Cymbopetalum brasiliense	beetle			1
	Duguetia flagellaris	beetle	1		
	Duguetia lanceolata	beetle	2		2
	Guatteria australis	beetle	5		1
	Guatteria nigrescens	beetle	4	1	3
	Guatteria pogonopus	beetle			2
	Guatteria seaustralis	beetle			1
	Guatteria sellowiana	beetle	3		1
	Guatteria villosissima	beetle			2
	Oxandra nitida	beetle	1		
	Rollinia emarginata	beetle		1	
	Rollinia laurifolia	beetle			2
	Rollinia mucosa	beetle	1	1	
	Rollinia sericea	beetle	2		1
	Rollinia sylvatica	beetle	5	1	3
	Trigynaea oblongifolia	beetle	1		
	Unonopsis guatterioides	beetle	2		1
	Xylopia aromatica	beetle			1
	Xylopia brasiliensis	beetle	4		2
	Xylopia sericea	beetle	3	1	5
Apocynaceae	*Aspidosperma camporum*	moth	3		
	Aspidosperma cylindrocarpon	moth	4	1	
	Aspidosperma discolor	moth	1		
	Aspidosperma dispermum	moth	1		
	Aspidosperma illustre	moth	1		
	Aspidosperma olivaceum	moth	1	1	

	Aspidosperma parvifolium	moth	3		2
	Aspidosperma polyneuron	moth	11	2	2
	Aspidosperma ramiflorum	moth	4	3	1
	Aspidosperma spruceanum	moth			2
	Himatanthus bracteatus	moth	1		
	Himatanthus lancifolius	moth			3
	Himatanthus phagedaenicus	moth	1		
	Malouetia arborea	moth	3		2
	Rauvolfia mattfeldiana	long tongue	1		
	Rauvolfia sellowii	insect			1
	Tabernaemontana catharinensis	moth	3		2
	Tabernaemontana fuchsiaefolia	moth		1	
	Tabernaemontana hystrix	moth	3		1
	Tabernaemontana laeta	moth	3		1
Aquifoliaceae	*Ilex cerasifolia*	insect			3
	Ilex paraguariensis	insect	1		
	Ilex pseudobuxus	insect	1		
	Ilex theezans	insect	1		
Araliaceae	*Aralia warmingiana*	insect	1		1
	Dendropanax cuneatus	insect	3	2	1
	Schefflera morototoni	insect		1	4
	Schefflera calva	insect	3		
Araucariaceae	*Araucaria angustifolia*	wind		1	
Arecaceae	*Acrocomia aculeata*	beetle		1	1
	Aiphanes horrida	insect-wind		1	
	Allagoptera caudescens	undetermined			1
	Archontophoenix cunninghamiana	bee		1	1
	Astrocaryum aculeatissimum	beetle	2		1
	Attalea dubia	undetermined		1	
	Bactris acanthocarpa	beetle			1
	Caryota urens	undetermined		1	
	Dypsis lutescens	undetermined		1	
	Euterpe edulis	bee	2	1	
	Geonoma schottiana	insect	2		
	Mauritia flexuosa	beetle		1	
	Phoenix reclinata	insect-wind		1	
	Roystonea oleracea	bee		1	
	Syagrus oleracea	beetle-bee	6		
	Syagrus romanzoffiana	beetle-bee	9	3	8
Asparagaceae	*Cordyline fruticosa*	insect	2		
Asteraceae	*Eremanthus erythropappus*	insect			1
	Eremanthus incanus	insect			2
	Eupatorium macrophyllum	insect	1		
	Gochnatia polymorpha	insect	2		2
	Morithamnus ganophyllus	insect			1
	Piptocarpha angustifolia	insect	1		
	Piptocarpha axillaris	insect	1		
	Piptocarpha macropoda	insect	2		3
	Piptocarpha ramiflora	insect	1		
	Piptocarpha sellowii	insect	2		
	Vernonanthura diffusa	insect	2		2
	Vernonanthura divaricata	insect			1
	Vernonia diffusa	insect	4	1	
	Vernonia polyanthes	insect			1
Bignoniaceae	*Cybistax antisyphilitica*	bee	2		1
	Handroanthus achraceus	bee	1		
	Handroanthus chrysotrichus	bee		4	
	Handroanthus heptaphyllus	bee	2	2	
	Handroanthus impetiginosus	bee		4	
	Handroanthus ochraceus	bee	1	4	
	Handroanthus vellosoi	bee		1	
	Jacaranda cuspidifolia	bee		2	
	Jacaranda macrantha	bee	6		4
	Jacaranda mimosifolia	bee		4	
	Jacaranda puberula	bee	1		5
	Paratecoma peroba	long tongue	1	1	
	Sparattosperma leucanthum	bee	3	2	7
	Spathodea campanulata	vertebrate		5	
	Tabebuia alba	bee			1
	Tabebuia arianeae	bee	1		

	Tabebuia avellanedae	bee			
	Tabebuia chrysotricha	bee	1		1
	Tabebuia heptaphylla	bee	2	2	1
	Tabebuia heterophylla	bee			
	Tabebuia impetiginosa	bee		1	1
	Tabebuia pentaphylla	bee			
	Tabebuia rosea	bee		1	
	Tabebuia roseoalba	bee	1	4	
	Tabebuia vellosoi	bee			2
	Tecoma stans	bee	1	3	2
	Zeyheria tuberculosa	bee	3	2	3
Bixaceae	*Bixa orellana*	bee		2	
Boraginaceae	*Cordia abyssinica*	insect		5	
	Cordia americana	insect	4	4	2
	Cordia ecalyculata	insect	6	1	3
	Cordia magnoliifolia	insect			2
	Cordia nodosa	insect			1
	Cordia sellowiana	insect	3		2
	Cordia superba	insect	3	2	1
	Cordia trichotoma	insect	2	2	2
Burseraceae	*Crepidospermum atlanticum*	insect	1		
	Protium brasiliense	insect			1
	Protium heptaphyllum	insect	6	2	4
	Protium warmingianum	insect	1	1	4
	Protium widgrenii	insect			1
	Protium spruceanum	insect	1		2
Cactaceae	*Opuntia brasiliensis*	bee	1		
Calophyllaceae	*Kielmeyera lathrophyton*	pollen consumer			1
Canellaceae	*Cinnamodendron dinisii*	beetle			1
Cannabaceae	*Celtis iguanaea (syn. ehrenbergiana)*	wind	3		2
	Trema micrantha	wind	6	3	3
Capparaceae	*Capparidastrum brasilianum*	big animal	1		
	Crateva benthamii	big animal		1	
Cardiopteridaceae	*Citronela megaphylla*	insect	1		
	Citronella paniculata	insect	4		
	Villaresia congonha	insect	1		
Caricaceae	*Carica papaya*	long tongue		1	
	Carica quercifolia	long tongue	1		
	Jacaratia heptaphylla	moth	1		
	Jacaratia spinosa	moth	7	1	1
Casuarinaceae	*Casuarina equisetifolia*	wind		1	
Celastraceae	*Maytenus alaternoides*	insect			1
	Maytenus cestrifolia	insect	1		
	Maytenus evonymoides	insect	4		1
	Maytenus glazioviana	insect			1
	Maytenus ilicifolia	insect	4		1
	Maytenus multiflora	insect	1		
	Maytenus robusta	insect	5		1
	Maytenus salicifolia	insect	4		2
Chrysobalanaceae	*Couepia meridionalis*	insect			2
	Hirtella hebeclada	moth	1		
	Licania hoehnei	insect	3		
	Licania hypoleuca	insect			2
	Licania kunthiana	insect	2		1
	Licania octandra	insect			1
	Licania tomentosa	insect		2	
Clethraceae	*Clethra scabra*	insect	4		2
Clusiaceae	*Calophyllum brasiliensis*	insect	1		2
	Garcinia garneriana	bee	1		
	Garcinia brasiliensis	bee	1	1	
	Tovomitopsis saldanhae	bee	1		2
Combretaceae	*Terminalia argentea*	insect	1	1	1
	Terminalia glabrescens	insect	1		3
	Terminalia kuhlmannii	insect	1		
	Terminalia phaeocarpa	insect	1		
	Terminalia triflora	insect	3	1	2
Connaraceae	*Connarus detersus*	insect	1		
Cycadaceae	*Cycas circinalis*	insect-wind		1	
Dichapetalaceae	*Stephanopodium engleri*	insect			1
Dilleniaceae	*Dillenia indica*	bee		3	

Ebenaceae	*Diospyros capreifolia*	moth	1		
	Diospyros hispida	moth			1
	Diospyros inconstans	moth	4		1
Elaeocarpaceae	*Sloanea guianensis*	bee	3		1
	Sloanea monosperma	bee	4		2
Erythroxylaceae	*Erythroxylum buxus*	insect	1		
	Erythroxylum citrifolium	insect	2		2
	erythroxylum pelleterianum	insect	2		6
	Erythroxylum pulchrum	insect	3	1	1
	Erytrhoxyllum campestre	insect	1		
Euphorbiaceae	*Acalypha sp.*	wind	1		
	Actinostemon communis	wind	1		
	Actinostemon concepcionis	wind	1		
	Actinostemon concolor	wind	7		2
	Actinostemon klotzschii	wind	6		1
	Alchornea glandulosa	wind	12	8	5
	Alchornea iricurana	wind	1		1
	Alchornea sidifolia	wind			1
	Alchornea triplinervia	wind	4		3
	Aleurites moluccana	insect		1	
	Aparisthmium cordatum	wind	2		3
	Cnidoscolus oligandrus	insect	1		
	Croton floribundus	insect	13	3	8
	Croton piptocalyx	insect	4		
	Croton salutaris	insect	2		1
	Croton urucurana	insect	1	5	2
	Croton verrucosus	insect			1
	Glycydendron amazonicum	insect	1		
	Hevea brasiliensis	insect		1	
	Hura crepitans	bat		1	
	Joannesia princeps	insect		7	
	Mabea fistulifera	big animal	1		5
	Mabea piriri	big animal	2		
	Manihot pilosa	insect	1	1	2
	Maprounea guiwindnsis	wind	3	1	2
	Pachystroma longifolium	wind	1	1	
	Philyra brasiliensis	undetermined	1		
	Ricinus communis	insect-wind		1	
	Sapium glandulosum	insect	3	1	5
	Sebastiana serrata	wind	2		1
	Sebastiania commersoniana	wind	6		
	Senefeldera verticillata	wind	3		
	Tetrorchidium rubrivenium	wind	5		
Leguminosae	*Abarema limae*	big animal	1		
	Acacia glomerosa	insect	2		
	Acacia polyphylla	insect	5	1	6
	Acosmium lentiscifolium	insect	1		
	Acosmium subelegans	insect	1		
	Albizia hasslerii	big animal	1		
	Albizia lebbeck	big animal		3	
	Albizia niopoides	big animal		1	1
	Albizia polycephala	big animal	7		7
	Anadenanthera colubrina	insect	1	3	3
	Anadenanthera falcata	insect			
	Anadenanthera macrocarpa	insect	1	1	1
	Anadenanthera peregrina	insect	1	3	3
	Anadenanthera peregrina var. falcata	insect		1	
	Andira anthelmia	bee			1
	Andira fraxinifolia	bee			2
	Andira legalis	bee			1
	Andira ormosioides	bee	2		1
	Apuleia leiocarpa	insect	1	1	7
	Bauhinia forficata	moth	4	3	1
	Bauhinia longifolia	vertebrate	3	1	3
	Bauhinia rufa	bat	1		
	Bauhinia variegata	vertebrate		1	
	Bowdichia virgilioides	bee			1
	Caesalpinia echinata	bee		3	
	Caesalpinia ferrea	bee		3	1
	Caesalpinia leiostachya	bee		1	

	Caesalpinia pluviosa	bee		3	
	Calliandra foliolosa	big animal	2		1
	Calliandra tweedii	bird	1		
	Cassia ferruginea	bee	5	2	3
	Cassia fistula	bee		1	
	Centrolobium robustum	bee		1	
	Centrolobium tomentosum	bee	8	5	3
	Chloroleucon tortum	big animal		1	
	Clitoria fairchildiana	bee		2	
	Copaifera langsdorffii	insect	5	2	6
	Copaifera lucens	insect	1		
	Copaifera trapezifolia	insect	1		
	Dahlstedtia pinnata	bird	1		
	Dalbergia brasiliensis	insect	1		
	Dalbergia elegans	insect	1		
	Dalbergia frutescens	insect			4
	Dalbergia nigra	insect	4	2	6
	Dalbergia villosa	insect			3
	Deguelia sp.	bee	1		
	Delonix regia	bird		1	
	Dimorphandra mollis	insect		1	
	Diplotropis incexis	bee	1		
	Dipteryx alata	bee		1	
	Enterolobium contortisiliquum	insect	2	5	1
	Enterolobium monjollo	insect			1
	Erythrina falcata	bird	2	1	
	Erythrina speciosa	bird		5	
	Erythrina verna	bird		1	1
	Exostyles venusta	insect	1		
	Gliricidia sepium	bee		1	
	Goniorrhachis marginata	bee	1		
	Holocalyx balansae	insect	8	5	1
	Hymenaea courbaril	bat	2	7	
	Hymenaea courbaril var. Stilbocarpa	bat			
	Hymenaea martiana	bee		1	
	Hymenolobium janeirense	bee	1		2
	Inga affinis	big animal	1		
	Inga capitata	big animal			2
	Inga cylindrical	insect	1		1
	Inga edulis	big animal	1		
	Inga hispida	big animal	1		
	Inga ingoides	big animal			1
	Inga laurina	moth		1	
	Inga leptantha	big animal			1
	Inga luschnathiana	big animal	3		
	Inga marginata	big animal	6	2	3
	Inga sessilis	big animal	2		1
	Inga striata	big animal	6		4
	Inga uruguensis	big animal	1		
	Inga vera	big animal		4	2
	Inga vera subespaffinis	big animal			1
	Inga vulpine	big animal			1
	Leicochloron incuriale	insect		1	
	Leucaena leucocephala	insect		4	
	Libidibia ferrea	bee		1	
	Lonchocarpus campestris	bee		2	
	Lonchocarpus cultratus	bee	5	3	3
	Lonchocarpus guilleminianus	bee	2		
	Lonchocarpus muehlbergianus	bee	4	7	1
	Luetzelburgia guaissara	bee	1		
	Machaerium acutifolium	bee	3		2
	Machaerium brasiliense	bee	2	1	4
	Machaerium dimorphandrum	bee			1
	Machaerium fulvovenosum	bee	1		
	Machaerium hirtum	bee	3		3
	Machaerium lanceolatum	bee			1
	Machaerium nictitans	bee	11	3	5
	Machaerium scleroxylon	bee	1	1	
	Machaerium stipitatum	bee	9	2	7
	Machaerium vestitum	bee	2		

	Machaerium villosum	bee	3	1	2
	beeanoxylon brauna	bee	2		3
	Mimosa artemisiana	insect			1
	Mimosa bimucronata	insect		3	
	Mimosa caesalpiniifolia	insect		3	
	Myrocarpus frondosus	insect	2	1	
	Myroxylon peruiferum	insect-bird	3	7	1
	Ormosia arborea	insect	3		
	Parapiptadenia pterosperma	insect	1		
	Parapiptadenia rigida	insect	3	3	2
	Parkia sp.	bat-bee		1	
	Peltogyne angustiflora	bee	1		
	Peltophorum dubium	bee	6	7	3
	Phyllocarpus riedelii	butterfly-moth-bird	1		
	Piptadenia gonoacantha	insect	12	6	10
	Piptadenia paniculata	insect	1		
	Plathymenia foliolosa	insect	1		
	Plathymenia reticulata	insect			3
	Plathymiscium floribundus	bee	4		
	Platycyamus regnellii	bee	1		
	Platymiscium pubescens	bee		1	2
	Platypodium elegans	bee	4	2	6
	Poecilanthe falcata	bee	1		
	Poecilanthe parviflora	bee		3	
	Poeppigia procera	insect	1		
	Poincianella pluviosa	bee		2	
	Pseudopiptadenia contorta	insect	5	1	3
	Pseudopiptadenia leptostachya	insect	2		
	Pseudopiptadenia warmingii	insect	1		1
	Pterocarpus rohrii	bee	1	1	
	Pterocarpus violaceus	bee		2	
	Pterodon emarginatus	bee	1		
	Pterogyne nitens	insect	1	5	2
	Samanea tubulosa	big animal		1	
	Schizolobium parahyba	bee	2	7	1
	Sclerolobium rugosum	insect			2
	Senegalia polyphylla	insect	1	2	
	Senna macranthera	bee	2	2	3
	Senna multijuga	bee	3	4	4
	Stryphnodendron guianense	insect			2
	Stryphnodendron obovatum	insect			1
	Stryphnodendron polyphyllum	insect			2
	Swartzia acutifolia	bee	1		1
	Swartzia apetala	bee	1		1
	Swartzia flaemingii	bee			1
	Swartzia macrostachya	bee			1
	Swartzia multijuga	bee			2
	Swartzia myrtifolia	bee	3		2
	Swartzia oblata	bee	1	1	
	Swartzia polyphylla	bee			2
	Sweetia fruticosa	insect	4		2
	Tachigali denudata	insect	2		1
	Tachigali paratyensis	insect	1		2
	Tachigali rugosa	insect	2		
	Tipuana tipu	bee		8	
	Vatairea heteroptera	bee	1		
	Zollernia glabra	bee	1		
	Zollernia ilicifolia	bee		1	
	Zollernia modesta	insect	1		
	Zygia latifolia	big animal			2
Fagaceae	*Castwinda sativa*	wind		1	
Humiriaceae	*Humiriastrum dentatum*	insect	1		
Hypericaceae	*Vismia brasiliensis*	bee			1
	Vismia guianensis	bee		1	2
Juglandaceae	*Juglans regia*	wind		1	
Lacistemataceae	*Lacistema pubescens*	wind	1	1	2
	Lacistema robustum	wind			1
Lamiaceae	*Callicarpa reevesii*	insect		1	
	Gbeeina arborea	bee		1	
Lauraceae	*Aniba formula*	insect	3		2

	Cinnamomum verum	insect		1	
	Cinnamomum triplinerve	insect			1
	Cryptocarya aschersoniana	insect	4		
	Cryptocarya moschata	insect	2		
	Cryptocarya saligna	insect	2		
	Endlicheria glomerata	insect			2
	Endlicheria paniculata	insect	7	1	3
	Nectandra grandiflora	insect	1		1
	Nectandra hihua	insect	1		
	Nectandra lanceolata	insect	1	1	2
	Nectandra megapotamica	insect	8	7	4
	Nectandra membranacea	insect	1		
	Nectandra oppositifolia	insect	10	2	7
	Nectandra puberula	insect			1
	Nectandra reticulata	insect			1
	Nectandra rigida	insect	1		
	Nectandra saligna	insect			1
	Nectandra warmingii	insect			1
	Ocotea beulahiae	insect	2		
	Ocotea bicolor	insect	1		
	Ocotea brachybotra	insect	3		
	Ocotea campininha	insect	2		
	Ocotea conferta	insect	1		
	Ocotea confertiflora	insect	1		
	Ocotea corymbosa	insect	9		4
	Ocotea diospyrifolia	insect	3		1
	Ocotea dispersa	insect			1
	Ocotea divaricata	insect			3
	Ocotea elegans	insect	3		
	Ocotea glaziovii	insect			1
	Ocotea indecora	insect	4		
	Ocotea lancifolia	insect	1		
	Ocotea laxa	insect			2
	Ocotea minarum	insect	1		
	Ocotea nitida	insect	1		
	Ocotea odorifera	insect	3		2
	Ocotea pretiosa	insect	1		1
	Ocotea puberula	insect	4	2	
	Ocotea pulchella	insect	1		
	Ocotea silvestris	insect	2		
	Ocotea teleiandra	insect			1
	Ocotea velloziana	insect	2		
	Ocotea velutina	insect	1		4
	Persea americana	insect	1	2	
	Persea pyrifolia	insect	1		
	Persea venosa	insect			1
	persea willdenowii	insect	1		
	Urbanodendron bahiense	insect	1		
	Urbanodendron verrucosum	insect			3
Lecythidaceae	*Cariniana estrellensis*	bee	14	5	6
	Cariniana legalis	bee	4	6	1
	Cariniana rubra	bee		1	
	Couratari asterotricha	bee	1		
	Lecythis lanceolata	bee		1	1
	Lecythis lurida	bee	1		
	Lecythis pisonis	bee	1	2	
Loganiaceae	*Strychnos brasiliensis*	insect			1
Lythraceae	*Lafoensia glyptocarpa*	bat		3	
	Lafoensia pacari	bat	2	1	
	Lagerstroemia speciosa	bee		2	
Magnoliaceae	*Magnolia champaca*	beetle		7	
	Magnolia ovata	beetle	1		
Malpighiaceae	*Bunchosia pallescens*	bee	1		
	Byrsonima ligustrifolia	bee	2		
	Byrsonima sericea	bee			2
	Heteropterys byrsonimifolia	bee			1
Malvaceae	*Adansonia digitata*	bat		1	
	Basiloxylon brasiliensis	bee		2	
	Bastardiopsis densiflora	insect		1	
	Ceiba glaziovii	bat	1		

	Ceiba speciosa	bat	6	7	5
	Christiana macrodon	insect	1		
	Eriotheca candolleana	bat			3
	Guazuma crinita	fly	1		
	Guazuma ulmifolia	fly	3	4	2
	Helicteres lhotzkyana	vertebrate		1	
	Helicteres ovata	vertebrate			1
	Heliocarpus americanus	insect	1		
	Heliocarpus popayanensis	insect		2	
	Luehea candicans	moth	2		1
	Luehea divaricata	big animal	5	3	5
	Luehea grandiflora	bat	4	5	6
	Luehea mediterranea	undetermined	1		
	Luehea speciosa	big animal		1	
	Pachira aquatica	bat		1	
	Pachira glabra	bat		5	
	Pseudobombax grandiflorum	bat	9	4	2
	Pseudobombax longiflorum	bat			1
	Pterygota brasiliensis	insect	1		
	Quararibea penduliflora	moth-bat	1		
	Sterculia curiosa	undetermined	1		
	Sterculia apetala	big animal		2	
Melastomataceae	*Miconia budlejoides*	bee	1		
	Miconia calvescens	bee			1
	Miconia candolleana	bee			1
	Miconia cinnamomifolia	bee	3	1	1
	Miconia discolor	bee			1
	Miconia fasciculata	bee			1
	Miconia hymenonervia	bee	2		
	Miconia inconspicua	bee	1		
	Miconia latecrenata	bee	1		
	Miconia lepidota	bee	2		
	Miconia pusilliflora	bee	1		
	Miconia theaezans	bee			1
	Miconia trianae	bee			1
	Miconia tristis	bee			1
	Tibouchina estrellensis	bee			1
	Tibouchina granulosa	bee		1	1
Meliaceae	*Cabralea canjerana*	moth	11	2	5
	Cedrela fissilis	insect	10	6	4
	Guarea guidonia	moth	2	4	4
	Guarea kunthiana	moth	6	2	4
	Guarea macrophylla	moth	5		3
	Melia azedarach	insect		3	1
	Toona ciliata	insect		1	
	Trichilia casaretti	insect	1		
	Trichilia catigua	insect	11	3	1
	Trichilia claussenii	insect	8	3	2
	Trichilia elegans	insect	5		2
	Trichilia emarginata	insect	1		
	Trichilia hirta	insect	1		1
	Trichilia lepidota	insect	2	1	2
	Trichilia pallens	insect	2		1
	Trichilia pallida	insect	9	1	8
	Trichilia quadrijuga	insect	1		
	Trichilia ramalhoi	insect	1		
	Trichilia silvatica	insect	2		
	Trichilia tetrapetala	insect	1		
Monimiaceae	*Mollinedia argyrogyna*	small insect	3		
	Mollinedia glabra	small insect	2		
	Mollinedia lanceolata	small insect	1		
	Mollinedia longifolia	small insect	2		
	Mollinedia schottiana	small insect	1	1	1
	Mollinedia triflora	small insect			1
	Mollinedia widgrenii	small insect	4		2
	Siparuna arianae	small insect	1		
	Siparuna guianensis	small insect	4	1	7
	Siparuna reginae	small insect			1
Moraceae	*Artocarpus heterophyllus*	insect-wind		1	
	Artocarpus integer	insect		1	

	Brosimum gaudichaudii	insect-wind	1		
	Brosimum glaziovii	insect-wind	3		
	Brosimum guianense	insect-wind	4		3
	Brosimum lactescens	insect-wind	1		3
	Clarisia ilicifolia	wind	2		
	Ficus citrifolia	wasp	2	1	
	Ficus clusiifolia	wasp	1		
	Ficus enormis	wasp			1
	Ficus eximia	wasp		2	
	Ficus glabra	wasp	4		2
	Ficus gomelleira	wasp	3		1
	Ficus guaranitica	wasp		3	
	Ficus insipida	wasp	3	2	2
	Ficus longifolia	wasp	1		
	Ficus microcarpa	wasp		1	
	Ficus organensis	wasp			1
	Ficus trigona	wasp		1	
	Maclura tinctoria	wind	5	3	5
	Morus nigra	wind		2	
	Naucleopsis oblongifolia	small insect	1		1
	Pseudolmedia hirtula	undetermined	1		
	Sorocea bonplandii	wind	7		5
	Sorocea guillerminiana	wind	1		3
Myristicaceae	*Bicuiba oleifera*	small insect	2		
	Virola bicuhyba	small insect			1
Myrtaceae	*Blepharocalyx salicifolius*	bee			1
	Calycorectes acutatus	insect	1		
	Calyptranthes clusiifolia	insect			3
	Calyptranthes concinna	insect	2		1
	Campomanesia dichotoma	bee			2
	Campomanesia espiritosantensis	bee	1		
	Campomanesia guaviroba	bee	6		1
	Campomanesia guazumaefolia	bee	7		2
	Campomanesia laurifolia	bee	1		
	Campomanesia rhombea	bee	1	1	
	Campomanesia xanthocarpha	bee	7		2
	Corymbia citriodora	big animal		1	
	Eucalyptus sp.	big animal		1	1
	Eugenia blastantha	pollen consumer	5		
	Eugenia brasiliensis	pollen consumer			1
	Eugenia cerasiflora	pollen consumer	3		1
	Eugenia cuprea	pollen consumer			1
	Eugenia dodoneaefolia	pollen consumer	1		
	Eugenia egensis	pollen consumer	2		
	Eugenia excelsa	pollen consumer	2		
	Eugenia florida	pollen consumer	1	1	3
	Eugenia francavilleana	pollen consumer	1		
	Eugenia gardneriana	pollen consumer			1
	Eugenia glazioviana	pollen consumer	2		
	Eugenia involucrata	pollen consumer			1
	Eugenia ligustrina	pollen consumer	1		
	Eugenia melanogyna	pollen consumer	3		
	Eugenia moraviana	pollen consumer	1		
	Eugenia myrcianthes	pollen consumer			
	Eugenia neoglomerata	pollen consumer			1
	Eugenia neolanceolata	pollen consumer			2
	Eugenia piryformis	pollen consumer	1		
	Eugenia platyphylla	pollen consumer	1		
	Eugenia platysema	pollen consumer	1		
	Eugenia pluriflora	pollen consumer	1		
	Eugenia prasina	pollen consumer	1		
	Eugenia racemulosa	pollen consumer	1		
	Eugenia repanda	pollen consumer	1		
	Eugenia speciosa	pollen consumer	1		
	Eugenia stictosepala	pollen consumer	4		1
	Eugenia subterminalis	pollen consumer	1		
	Eugenia tinguyensis	pollen consumer	2		
	Eugenia uniflora	pollen consumer	2	3	1
	Eugenia vattimoana	pollen consumer	1		
	Eugenia verrucosa	pollen consumer	1		

	Marlierea excoriata	pollen consumer	2		
	Marlierea racemosa	pollen consumer			1
	Marlierea warmingiana	pollen consumer			2
	Marlieria tomentosa	pollen consumer	1		
	Myrceugenia myrcioides	pollen consumer	1		
	Myrceugenia ovata	pollen consumer			1
	Myrcia albotomentosa	pollen consumer	1		
	Myrcia anacardiifolia	pollen consumer			2
	Myrcia detergens	pollen consumer			2
	Myrcia eriopus	pollen consumer			1
	Myrcia fallax	pollen consumer	2	1	3
	Myrcia glabra	pollen consumer			1
	Myrcia hebepetala	pollen consumer	1		1
	Myrcia laruotteana	pollen consumer			1
	Myrcia lineata	pollen consumer	1		
	Myrcia multiflora	pollen consumer	1		
	Myrcia riatenella	pollen consumer			1
	Myrcia richardiana	pollen consumer			1
	Myrcia rostrata	pollen consumer	1		3
	Myrcia rufula	pollen consumer			1
	Myrcia selloi	pollen consumer	1		
	Myrcia sphaerocarpa	pollen consumer	1		
	Myrcia splendens	pollen consumer	8	1	1
	Myrcia tijucensis	pollen consumer	1		
	Myrcia tomentosa	pollen consumer	3		
	Myrcianthes pungens	insect	1		
	Myrciaria ciliolata	bee			1
	Myrciaria floribunda	pollen consumer	12		1
	Myrciaria glomerata	pollen consumer		2	2
	Neomitranthes glomerata	pollen consumer	2		
	Neomitranthes langsdorffii	pollen consumer	1		
	Neomitranthes stictophylla	pollen consumer	1		
	Pimenta pseudocaryophyllus	pollen consumer			2
	Plinia cauliflora	insect	2		2
	Plinia grandifolia	insect	1		
	Plinia involucrata	insect	1		
	Psidium cattheianum	bee		2	1
	Psidium guajava	bee		5	2
	Psidium guineense	bee	1	1	
	Psidium myrtoides	bee	1		
	Psidium robustum	bee			1
	Psidium rufum	bee			3
	Syzygium cumini	bee		7	1
	Syzygium jambos	big animal	2		
Nyctaginaceae	*Andradea floribunda*	undetermined	1		
	Guapira hirsuta	insect	3		2
	Guapira noxia	insect	1		
	Guapira opposita	insect	14	2	7
	Guapira tomentosa	insect	1		
	Pisonia ambigua	insect	7		1
	pisonia zapallo	insect			1
	Ramisia brasiliensis	undetermined	1		
Ochnaceae	*Ouratea parviflora*	bee			1
	Ouratea polygyna	bee			1
	Ouratea semiserrata	bee			1
Olacaceae	*Cathedra rubricaulis*	insect	1		
	Dulacia sp.	insect	1		
	Heisteria ovata	insect	1		
	Heisteria silvianii	insect	1		
Oleaceae	*Ligustrum lucidum*	insect		4	
Opiliaceae	*Agonandra excelsa*	wind	4		1
Peraceae	*Chaetocarpus echinocarpus*	insect			2
Peraceae	*Pera glabrata*	insect	3	1	4
	Pera heteranthera	insect	2		
	Pogonophora schomburgkiana	insect			2
Phyllanthaceae	*Hieronyma alchorneoides*	insect	3		2
	Hieronyma oblonga	insect	1		
	margaritaria nobilis	small insect	1		1
	Phyllanthus acuminatus	small insect	4		
	Savia dictyocarpa	insect	3		3

Phytolaccaceae	*Gallesia integrifolia*	insect	7	4	
	Seguieria langsdorffii	insect	4		1
Picramniaceae	*Picramnia ciliata*	insect	1		
	Picramnia parvifolia	insect			1
	Picramnia regnelli	insect	1		
	Picramnia warmingiana	insect	1		
Pinaceae	*Pinus strobus*	wind		1	
Piperaceae	*Piper aduncum*	pollen consumer		2	
	Piper amalago	pollen consumer	3	2	1
	Piper arboreum	insect-wind	2		1
	Piper cernuum	insect-wind	1		
	Piper gaudichaudianum	insect-wind	1		
Pittosporaceae	*Pittosporum undulatum*	insect		2	
Poaceae	*Guadua angustifolia*	wind			1
Podocarpaceae	*Podocarpus sellowii*	wind	1		
Polygalaceae	*Acanthocladus pulcherrimus*	insect	1		
Polygonaceae	*Triplaris americana*	insect		5	
	Coccoloba glaziovii	insect	1		
	Coccoloba laevis	insect	1		
	Coccoloba warmingii	insect	1		
	Ruprechtia laurifolia	insect	1		
	Ruprechtia laxiflora	insect	2		
Primulaceae	*Ardisia sp*	insect	1		
	Myrsine coriacea	wind	2	1	2
	Myrsine gardneriana	wind			1
	Myrsine guiwindnsis	wind			1
	Myrsine umbellata	wind	7	2	3
Proteaceae	*Euplassa incana*	moth			1
	Euplassa legalis	moth			1
	Euplassa organensis	moth			1
	Grevillea robusta	mammal-bird		2	
	Roupala brasiliensis	moth			1
	Roupala montana	moth	1		2
Proteaceae	*Roupala montana var. paraensis*	moth	3		
Putranjivaceae	*Drypetes sp.*	insect	1		
Rhamnaceae	*Colubrina glandulosa*	insect	5	2	2
	Hovenis dulcis	insect		2	
	Rhamnidium elaeocarpum	insect	5	3	2
	Ziziphus glaziovii	insect	1		
Rhyzophoraceae	*Paradrypetes ilicifolia*	insect	1		
Rosaceae	*Eriobotrya japonica*	insect		2	
	Prunus myrtifolia	insect	3	1	2
	Prunus sellowii	insect	5	1	3
Rubiaceae	*Alseis floribunda*	insect		1	1
	Amaioua guianensis	insect	3		5
	amaioua intermedia	insect	5		1
	Bathysa australis	insect	4		1
	Bathysa gymnocarpa	insect			1
	Bathysa mendoncae	insect			1
	Bathysa nicholsonii	insect			4
	Bathysa stipulata	insect	2		
	Calycophyllum spruceanum	long tongue		1	
	Chomelia obtusa	long tongue	1		
	Chomelia parvifolia	long tongue			1
	Chomelia pubescens	long tongue	1		
	Chomelia sericea	long tongue	1		
	Coffea arabica	insect	4		1
	Cordiera elliptica	insect	1		
	Coutarea hexandra	big animal	3		5
	Faramea cyanea	long tongue	1		
	Faramea montevidensis	long tongue			1
	Genipa americana	bee		4	
	Genipa infundibuliformis	bee	1		2
	Guettarda angelica	long tongue	1		
	Guettarda uruguensis	long tongue			2
	Guettarda viburnoides	long tongue	4		2
	Ixora brevifolia	long tongue	1		
	Ixora gardneriana	long tongue	1	1	
	Ixora venulosa	long tongue	2		1
	Ixora warmingii	long tongue	1		1

	Melanopsidium nigrum	long tongue	1		
	Posoqueria acutifolia	moth			1
	Posoqueria latifolia	moth	5		1
	Psychotria carthagenensis	insect	2		1
	Psychotria mapourioides	insect	3		
	Psychotria myriantha	insect	1		
	Psychotria nuda	long tongue	2		
	Psychotria sessilis	insect	1		
	Psychotria suterella	insect	2		
	Psychotria vauthieri	insect	1		
	Psychotria vellosiana	insect			2
	Randia armata	moth	2		
	Rudgea jasminoides	long tongue	6		4
	Schizocalyx cuspidatus	insect	2		
	Simira corumbensis	insect	1		
	Simira viridiflora	insect	2		
	Sphinctanthus insignis	long tongue	2		
	Tocoyena sellowiana	moth			2
	Warszewiczia longistaminea	butterfly-moth-bird			1
Rutaceae	*Almeidea lilacina*	long tongue		1	
	Balfourodendron riedelianum	insect	6	4	1
	Citrus x aurantium	insect			2
	Clausena excavata	insect		1	
	Conchocarpus pentandrus	long tongue	2		
	Dictyoloma vandellianum	insect			2
	Esenbeckia febrifuga	insect	4	2	2
	Esenbeckia grandiflora	insect	6		
	Esenbeckia leiocarpa	insect	3	4	
	Galipea jasminiflora	long tongue	5		
	Galipea laxiflora	long tongue	1		
	Galipea multiflora	long tongue			1
	Helietta apiculata	insect	1	1	
	Metrodorea nigra	fly	8	1	
	Metrodorea stipularis	insect	2		1
	Murraya paniculata	insect		1	
	Neoraputia alba	insect	1		
	Pilocarpus giganteus	insect			3
	Pilocarpus pauciflorus	insect	2		
	Pilocarpus pennatifolius	insect	1		
	Zanthoxyllum hiemale	insect	1		
	Zanthoxyllum petiolare	insect			1
	Zanthoxylum acuminatum	insect	4		
	Zanthoxylum caribaeum	insect	2	1	3
	Zanthoxylum chiloperone	insect	1		
	Zanthoxylum fagara	insect	2	1	2
	Zanthoxylum monogynum	insect	1		
	Zanthoxylum rhoifolium	insect	3	3	6
	Zanthoxylum riedelianum	insect	3	2	
	Zanthoxylum tingoassuiba	insect			1
Sabiaceae	*Meliosma itatiaiae*	insect	1		
	Meliosma sellowii	insect	2		
Salicaceae	*Banara serrata*	insect	2		
	Casearia arborea	insect	2	1	2
	Casearia commersoniana	insect	1		
	Casearia decandra	insect	4		2
	Casearia gossypiosperma	insect	4	2	5
	casearia lasiophylla	insect			1
	Casearia obliqua	insect	5		1
	Casearia oblongifolia	insect	1		
	Casearia selloana	insect	1		
	Casearia sylvestris	insect	11	4	8
	Casearia ulmifolia	insect	1		3
	Macrothumia kuhlmannii	insect	1		
	Prockia crucis	insect	4		
	Xylosma ciliatifolia	wind			2
	Xylosma prockia	wind		1	3
	Xylosma salzmannii	wind	1		
	Xylosma pseudosalzmanii	wind	4		
Sapindaceae	*Allophylus edulis*	insect	10	3	6
	Allophylus laevigatus	insect	1		

	Allophylus racemosus	insect	2		1
	Cupania concolor	insect	1		
	Cupania emarginata	insect			3
	Cupania ludowigii	insect	3		
	Cupania oblongifolia	insect	3		3
	Cupania rugosa	insect	1		
	Cupania tenuivalvis	insect	1		
	Cupania vernalis	insect	8		8
	Diatenopteryx sorbifolia	insect	6		
	Dilodendron bipinnatum	insect		1	
	Dilodendron elegans	insect			1
	Koelreuteria bipinnata	insect		1	
	Koelreuteria paniculata	insect		1	
	Matayba elaeagnoides	insect	7	1	5
	Matayba guianensis	insect			2
	Matayba juglandifolia	insect			2
	Matayba leocodictya	insect	1		
	Matayba talisioides	insect	1		
	Melicoccus oliviformis subsp. intermedius	insect	1		
	Pseudima frutescens	insect	1		
	Sapindus saponaria	insect		3	
	Toulicia laevigata	insect			2
Sapotaceae	*Chrysophyllum flexuosum*	insect	1		
	Chrysophyllum gonocarpum	insect	8	1	2
	Chrysophyllum lucentifolium	insect	1		
	Chrysophyllum marginatum	insect	1		
	Ecclinusa ramiflora	insect	2		
	Manilkara salzmannii	insect	1		
	Micropholis crassipedicellata	insect	1		
	Micropholis cuneata	insect	1		
	Micropholis gardneriana	insect			2
	Pouteria caimito	insect	1	1	1
	Pouteria filipes	insect	1		
	Pouteria gardneri	insect	1		
	Pouteria gardneriana	insect	1		
	Pouteria reticulata	insect	1		
	Pradosia lactescens	insect	1		
Schoepfiaceae	*Schoepfia brasiliensis*	insect	1		2
Simaroubaceae	*Simaba cedron*	undetermined	1		
Solanaceae	*Brunfelsia uniflora*	long tongue			1
	Cestrum intermedium	long tongue	1		
	Cestrum mariquitense	long tongue		1	
	Cestrum schlechtendahlii	long tongue	3		1
	Cyphomandra fragrans	bee	1		
	Sessea brasiliensis	moth	2		
	Solanum argenteum	bee	2	1	
	Solanum bullatum	bee	4		1
	Solanum cernuum	bee			3
	Solanum cinnamomeum	bee	1		
	Solanum erianthum	bee			1
	Solanum granuloso-leprosum	bee		2	
	Solanum leucodendron	bee		1	4
	Solanum mauritianum	bee		1	
	Solanum pseudoquina	bee	1	2	
	Solanum rufescens	bee	2		1
	Solanum swartzianum	bee	3		1
Styracaceae	*Styrax camporum*	insect	1		
	Styrax glaber	insect	2		
	Styrax pohlii	insect	1		
Symplocaceae	*Symplocos pubescens*	insect	2		
	Symplocos tenuifolia	insect	1		
	Symplocos uniflora	insect	1		
Theaceae	*Laplacea tomentosa*	bee			1
Thymelaeaceae	*Daphnopsis fasciculata*	insect	1		
Trigoniaceae	*Trigoniodendron spiritusanctense*	bee	1		
Ulmaceae	*Ampelocera glabra*	wind	1		
	Cecropia glaziovii	insect-wind	4	1	4
	Cecropia hololeuca	insect-wind	4		4
	Cecropia pachystachya	insect-wind	4	4	2
	Coussapoa curranii	wind	1		

	Pourouma cecropiifolia Mart.	insect-wind		1	
	Pourouma guianensis	insect-wind	1		1
	Urera baccifera	wind	7	1	1
Verbenaceae	*Aegiphila sellowiana*	long tongue	3	2	4
	Aloysia virgata	long tongue	4	2	6
	Citharexylum myrianthum	long tongue		6	
	Vitex megapotamica	long tongue	1		1
	Vitex orinocensis	long tongue	1		
	Vitex polygama	long tongue	2	1	1
Violaceae	*Rinorea bahiensis*	insect	1		
Vochysiaceae	*Callisthene minor*	insect	1		
	Qualea jundiahy	big animal	1		2
	Qualea megalocarpa	big animal	1		
	Qualea multiflora subsp. Pubescens	big animal	2		
	Vochysia magnifica	big animal	1		1
	Vochysia schwackeana	big animal	1		
	Vochysia tucanorum	big animal	4		

APPENDIX 2.1. LIST OF SAMPLED BEE SPECIES AND THE FUNCTIONAL GROUPS WHERE THESE WERE CLASSIFIED.

Bee species	Functional Group
Andrenidae	
Oxaea flavescens	16
Psaenythia sp. 1	1
Psaenythia sp. 2	1
Apidae	
Apis mellifera	13
Centris	15
Ceratina sp. 1	5
Ceratina sp. 2	5
Ceratina sp. 3	5
Diadasina	10
Doeringiella	14
Eucerini	
Eufriesea violacea	17
Euglossa annectans	12
Euglossa cordata	12
Euglossa fimbriata	12
Euglossa pleiosticta	12
Euglossa truncate	12
Eulaema cingulate	18
Eulaema nigrita	18
Exaeretes maragdina	19
Exomalopsis aff. analis	1
Exomalopsis aff. auropilosa	1
Exomalopsis aff. vernoniae	1
Exomalopsis sp. 1	1
Exomalopsis sp. 2	1
Exomalopsis sp. 3	1
Exomalopsis sp. 4	1
Exomalopsis sp. 5	1
Exomalopsis sp. 6	1
Exomalopsis sp. 7	1
Exomalopsis sp. 8	1
Florilegus	10
Lophothygater	
Melissodes sp. 1	9
Melissodes sp. 2	9
Melissoptila	10
Melitoma segmentaria	10
Nomada sp. 1	8
Nomada sp. 2	8
Nomada sp. 3	8
Protosiris	8
Pseudepeolus	
Ptilothrix aff. Tricolor	10
Ptilothrix relata	10
Ptilothrix sp. 1	10
Thalestria aff. spinosa	19
Thygater analis	9
Thygater sp. 1	9
Thygater sp. 2	9
Trigona hyalinata	6
Trigona sp. 1	6
Trigona sp. 2	6
Trigona spinipes	6
Xylocopa	17
Colletidae	
Ptiloglossa	
Halictidae	
Augochlora sp. 1	7
Augochlora sp. 2	7
Augochlora sp. 3	7
Augochlora sp. 4	7
Augochlora sp. 5	7
Augochlora sp. 6	7
Augochlora sp. 7	7
Augochlorella sp. 1	4
Augochlorella sp. 2	4
Augochlorella sp. 3	4
Augochlorella sp. 4	4
Augochlorella sp. 5	4
Augochlorella sp. 6	4
Augochlorella sp. 7	4
Augochlorella sp. 8	4
Augochlorella sp. 9	4
Augochlorini sp.1	
Augochlorini sp. 2	
Augochlorini sp. 3	
Augochloropsis sp. 1	4
Augochloropsis sp. 2	4
Dialictus sp. 1	3
Dialictus sp. 2	3
Dialictus sp. 3	3
Dialictus sp. 4	3
Pseudoagapostemon	2
Pseudoaugochlora	
Megachilidae	
Megachile laeta	11
Megachile	11

APPENDIX 2.2. LIST OF POLLEN TYPES FOUND ON THE BODIES OF SAMPLED BEES, AND THE FUNCTIONAL GROUPS WHERE THESE WERE CLASSIFIED.

Pollen species	Functional Group
Acanthaceae	
Acanthaceae	
Herpetacanthus Type	3
Mendoncia Type	12
Thunbergia	13
Alismataceae	
Echinodorus Type	1
Sagittaria Type	1
Amaranthaceae	
Alternanthera	1
Amaranthaceae	3
Chamissoa Type	10
Chenopodium Type	3
Anacardiaceae	
Manguifera indica Type	17
Schinus therebinthifolius	14
Spondias	14
Apiaceae	
Apiaceae	1
Apocynaceae	
Allamanda Type	3
Apocynaceae sp. 1	
Apocynaceae sp. 2	
Aspidosperma Type	22
MandevillaType	3
NeriumType	
Araceae	
Spatiphyllum	3
Araliaceae	
Araliaceae	
Arecaceae	
AstrocaryumType	
CocosType	
Euterpe Type	
MauritiaType	16
Syagrus romanzoffiana	16
Asparagaceae	
Asparagaceae	5
Asteraceae	
Ambrosia Type	
Asteraceae sp. 1	
Asteraceae sp. 2	
Asteraceae sp. 3	
Bidens Type	
Conyza bonariensis	1
Cyrtocymura scorpioides	1
Eirmocephala Type	
Elephantopus Type	1
Emilia Type	1
Jungia Type	1
Parthenium hysterophorus	4
Sonchus Type	4
Sphagneticola trilobata	1
Tridax procumbens	1
Begoniaceae	
Begonia Type	2
Bignoniaceae	
Amphilophium Type	9
Anemopaegma Type	9
Anemopaegma Type	9
Bignonia binata Type	9
Bignoniaceae sp. 1	
Bignoniaceae sp. 2	
Bignoniaceae sp. 3	
Bignoniaceae sp. 4	
Jacaranda Type	15
Mansoa difficilis Type	9
Spatodea Type	19
Tecoma Type	18
Bixaceae	
Bixa orellana	15
Boraginaceae	
Cordia	17
Brassicaceae	
Brassicaceae	
Cannabaceae	
Cannabaceae Type	
Trema micrantha	16
Caricaceae	
Carica	19
Caryocaraceae	
Caryocar brasiliense	16
Caryophyllaceae	
Caryophyllaceae	4
Spergula	4
Celastraceae	
Hippocratea volubilis	8
Cleomaceae	
Tarenaya spinosa Type	6
Commelinaceae	
Tradescantia	7
Convolvulaceae	
Convolvulaceae	8
Ipomoea sp. 1	8
Ipomoea sp. 2	8
Ipomoea sp. 3	8
Ipomoea sp. 4	8
Ipomoea sp. 5	8
Ipomoea cairica	8
Merremia Type	8

Cucurbitaceae	
Cayaponia Type	8
Melothria Type	8
Momordica charantia	11
Cyperaceae	
Cyperaceae	3
Rynchospora Type	1
Scleria Type	3
Ericaceae	
Gaulteria Type	16
Euphorbiaceae	
Alchornea Type	16
Croton floribundus	14
Croton urucurana	14
Dalechampia sp. 1	9
Dalechampia sp. 2	9
Euphorbiaceae	
Euphorbia hirta	1
Ricinus communis	17
Sapium	14
Gentianaceae	
Gentianaceae	1
Heliconiaceae	
Heliconiaceae	
Lamiaceae	
Hyptis Type	1
Lamiaceae sp. 1	
Lamiaceae sp. 2	1
Lamiaceae sp. 3	
Leonorus sibiricus	4
Tectona grandis Type	
Lauraceae	
Lauraceae Type	
Leguminosae	
Anadenanthera	14
Bauhinia forficate	16
Centrolobium Type	15
Clitoria fairchildiana	15
Crotalaria Type	
GliricidiaType	
Inga semialata Type	16
Inga Type	16
Leguminosae sp. 1	
Leguminosae sp. 2	
Leucaena leucacephala	17
Lonchocarpus Type	
macroptilium lathyroides	2
MimosapudicaType	1
MimosaType	14
MimosaType	14
Ormosiatype	
Peltophorum dubium	15
Piptadenia gonoacantha	14
Poincianella libidibia Type	21
Schizolobium parahyba	15
Senegalia	14
Senna	15
Tipuana tipu	15
Loganiaceae	
Spigelia Type	1
Loranthaceae	
Struthanthus	
Lythraceae	
Cuphea melvilla Type	3
CuphearacemosaType	3
Lagestroemia	
Malpighiaceae	
Heteropterys pteropetala Type	
Malpighiaceae sp. 1	
Malpighiaceae sp. 2	
Malpighiaceae sp. 3	
Malpighiaceae sp. 4	
Malpighiaceae sp. 5	
Malvaceae	
Apeiba tibourbou	15
Hibiscus sp. 1	19
Hibiscus sp. 2	19
Luehea Type	16
Pachira Type	
Sida	1
Waltheria Type	
Melastomataceae	
Melastomataceae sp. 1	
Melastomataceae sp. 2	15
Tibouchina granulosa	15
Meliaceae	
Meliaceae	
Trichilia elegans	20
Menispermaceae	
Menispermaceae	1
Muntingiaceae	
Muntingia calabura	14
Myrtaceae	
Eucalyptus sp. 1	26
Eucalyptus sp. 2	26
Eugenia Type	
Myrtaceae	
Psidium Type	18
Syzygium cumini	25
Onagraceae	
Ludwigia sp. 1	2
Ludwigia sp. 2	2
Oxalidaceae	
Oxalis Type	1
Passifloraceae	
Passiflora	
Phytolaccaceae	
Phytolacca Type	1
Piperaceae	
Piper	14
Poaceae	
Brachiaria	5
Poaceae sp. 1	5
Poaceae sp. 2	5

Zeamays Type	5
Polygonaceae	
Polygonaceae	
Polygonum	1
Triplaris Type	14
Portulacaceae	
Portulaca oleacea	1
Primulaceae	
Myrsine Type	16
Rhamnaceae	
Colubrina glandulosa	20
Rosaceae	
Prunus Type	14
Rubiaceae	
Coffea Arabica	24
Declieuxia fruticosa Type	3
Genipa Americana	23
HilliaType	
Psychotria sp. 1	20
Psychotria sp. 2	20
Psychotria sp. 3	
Richardia Type	1
Rubiaceae sp. 1	
Rubiaceae sp. 2	
Rubiaceae sp. 3	
Rubiaceae sp. 4	
Rutaceae	
Citrus	24
Citrus aff. lemon	24
Zanthoxylum Type	14
Sapindaceae	
Paullinia Type	8
Sapotaceae	
Chrysophyllum	20
Scrophulariaceae	
Scrophulariaceae sp. 1	
Scrophulariaceae sp. 2	
Solanaceae	
Solanaceae sp. 1	
Solanaceae sp. 2	
Solanaceae sp. 3	
Solanaceae sp. 4	
Solanum sp. 1	15
Solanum sp. 2	
Solanum mauritianum	15
Styracaceae	
Styrax Type	14
Urticaceae	
Cecropia	14
Urera Type	16
Verbenaceae	
Lantana Type	1
Stachytarpheta	1
Vitaceae	
Cissus Type	8
Vochysiaceae	
Vochysia	16

APPENDIX 2.3 EFFECTS OF HABITAT CHANGES AND ISOLATION ON BEE FUNCTIONAL GROUPS.

Table 2.3.1. Specific responses of bee functional groups to the different habitat types. Significant effects are indicated in bold.

	Coef.	S.E.	z value	Pr(>|z|)
Reference Fragment				
group 1	0.044	0.020	-6.843	<0.01
group 2	0.000	0.000	-0.008	0.994
group 3	0.053	0.022	-7.03	<0.01
group 4	0.070	0.026	-7.264	<0.01
group 5	0.009	0.009	-4.716	<0.01
group 6	0.018	0.013	-5.668	<0.01
group 7	0.018	0.013	-5.668	<0.01
group 8	0.000	0.000	-0.008	0.994
group 9	0.018	0.013	-5.668	<0.01
group 10	0.123	0.035	-7.405	<0.01
group 11	0.000	0.000	-0.008	0.994
group 12	0.175	0.043	-7.179	<0.01
group 13	0.053	0.022	-7.03	<0.01
group 14	0.000	0.000	-0.008	0.994
group 15	0.000	0.000	-0.008	0.994
group 16	0.000	0.000	-0.008	0.994
group 17	0.035	0.018	-6.585	<0.01
group 18	0.298	0.058	-6.191	<0.01
group 19	0.088	0.029	-7.379	<0.01
Degraded Fragment				
group 1	0.000	0.000	-0.007	0.994
group 2	2.065	7921.012	0	1.000
group 3	1.377	0.860	0.512	0.609
group 4	2.478	1.193	1.886	0.059
group 5	0.000	0.000	-0.006	0.995
group 6	0.000	0.000	-0.007	0.995
group 7	1.652	1.671	0.496	0.620
group 8	2.065	7921.012	0	1.000
group 9	3.304	2.906	1.359	0.174
group 10	0.826	0.403	-0.392	0.695
group 11	2.065	7921.013	0	1.000
group 12	1.404	0.510	0.934	0.350
group 13	0.275	0.300	-1.182	0.237
group 14	2.065	7921.012	0	1.000
group 15	2.065	7921.012	0	1.000
group 16	2.065	7921.011	0	1.000
group 17	0.000	0.000	-0.007	0.995
group 18	0.875	0.288	-0.407	0.684
group 19	0.496	0.335	-1.039	0.299
Restored Corridor				
group 1	0.552	0.340	-0.966	0.334
group 2	1.724	5546.183	0.000	1.000
group 3	**4.367**	**1.938**	**3.321**	**0.001**
group 4	**3.677**	**1.440**	**3.325**	**0.001**
group 5	1.379	1.600	0.277	0.782
group 6	0.690	0.634	-0.404	0.686
group 7	1.149	0.970	0.165	0.869
group 8	1.02E+7	2.919E+10	0.006	0.995
group 9	1.839	1.468	0.763	0.446
group 10	**0.394**	**0.161**	**-2.275**	**0.023**
group 11	1.02E+7	2.919E+10	0.006	0.995
group 12	0.827	0.249	-0.629	0.529
group 13	0.383	0.236	-1.558	0.119
group 14	1.724	5546.184	0.000	1.000
group 15	1.724	5546.183	0.000	1.000
group 16	2.042E+7	5.839E+10	0.006	0.995
group 17	0.230	0.201	-1.684	0.092
group 18	**0.487**	**0.129**	**-2.722**	**0.006**
group 19	**0.322**	**0.163**	**-2.243**	**0.025**
Secondary Corridor				
group 1	1.285	0.750	0.429	0.668
group 2	1.783E+7	5.098E+10	0.006	0.995
group 3	**5.218**	**2.381**	**3.622**	**<0.01**
group 4	1.405	0.647	0.738	0.461
group 5	0.000	0.000	-0.010	0.992
group 6	0.803	0.809	-0.218	0.827
group 7	1.204	1.110	0.202	0.840
group 8	5.350E+7	1.529E+11	0.006	0.995
group 9	**4.817**	**3.729**	**2.031**	**0.042**
group 10	1.434	0.511	1.010	0.313
group 11	2.408	7950.343	0.000	1.000
group 12	**0.442**	**0.175**	**-2.065**	**0.039**
group 13	1.204	0.652	0.343	0.732
group 14	2.408	7950.342	0.000	1.000
group 15	1.783E+7	5.098E+10	0.006	0.995
group 16	7.134E+7	2.039E+11	0.006	0.995
group 17	0.000	0.000	-0.011	0.992
group 18	**0.165**	**0.072**	**-4.151**	**<0.01**
group 19	**0.241**	**0.161**	**-2.124**	**0.034**
Sugarcane Field				
group 1	**5.013**	**2.497**	**3.236**	**0.001**
group 2	3.234	10336.64	0.000	1.000
group 3	**2.560**	**1.242**	**1.939**	**0.053**

group 4	**3.032**	**1.265**	**2.658**	**0.008**
group 5	0.000	0.000	-0.011	0.991
group 6	0.404	0.498	-0.736	0.462
group 7	0.000	0.000	-0.011	0.991
group 8	1.796E+7	5.135E+10	0.006	0.995
group 9	1.617	1.415	0.549	0.583
group 10	0.866	0.340	-0.366	0.714
group 11	3.592E+7	1.027E+11	0.006	0.995
group 12	**0.121**	**0.077**	**-3.339**	**0.001**
group 13	1.887	0.951	1.260	0.208
group 14	1.796+7	5.135E+10	0.006	0.995
group 15	3.234	10336.64	0.000	1.000
group 16	2.694E+8	7.702E+11	0.007	0.995
group 17	0.000	0.000	-0.012	0.990
group 18	**0.095**	**0.052**	**-4.330**	**<0.01**
group 19	**0.081**	**0.085**	**-2.381**	**0.017**

Table 2.3.2. ANOVA table of the best model selected for the effect of functional group (“group”), habitat change (“habitat”) and habitat isolation (“fragment”) on bee abundance.

	Df	**Deviance**	**Resid. Df**	**Resid. Dev**	**Pr(>Chi)**
NULL			859	1819.56	
habitat	2	40.46	857	1779.1	1.64E-09
group	19	1109.74	838	669.36	< 2.2e-16
fragment	1	12.11	837	657.25	0.000502
habitat: group	38	111.82	799	545.43	3.39E-09

APPENDIX 2.4. EFFECTS OF HABITAT CHANGES AND ISOLATION ON PLANT FUNCTIONAL GROUPS.

Table 2.4.1. Specific responses of plant functional groups to the different habitat types. Significant effects are indicated in bold.

	Estimate	Std. Error	z value	Pr(>|z|)
Reference Fragment				
group 1	11.750	1.714	16.891	<0.001
group 2	0.128	0.055	-4.748	<0.001
group 3	0.191	0.070	-4.543	<0.001
group 4	0.553	0.135	-2.422	0.015
group 5	0.809	0.176	-0.974	0.330
group 6	0.000	0.000	-0.011	0.991
group 7	0.043	0.031	-4.373	<0.001
group 8	0.383	0.106	-3.463	0.001
group 9	0.255	0.083	-4.221	<0.001
group 10	0.000	0.000	-0.011	0.991
group 11	0.021	0.022	-3.810	<0.001
group 12	0.021	0.022	-3.810	<0.001
group 13	0.021	0.022	-3.810	<0.001
group 14	0.894	0.190	-0.530	0.596
group 15	2.128	0.376	4.269	<0.001
group 16	0.638	0.149	-1.921	0.055
group 17	0.213	0.074	-4.444	<0.001
group 18	0.447	0.117	-3.069	0.002
group 19	0.064	0.038	-4.621	<0.001
group 20	0.170	0.065	-4.630	<0.001
group 21	0.000	0.000	-0.011	0.991
group 22	0.000	0.000	-0.011	0.991
group 23	0.149	0.060	-4.700	<0.001
group 24	0.149	0.060	-4.700	<0.001
group 25	0.128	0.055	-4.748	<0.001
group 26	0.149	0.060	-4.700	<0.001
Degraded Fragment				
group 1	**0.477**	**0.114**	**-3.104**	**0.002**
group 2	0.280	0.309	-1.152	0.250
group 3	0.933	0.566	-0.115	0.908
group 4	0.710	0.307	-0.793	0.428
group 5	0.618	0.243	-1.222	0.222
group 6	2.098	4881.097	0.000	1.000
group 7	0.000	0.000	-0.010	0.992
group 8	1.026	0.463	0.056	0.955
group 9	0.699	0.408	-0.613	0.540
group 10	2.098	4881.098	0.000	1.000
group 11	3.357	4.189	0.971	0.332
group 12	1.679	2.407	0.361	0.718
group 13	1.679	2.407	0.361	0.718
group 14	1.679	0.543	1.601	0.109
group 15	1.444	0.405	1.309	0.190
group 16	1.007	0.385	0.019	0.985
group 17	**3.021**	**1.393**	**2.398**	**0.016**
group 18	1.519	0.602	1.054	0.292
group 19	1.119	1.056	0.119	0.905
group 20	0.210	0.228	-1.436	0.151
group 21	1.372E+07	2.379E+10	0.009	0.992
group 22	1.372E+07	2.379E+10	0.009	0.992
group 23	1.199	0.758	0.287	0.774
group 24	0.959	0.643	-0.062	0.950
group 25	2.518	1.457	1.596	0.110
group 26	0.480	0.401	-0.878	0.380
Restored corridor				
group 1	**0.494**	**0.089**	**-3.900**	**<0.001**
group 2	0.360	0.241	-1.523	0.128
group 3	0.780	0.367	-0.528	0.598
group 4	0.665	0.213	-1.275	0.202
group 5	**0.455**	**0.137**	**-2.620**	**0.009**
group 6	2.026	3953.415	0.000	1.000
group 7	0.000	0.000	-0.018	0.986
group 8	0.840	0.296	-0.494	0.621
group 9	0.585	0.257	-1.219	0.223
group 10	3.532E+07	6.124E+10	0.010	0.992
group 11	5.943	6.299	1.681	0.093
group 12	0.000	0.000	-0.017	0.986
group 13	1.080	1.338	0.063	0.950
group 14	1.428	0.366	1.390	0.164
group 15	1.156	0.252	0.666	0.505
group 16	0.774	0.231	-0.856	0.392
group 17	1.513	0.621	1.008	0.313
group 18	0.926	0.305	-0.233	0.815
group 19	0.360	0.335	-1.097	0.272
group 20	**0.203**	**0.142**	**-2.278**	**0.023**
group 21	4.415E+06	7.655E+09	0.009	0.993
group 22	2.026	3953.415	0.000	1.000
group 23	0.540	0.305	-1.091	0.275
group 24	0.617	0.339	-0.880	0.379
group 25	1.621	0.818	0.956	0.339
group 26	**0.232**	**0.165**	**-2.051**	**0.040**
Secondary corridor				
group 1	**0.652**	**0.117**	**-2.381**	**0.017**
group 2	1.107	0.581	0.193	0.847
group 3	0.568	0.280	-1.148	0.251
group 4	1.100	0.327	0.321	0.748

group 5	0.605	0.172	-1.769	0.077
group 6	4.175E+06	7.239E+09	0.009	0.993
group 7	0.255	0.316	-1.103	0.270
group 8	1.022	0.347	0.063	0.950
group 9	**0.383**	**0.182**	**-2.015**	**0.044**
group 10	3.340E+07	5.791E+10	0.010	0.992
group 11	**8.174**	**8.552**	**2.008**	**0.045**
group 12	0.511	0.728	-0.471	0.638
group 13	0.000	0.000	-0.015	0.988
group 14	0.730	0.197	-1.169	0.242
group 15	**0.485**	**0.111**	**-3.150**	**0.002**
group 16	**0.443**	**0.143**	**-2.527**	**0.012**
group 17	1.430	0.586	0.874	0.382
group 18	0.511	0.182	-1.882	0.060
group 19	0.341	0.317	-1.158	0.247
group 20	**0.255**	**0.163**	**-2.139**	**0.032**
group 21	4.175E+06	7.239E+09	0.009	0.993
group 22	1.533	3068.542	0.000	1.000
group 23	0.292	0.190	-1.889	0.059
group 24	0.292	0.190	-1.889	0.059
group 25	1.277	0.658	0.475	0.635
group 26	0.949	0.476	-0.105	0.917
Sugarcane field				
group 1	**0.484**	**0.087**	**-4.039**	**<0.001**
group 2	**0.086**	**0.094**	**-2.240**	**0.025**
group 3	0.402	0.215	-1.705	0.088
group 4	**1.748**	**0.501**	**1.949**	**0.051**
group 5	**0.381**	**0.117**	**-3.146**	**0.002**
group 6	2.066	4005.003	0.000	1.000
group 7	0.000	0.000	-0.018	0.985
group 8	0.689	0.248	-1.037	0.300
group 9	**0.129**	**0.087**	**-3.055**	**0.002**
group 10	2.533E+07	4.391E+10	0.010	0.992
group 11	4.648	4.970	1.437	0.151
group 12	0.000	0.000	-0.018	0.986
group 13	0.000	0.000	-0.018	0.986
group 14	**0.578**	**0.161**	**-1.971**	**0.049**
group 15	**0.527**	**0.120**	**-2.809**	**0.005**
group 16	**0.275**	**0.099**	**-3.602**	**<0.001**
group 17	1.240	0.517	0.515	0.607
group 18	0.639	0.220	-1.300	0.194
group 19	0.344	0.320	-1.146	0.252
group 20	0.452	0.248	-1.450	0.147
group 21	8.442E+06	1.464E+10	0.009	0.993
group 22	2.066	4005.003	0.000	1.000
group 23	**0.148**	**0.121**	**-2.329**	**0.020**
group 24	0.516	0.291	-1.172	0.241
group 25	1.205	0.627	0.359	0.720
group 26	0.443	0.259	-1.394	0.163

Table 2.4.2. ANOVA table of the best model selected for the effect of functional group (“group”), habitat change (“habitat”) and habitat isolation (“fragment”) on pollen frequency.

	Df	**Deviance**	**Resid. Df**	**Resid. Dev**	**Pr(>Chi)**
NULL			1117	4861.8	
habitat	2	55.66	1115	4806.1	8.20E-13
group	25	2727.99	1090	2078.2	< 2.2e-16
fragment	1	12.81	1089	2065.3	0.000345
habitat: group	50	160.15	1039	1905.2	1.85E-13
habitat: Fragment	2	16	1037	1889.2	0.000336

Received: 4 January 2017 | Accepted: 16 August 2017
DOI: 10.1111/avsc.12335

RESEARCH ARTICLE

Applied Vegetation Science
IAVS

Are the assemblages of tree pollination modes being recovered by tropical forest restoration?

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Funding information
Departamento Administrativo de Ciencia, Tecnología e Innovación, Grant/Award Number: 568/2012

Co-ordinating Editor: Gerhard Overbeck

Abstract

Questions: Do the assemblages of pollination modes in restored (tree plantings) and secondary (naturally regenerated) forests change in comparison to primary forests, and how do these assemblages relate to species turnover at regional scale?

Location: Southeast region of Brazil.

Methods: We classified tree species found in a total of 40 forest sites (18 primary, 11 restored, 11 secondary) according to pollination mode, based on the literature. We calculated and compared functional dissimilarity distances, amounts of species and accumulated abundance of pollination modes, and functional indices of richness and evenness between forest types.

Results: Functional dissimilarity distances were much smaller than species dissimilarity distances within forest types (mean <20%, >80%, respectively), indicating a small variation in pollination modes between sites. Functional indices of richness and evenness did not differ between forest types. However, significant changes were found in the species and abundance proportions of several pollination modes. Primary forests were characterized by the predominance of generalized insect-pollinated species, followed by secondary proportions of bee, wind and moth pollination; other pollination modes were underrepresented. In restored forests, reductions were found in generalized insect, moth, wind, fly, pollen-consuming insect and very-small insect pollination, whereas the species pollinated by bees and bats more than doubled. Smaller changes were found among secondary forests, including reductions in moth, fly and fig-wasp pollination, whereas there were incremental changes in bee, beetle, big animal and small insect pollination.

Conclusions: Our results indicate a rather stable assemblage of pollination modes and also high ecological redundancy among trees regardless of the species replacement at the regional scale. Major changes among restored forests are probably in response to larger disturbance effects and/or restoration practices conducted in these sites. In contrast, smaller changes among secondary forests could be in response to smaller disturbance effects and natural selection processes, and also seem to suggest that highly resilient degraded areas are more likely to recuperate their functional diversity through natural regeneration alone. In both cases, however, efforts to recover such

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Nomenclature: Carvalho et al. (2010)

patterns should be encouraged to avoid possible negative effects in plant–pollinator interactions.

KEYWORDS
Atlantic forest, Brazil, community structure, ecosystem management, forest fragmentation, functional diversity, human disturbance, meta-analysis, natural regeneration, plant–animal interactions, pollination syndromes, reproductive traits, restoration ecology, semi-deciduous forest

1 | INTRODUCTION

Tropical forests are rapidly being degraded worldwide, affecting biodiversity, ecosystem functioning and the provision of ecosystem services. Consequently, their recuperation by means of ecological restoration is becoming a pressing necessity to recreate lost habitats for endangered species, while promoting human welfare and economic development (SER, 2004). The success and sustainability of restoration programmes depends on not only the retrieval of species diversity but also the diversity of functional traits, i.e. morphological, physiological, behavioral, structural and phenological characteristics, considered relevant to their response to the environment and/or their effect on ecosystem properties and services (Cadotte, Carscadden, & Mirotchnick, 2011; Lugo, 1992; Rodrigues, Lima, Gandolfi, & Nave, 2009; Silver, Brown, & Lugo, 1996; Violle et al., 2007). These include, for example, traits involved in the ability of a plant to colonize, compete and regenerate, to establish and persist in a restored community (e.g. seed viability, dispersal strategy, light tolerance and growth rate) or traits associated with ecosystem services like water purification, carbon sequestration or wood provision (e.g. nutrient fixation, wood density and growth rate), from which landholders would benefit.

Plant pollination modes, comprising strategies and adaptations for attracting pollinators, have received little attention in the context of restoration ecology (Ceccon & Varassin, 2014; Garcia, Cianciaruso, Ribeiro, dos Santos, & Rodrigues, 2015; Girão, Lopes, Tabarelli, & Bruna, 2007; Martins & Antonini, 2016). Yet, the restoration of floral source diversity and availability in plant communities guarantees the wellbeing of their pollinators (Carvalheiro et al., 2013; Dicks et al., 2015; Heithaus, 1974) and subsequently, the maintenance of the functions and services derived from plant species (Ashman et al., 2004; Fontaine, Dajoz, Meriguet, & Loreau, 2006; Kremen et al., 2007). The intraspecific genetic diversity in plants, which is indispensable for the preservation and evolution of restored forests, sometimes relies more on pollen vectors than on seed vectors (e.g. in the case of autochoric species; Helsen et al., 2016; Lexer et al., 2016) or may be dissimilarly affected by both when these exhibit different dispersal patterns, occurring at different distances and directions (Beckie, Blackshaw, Hall, & Johnson, 2016; Miller, 2016; Wang et al., 2016). Moreover, pollinators may sometimes indirectly benefit seed dispersal and seedling recruitment through the enhancement of seed and fruit set/size (Bond, 1994; Lundgren, Totland, & Lázaro, 2016). Pollinator conservation by ecological restoration has also been shown to improve crop pollination services, which could be translated into additional incentives and revenue for the implementation of restoration programmes in agricultural regions (Carvalheiro et al., 2013; Dicks et al., 2015; Heithaus, 1974).

Different restoration scenarios may lead to variable species assemblages with possible detrimental effects on the diversity of pollination modes. For instance, highly devastated areas that have lost their capacity to automatically recuperate and require tree plantings for restoration would probably generate plant communities diverging more from the original ones. In contrast, less disturbed areas that are still highly resilient and capable of automatically regenerating naturally, without the necessity to implement active restoration practices, would probably generate plant communities diverging less from the original ones (Brancalion, Gandolfi, & Rodrigues, 2015; Rodrigues et al., 2009). The consequences of these possible scenarios have been explored to a small extent (Chazdon, Careaga, Webb, & Vargas, 2003; Girão et al. 2009; Lopes, Girão, Santos, Peres, & Tabarelli, 2009; Kimmel et al., 2010; Garcia et al., 2015; Martins & Antonini, 2016). Hence, in the present study, we compared the diversity of pollination modes in restoration plantings and naturally regenerated forests with that in primary forests in Brazil. Given that species assemblages vary spatially in response to local environmental and landscape conditions and the geographic distribution of species (Brancalion et al., 2015; Torres, Martins, & Kinoshita, 1997), we included plant communities from several locations to understand how the diversity of pollination modes relates to species turnover at a regional scale, as well as to search for patterns that could be used as a model for restoration planning in tropical forests.

2 | METHODS

The present study was based on data from 40 floristic surveys conducted in tree communities within the domain of tropical semi-deciduous forests in the Atlantic forest biome in Brazil (Veloso, Rangel Filho, & Lima, 1991). These surveys were selected because they used a similar methodology (phytosociological data obtained from trees >4.5 cm DBH) and the species importance values (used herein as a proxy for abundance) were available. A total of 18 surveys were conducted in relatively well-conserved primary forest fragments, although some of them were slightly affected by selective logging and livestock grazing (named herein as “remnants”). A total of 11 surveys were conducted in degraded sites restored with tree plantings of various native and exotic species (named herein as "restored"). The remaining 11 surveys were conducted in less degraded areas restored by natural regeneration alone (named herein as "secondary"). The maximum distance between sites was 986 km and the minimum was 100 m (19°26′–23°33′S, 41°13′–50°27′W). The elevation varied between 100 and 1025 m a.s.l. The climate of the region was classified as Cwa, Cwb or Cfa in the Köppen (1948), with a dry winter from June to September, a rainy summer from December to March, a mean annual temperature of 18–22°C, and annual precipitation of 1100–1730 mm. The references are summarized in Appendix S1.

The species recorded in these surveys were classified into the following pollination modes: "bird", "bat", "wasp", "fly", "moth", "beetle", "small insect" (trips, rove beetles, etc.), "bee", "mammal" (non-flying) and "wind." Mixed pollination modes are indicated by the conjunction of two or more of the above, but the most common modes received different names: "insect" (various types), "pollen consumer" (various types of insects excluding nectar consumers like lepidopterans), "big animal" (large bees, birds, lepidopterans and bats), "long tongue" (bees, lepidopterans and birds) and "vertebrate" (hummingbirds and bats). These pollination modes were established after conducting an extensive literature review on the pollinators of each species. The species without any information were classified into the category of another in the same genus or family showing similar floral morphology (see Appendix S2). We decided not to use the traditional pollination syndromes of Fægri and van der Pijl (1979) that are based on floral trait combinations alone, given their inability to predict the pollinators of several species (Mayfield, Waser, & Price, 2001; Ollerton et al., 2009; Rosas-Guerrero et al., 2014). Likewise, taking into account the recommendations of many authors (Ollerton, Rech, Waser, & Price, 2015; Ollerton et al., 2009; Rosas-Guerrero et al., 2014; Waser, Chittka, Price, Williams, & Ollerton, 1996), we considered not only the most efficient pollinators but also the secondary or less effective ones because pollinator efficiency can vary in space and time (Ollerton et al., 2015; Price, Waser, Irwin, Campbell, & Brody, 2005; Waser et al., 1996) and because secondary pollinators represent important selecting forces in the expression and evolution of many flower phenotypes (Sargent & Otto, 2006; Strauss & Whittall, 2006). In addition, pollination modes represent an ecological function of resource provision from which both primary and secondary pollinators benefit.

Comparisons between sites and forest types (remnants, restored and secondary) were conducted using Morisita–Horn dissimilarity distances, as suggested by Wolda (1981), for dealing with different sample sizes. Species dissimilarity distances were calculated on a matrix containing the species abundances by site (i.e., importance value × sample area/100). Functional dissimilarity distances were calculated on two matrices: one containing the species quantities from each pollination mode by site (functional dissimilarity for species) and the other containing the accumulated abundances of pollination modes by site (functional dissimilarity for abundances). Spatial autocorrelations were tested using Mantel tests with dissimilarity and geographic distances between sites (significance level = 0.05). Overall differences in the assemblages of species and pollination modes among forest types were tested using MANOVA (significance level = 0.05). The functional diversity of each site was estimated using the indices of functional richness and evenness provided by Villéger, Mason, and Mouillot (2008) and Schleuter, Daufresne, Massol, and Argillier (2010). Particular differences in functional indices and pollination modes were tested separately using GLM. Beta models were fitted to functional indices, Poisson and negative binomial models to species quantities, and Gaussian models to accumulated abundances. Binomial-Gamma hurdle models were fitted to rare pollination modes with zero-inflated data (>30% zero values). Forest type was included as the explanatory variable with a significance level of 0.05. Sample area was added as an offset variable in Poisson and binomial models and as an explanatory variable in beta and gamma models to control for unequal sampling. Model fitting was measured with R^2 values, the ratio deviance: degrees of freedom, residual analysis and AUC values. All analyses were performed using R, packages FD, vegan, lme4, betareg, and ggplot2 (R Foundation for Statistical Computing, Vienna, Austria).

3 | RESULTS

From a total of 974 tree species recorded in the floristic surveys, 660 species were found in remnants, 305 in restored forests and 452 in secondary forests. The species were spatially structured (Mantel test, $r = .42$, $p < .01$) and varied greatly between sites (mean dissimilarity distances were >0.8, see Figure 1) and forest types (MANOVA, $F = 2.57$, $p < .01$).

In contrast, the assemblages of pollination modes were not spatially structured (species, $r = .04$; abundance, $r = .08$; $p > .1$) and varied less between sites (mean functional dissimilarity distances were < 0.2; Figure 1), although they differed significantly between forest types (MANOVA, species, $F = 7.26$; abundance, $F = 3.57$; $p < .01$). The functional indices of richness and evenness were not different between forest types (GLM, $p > .05$; Figure 2).

Remnant forests were particularly characterized by the predominance of insect-pollinated trees, represented by nearly half the species and individuals in every site (Figure 3) and by 48 families, among which *Lauraceae*, *Leguminosae* (mimosoid species), *Sapindaceae*, *Sapotaceae* and *Rutaceae* were some of the most important. This pollination mode was followed by bee pollination, mainly represented by species from the families *Leguminosae* (sf. Caesalpinoidae, Papilionoidae), *Bignoniaceae*, *Solanaceae* and *Melastomataceae*; wind pollination, with various common *Moraceae*, *Euphorbiaceae* and *Urticaceae* species; moth pollination in many *Apocynaceae* (genera *Aspidosperma*, *Himatanthus*, and *Tabernaemontana*), *Meliaceae* (*Guarea* and *Cabralea*), *Ebenaceae* (*Diospyros*), *Proteaceae* (*Euplassa* and *Roupala*) and *Rubiaceae* (*Posoqueria*, *Randia* and *Tocoyena*) species; and pollen-consumer pollination in *Myrtaceae*. Other pollination modes were found in mean proportions <0.04.

In restored forests, the prevalent abundance of insect-pollinated trees was maintained, although a significant reduction of about 6% was found in the amount of species (Figure 3). From a total of 48 families of

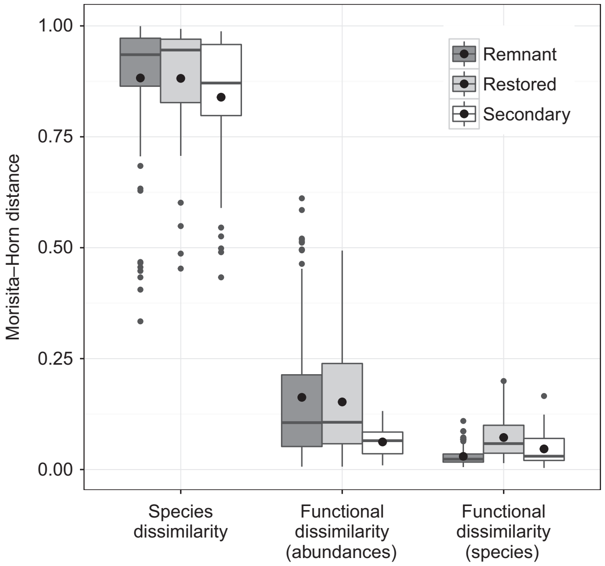

FIGURE 1 Box-plot of species and functional dissimilarities in remnants (primary forest), restored (tree plantings) and secondary (naturally regenerated) tropical semi-deciduous forests. Central boxes span the first quartile to the third quartile (the inter-quartile range or IQR). Segments and points inside the boxes show the median and mean values, respectively, and "whiskers" below and above the boxes show the location of the smallest and the largest values no further than 1.5 × IQR from the first and the third quartiles. Small points indicate data beyond the whiskers or "outliers". Species dissimilarity indicates the differences in the tree species composition among sites, whereas functional dissimilarity indicates the differences in the abundances and the number of species from different pollination modes among sites. No statistical differences were found among forest types, but the figure indicates much higher dissimilarities in the species composition than in the assemblages of pollination modes in all forest types

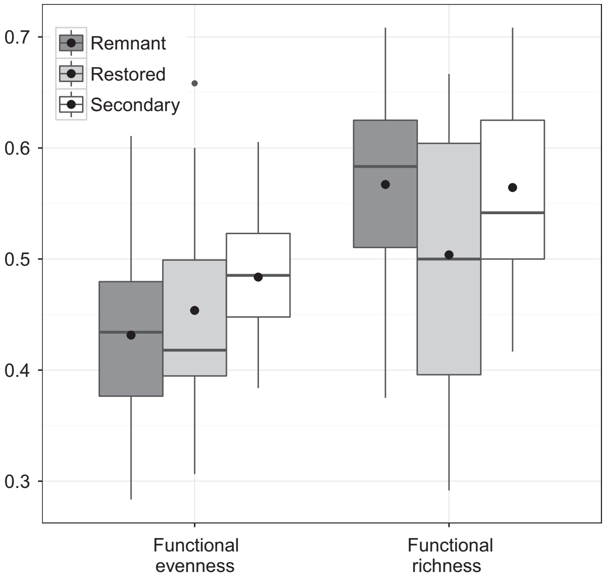

FIGURE 2 Box-plot of the functional indices of richness and evenness of pollination modes in remnants (primary forests), restored (tree plantings) and secondary (naturally regenerated) tropical semi-deciduous forests. Central boxes span the first quartile to the third quartile (the inter-quartile range or IQR). Segments and points inside the boxes show the median and the mean values, respectively, and "whiskers" below and above the boxes show the location of the smallest and the largest values no further than 1.5 × IQR from the first and the third quartiles. The small point indicates a datum beyond the whisker or "outlier". No statistical differences were found among forest types

insect-pollinated species in remnants, only 28 were found in restored forests. Some families with the largest reductions in species included *Lauraceae* (7/36 spp.), *Rubiaceae* (1/15 spp.) and *Sapotaceae* (2/14 spp.). Wind-pollinated species and abundance were reduced by more than one-third, probably because only three of 15 wind-pollinated euphorbs found in remnants were also found in restored forests. Moth-pollinated species fell by a half, and their abundance by more than a half (11/31 spp.). The *Apocynaceae* family, which had the largest number of moth-pollinated species, was represented here by only five species, compared with 15 species found in remnants. Other families of moth-pollinated species that were absent in restored forests included *Rubiaceae* (e.g. *Posoqueria* spp.), *Ebenaceae* (e.g. *Diospyros* spp.) and *Proteaceae* (e.g. *Roupala montana*). The species and abundances for pollen-consuming insects decreased, mainly because of reductions in *Myrtaceae* species (7/43 spp.). Flowers specialized in very small insects significantly decreased, probably as a result of the absence of *Monimiaceae* species (2/8 spp., genera *Mollinedia* and *Siparuna*). The abundance of fly-pollinated species reduced as well, in response to the scarcity of individuals of *Metrodorea nigra*, which was an important species among remnants. These reductions in pollination modes were replaced by much higher abundances and species pollinated by bees (mainly *Caesalpinoidae*, *Papilionoidae* and *Bignoniaceae* species) and bats (mostly *Malvaceae* sf. *Bombacoideae* species). The mean number of bird-pollinated species increased, although not significantly, because of the presence of the introduced species *Erythrina speciosa* in many restored forests.

Secondary forests also differed from remnants but changed to a lesser extent than restored forests (Figure 3). Bee-pollinated species significantly increased. Moth-pollinated species significantly fell by one half, and important reductions were found in the abundances of *Apocynaceae* (e.g. genera *Aspidosperma* and *Tabernaemontana*) and *Meliaceae* species (particularly *Cabralea canjerana*). The occurrence of fly pollination decreased due to the absence of *Metrodorea nigra*. Abundances were smaller in fig-wasp pollination (*Ficus* spp.) and wind pollination (various *Euphorbiaceae* species such as *Actinostemon* spp., *Sebastiana commersoniana* and *Tetrorchidium rubrivenium*) but larger in beetle (*Xylopia sericea* and other *Annonaceae* species), small insect (higher frequency of *Siparuna guianensis* trees) and big animal pollination (*Inga* spp.).

4 | DISCUSSION

We observed several patterns that are helpful in understanding the processes governing the assemblage of pollination modes among species, as well as in the decision-making processes aimed at restoring functionally diverse ecosystems.

First, species dissimilarity was much higher than functional dissimilarity among forest locations (Figure 1). High species dissimilarity

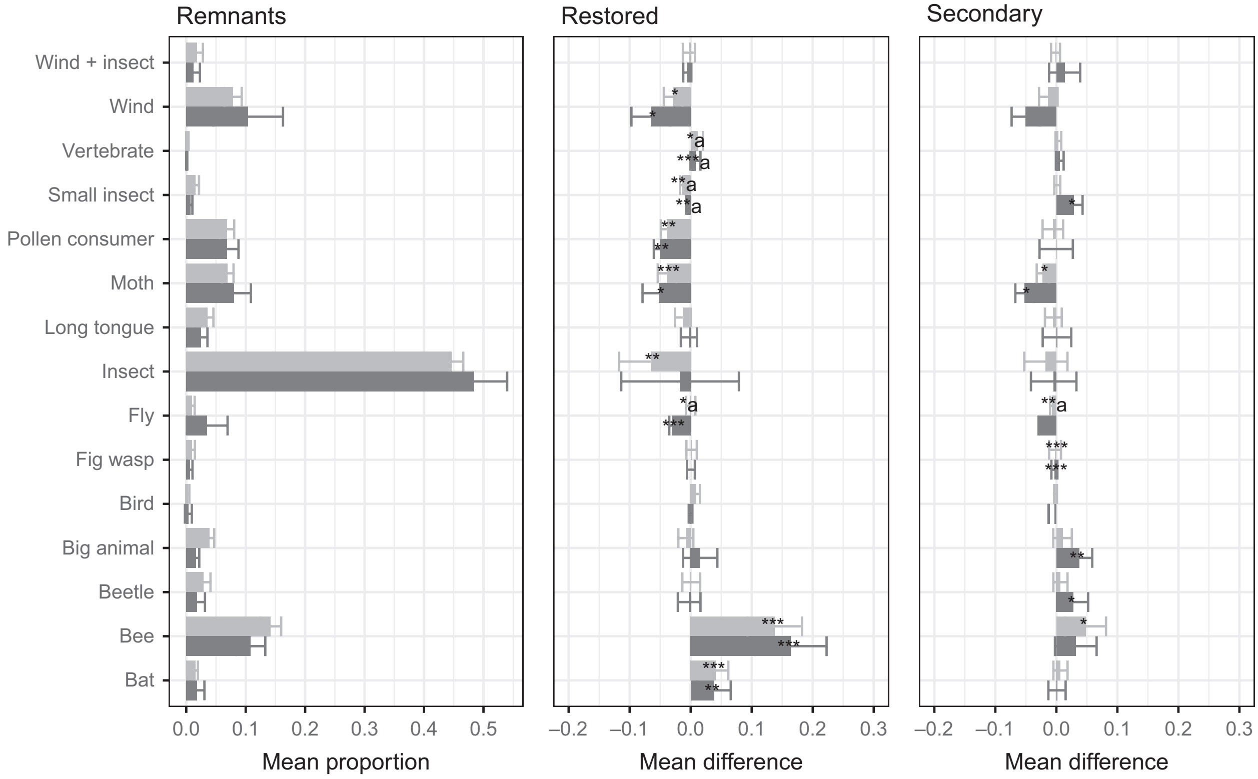

FIGURE 3 Mean values and CIs (95%) of species (light-grey) and abundance (dark-grey) proportions of pollination modes at remnants (primary forest) and the differences found among restored (tree plantings) and secondary (naturally regenerated) tropical semi-deciduous forests. The figure shows greater changes among restored forests than secondary forests, compared with primary forests. Asterisks (*) denote significant differences in GLM: *0.05, **0.01, ***0.001. "a" indicates changes in the presence–absence of pollination modes using zero-inflated binomial models

could be explained by the large distances between some of our study areas; however, the restricted geographic distribution of many species responding to specific environmental requirements (i.e. topography, soil types and pluviometric regimes), in conjunction with possible stochastic events, can also contribute to a high species turnover between communities on a minor scale (Brancalion et al., 2015; Torres et al., 1997). Small degrading effects in our remnants relating to fragmentation, border effects or other human pressures could be additional causes of variation in species composition. However, the significant differences among the three forest types demonstrated that the major causes of differentiation reside in the processes of total deforestation, land-use practices and subsequent restoration.

In contrast, the smaller functional dissimilarity indicates a rather stable functional assemblage of pollination modes and also a high ecological redundancy among communities (Petchey & Gaston, 2002; Pillar et al., 2013), regardless of the species replacement. The lack of spatial autocorrelation confirms this result because the variations in pollination modes were not related to the differences in species composition (and its spatial autocorrelation) among locations. Comparable studies support our findings and suggest that, among communities, differentiation for particular traits can be relatively small because of habitat-filtering forces selecting species with similar adaptations from the regional pool, as opposed to within communities, where the interactions between co-existing species are supposed to augment functional diversity by niche segregation (de Bello et al., 2009; Pavoine & Dolédec, 2005).

Second, pollination systems were characterized by the high predominance of generalist insect pollination and the secondary incidences of bee, wind, moth and pollen-consuming insect pollination, whereas many other specialized and mixed modes were underrepresented. This fairly low functional diversity of tree communities could possibly be ascribed to an environmental filtering mechanism where several selecting forces, perhaps including both pollinator and non-pollinator agents (i.e. herbivores, pathogens and abiotic stressors), may be interacting (Sargent & Otto, 2006; Strauss & Whittall, 2006). Underrepresented modes such as beetle, bat and bird pollination seem to be more common in understorey plants (Bawa, 1990; Buzato, Sazima, & Sazima, 2000; Diogo, Martins, Verola, & Costa, 2016; Fleming & Muchhala, 2008; Frankie et al., 1990; Sazima, Buzato, & Sazima, 1999; Schatz, 1990), for example, in many herbaceous monocots (*Costaceae* and *Heliconiaceae* by hummingbirds and bats and *Cyclantaceae* by beetles) and epiphytes (*Araceae* by beetles and bromeliads by hummingbirds and bats). Such large trait divergence among plant growth forms is expected and seems to be a pattern for various functional traits (de Bello et al., 2009). In the context of ecological restoration, this issue is of high concern and highlights the importance of encouraging projects aimed at reintroducing plants with different habits into restored and secondary forests (e.g. Duarte & Gandolfi, 2013; Le Bourlegat, Gandolfi, Brancalion, & dos Santos Dias, 2013) to fully recover functional diversity.

Third, restored forests showed more accentuated and variable changes in the assemblages of pollination modes than secondary forests, as was expected. One of the possible causes could be the artificial selection of species for plantings, which is generally performed to recover functional traits more relevant during the initial establishment of seedlings (e.g. light requirements) and/or which depend on the cost and availability of seedlings in nurseries; hence, it sometimes includes both native and exotic species (Brancalion et al., 2015). As a result, many functional traits essential for the stability of the ecosystem in the long term (e.g. reproductive traits) could remain neglected. Other causes could be the major disturbance impacts associated with these areas, causing alterations, for example, in soil seed banks, soil properties and the loss of connectivity with the surrounding forests that facilitate propagule arrival. The smaller changes found among secondary forests, in turn, seem to be reflected in the minor disturbance impacts and the lack of human intervention in these areas. In the present study, we could not test how specific restoration practices, ages of restoration and other local environmental variables explain variations in pollination modes within forest types because of the small number of sites and a lack of detailed information. However, our results suggest that highly resilient degraded sites could easily recuperate their functional diversity through natural regeneration alone, whereas at more disturbed sites, selecting better species for plantings and monitoring natural regenerants is recommended to better reassemble functional diversity.

Despite the changes found in several pollination modes, the functional richness among restored and secondary forests did not significantly differ from remnants, although we found lower values among several restored sites. Similarly, the functional evenness did not significantly differ among forest types, probably because of the predominance of the most important pollination modes, as well as the underrepresentation of the less common ones, was still maintained. This lack of variation seems to be concordant with the suggestion of Schleuter et al. (2010) that functional diversity indices are not so reliable when using categorical data because they were specifically developed for numerical traits. In this case, the variation in functional diversity indices alone would probably not be able to detect significant changes in particular functional attributes that may have important implications for biodiversity conservation.

Some of the changes we found in pollination modes are reinforced by previous studies, such as the negative effect of forest fragmentation on moth pollination found by Girão et al. (2009) and the higher representation of beetle-pollinated species (i.e. *X. aromatica*) in secondary areas found by Martins and Antonini (2016). However, divergent results appear when comparing our findings with those of studies that include different plant growth forms and strata. For example, Chazdon et al. (2003) and Lopes et al. (2009) have found major proportions of generalized insect pollination among secondary wet forests in Costa Rica and Brazil, but in the present study, we found this was predominant even among primary forests. Other specialized modes, such as bird, bat and non-flying mammal pollination, have been reported to be intensely reduced by human disturbances in other tropical wet forests (Girão et al. 2009; Lopes et al., 2009; Kimmel et al., 2010; Chazdon et al., 2003). In the present study, such pollination modes were underrepresented in general among tree species and did not significantly change in secondary areas.

Conflicting results may also occur as a consequence of ambiguous methods for plant classification. In previous studies conducted in semi-deciduous (Kinoshita et al., 2006; Yamamoto, Kinoshita, & Martins, 2007) and other tropical forests (Araújo, Gadelha Neto, Quirino, & Araújo, 2009; Diogo et al., 2016; van Dulmen, 2001; Girão et al., 2007; Kress & Beach, 1994), there was a predominance of bee pollination instead of generalized insect pollination because the authors used the traditional pollination syndromes (i.e. Fægri & van der Pijl, 1979) or just included the most efficient pollinators during plant species classification. We do not deny that bees are the preponderant pollinators of tropical wild species (i.e. according to these studies, bees pollinate >50% of species), but this does not necessarily mean that bee-pollinated plants are particularly adapted to bee pollination or that these plants prevent visits from other types of pollinators (e.g. Mayfield et al., 2001). Similarly, Kimmel et al. (2010) have found an overrepresentation of moth pollination in two secondary fragments because of the high dominance of *Inga ingoides* and *Albizia saman* trees. In the present study, we found an increase in the abundance of various *Inga* species among secondary forests, but we classified them as big animal-pollinated trees because they are secondarily pollinated by birds, bats and butterflies (Amorim, Galetto, & Sazima, 2013; Koptur, 1983).

In conclusion, we found that the assemblages of pollination modes in these tropical forests describe a pattern that is maintained at regional scale, and can be recovered throughout natural regeneration after low disturbance, but could remain altered after high disturbance and subsequent restoration practices. Several effects resulting from alterations in these assemblages can be expected. Reductions among specialized pollination modes (principally moth, fly and small insect) are likely to cause major competition between animal vectors. Pollinators have been seen to change their foraging behaviour to more generalized visitation patterns in less diverse plant communities (Heithaus, 1974). Under the former conditions, plant pollination would be negatively affected by smaller visitation frequency and the arrival of alien pollen to the stigmas. At the community level, less stable and robust interaction networks would be anticipated, as well as mismatches in flowering periods (Miller-Rushing, Høye, Inouye, & Post, 2010). Increases in the species and abundance proportions of pollination modes (particularly bees and bats in our case) are expected to be advantageous for their pollinators because of major resource availability (Carvalheiro et al., 2013; Dicks et al., 2015). Plant species having such pollination modes would be enhanced by means of facilitation and by higher attraction of their pollinators (Ghazoul, 2006). Still, plant species could be negatively affected as well because of major competition for pollination (Mitchell, Flanagan, Brown, Waser, & Karron, 2009).

ACKNOWLEDGEMENTS

We are grateful to Pedro Brancalion, Silvana Buzato, Paulo R. Guimarães Jr. and the two anonymous referees for their suggestions on the first version of the manuscript, as well as to The Administrative Department of Science, Technology and Innovation from Colombia (Colciencias) for the grant to P.M.M.P.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Location and description of the studied sites
Appendix S2 Tree species with pollination modes and number of sites present on each forest type

How to cite this article: Montoya-Pfeiffer PM, Rodrigues RR, Metzger JP, da Silva CI, Santos Baquero O, Alves dos Santos I. Are the assemblages of tree pollination modes being recovered by tropical forest restoration? *Appl Veg Sci*. 2018;21:156–163. https://doi.org/10.1111/avsc.12335