Title: Ecological outcomes of agroforests and restoration 15 years after planting

Running head: Ecological outcomes of agroforests and restoration

Authors and addresses: Carolina Giudice Badari[1], Luis Eduardo Bernardini[1], Danilo R. A. de Almeida[1], Pedro H. S. Brancalion[1], Ricardo Gomes César[2], Victoria Gutierrez[2], Robin L. Chazdon[3,4], Haroldo Borges Gomes[5], Ricardo A. G. Viani[6,7].

[1] Department of Forestry Sciences, University of São Paulo, ESALQ, Av. Pádua Dias, 11, 13418-900 Piracicaba, SP, Brazil

[2] WeForest asbl, Ogentroostlaan 15, 3090 Overijse, Belgium

[3] Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269–3043, USA

[4] Tropical Forests and People Research Centre, University of the Sunshine Coast, 90 Sippy Downs Drive, Sippy Downs Qld 4556, Australia

[5] Programa de Restauração Ecológica, Sistemas Agroflorestais e Extensão Rural do IPÊ - Instituto de Pesquisas Ecológicas, base no Pontal do Paranapanema – SP. Rua Ricardo Fogaroli, 387, 19280-000 Teodoro Sampaio, SP, Brazil.

[6] Department of Biotechnology and Plant and Animal Production, Federal University of São Carlos, CCA, Rodovia Anhanguera, Km 174, 13604-900, Araras, SP, Brazil

[7] Address correspondence to R. A. G. Viani, email ragviani@gmail.com

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/rec.13171

Author contributions: RAGV, CGB conceived and designed the research; CGB, LEB, performed the experiments; CGB, LEB, DRAA analyzed the data; RAGV, LEB, CGB, DRAA, HBG contributed with materials/analysis tools; CGB, LEB, DRAA, RC, RAGV, PHSB, RC, VG wrote and edited the manuscript.

Abstract

Large-scale forest restoration relies on approaches that are cost-effective and economically attractive to farmers, and in this context agroforestry systems may be a valuable option. Here, we compared ecological outcomes among (1) 12-15 year old coffee agroforests established with several native shade trees, (2) 12-15 year old high-diversity restoration plantations, and (3) reference, old-growth forests, within a landscape restoration project in the Pontal do Paranapanema region, in the Atlantic Forest of southeastern Brazil. We compared the aboveground biomass, canopy cover, and abundance, richness and composition of trees, and the regenerating saplings in the three forest types. In addition, we investigated the landscape drivers of natural regeneration in the restoration plantations and coffee agroforests. Reference forests had a higher abundance of trees and regenerating saplings, but had similar levels of species richness compared to coffee agroforests. High-diversity agroforests and restoration plantations did not differ in tree abundance. However, compared to restoration plantations agroforests showed higher abundance and species richness of regenerating saplings, a higher proportion of animal-dispersed species, and higher canopy cover. The abundance of regenerating saplings declined with increasing density of coffee plants, thus indicating a potential trade-off between productivity and ecological benefits. High-diversity coffee agroforests provide a cost-effective and ecologically viable alternative to high-diversity native tree plantations for large-scale forest restoration within agricultural landscapes managed by local communities, and should be included as part of the portfolio of reforestation options used to promote the global agenda on forest and landscape restoration.

Key words: agroforestry; *Coffea arabica* L.; ecological indicators; forest landscape restoration; natural regeneration; shade coffee;

Implications for practice

- High-diversity coffee agroforestry systems can facilitate forest and landscape restoration in the Atlantic Forest region while providing income for landowners during their first years;
- High-diversity coffee agroforestry systems can have equivalent (or better) ecological outcomes as restoration plantations established within the same region;
- The ecological restoration value of high-diversity coffee agroforests can be reduced in intensively-managed systems, indicating a trade-off between ecological and productive benefits.

Introduction

The loss and fragmentation of native forest ecosystems has been primarily driven by agriculture expansion, as a consequence of the growing demand for food, fuel, and fiber to sustain the rapidly increasing global human population (Lamb et al. 2005; Báez et al. 2011). Intensively managed production systems that remove all trees from the landscape have particularly negative consequences, while traditional agroforestry, such as shade-coffee production, re-establish trees in the landscapes and use eco-friendly approaches of production that can aid forest conservation (Garrity et al. 2006; Latawiec et al. 2016; Kremen & Merenlender 2018). In this context, we address the potential for agroforestry systems to mitigate the degradation caused by intensive agriculture and restore native forest ecosystems in degraded landscapes (Moguel et al. 1999; Vieira et al. 2009).

To reach ambitious global restoration goals while supporting the needs of a growing population, forest restoration initiatives should be integrated with other land uses (e.g. agricultural activities) as a strategy for improving restoration cost-effectiveness and attractiveness to farmers (Adams et al. 2016, Brancalion & Chazdon 2017), thereby improving both biodiversity conservation and human well-being at the landscape scale, an approach known as Forest and Landscape Restoration (FLR) (Mansourian et al. 2005). Although recent studies have explored the cost-effectiveness of different restoration approaches for ecosystem services provisioning (Birch et al. 2010; Molin et al. 2018), more information is needed about the differential performance of restoration approaches that include food producing species. The inclusion of food trees in restoration, including exotic species, was already recommended for improved restoration success in terms of human population involvement (Brancalion et al. 2014;

Muler et al. 2018), but this approach has not been rigorously assessed so far. By integrating restoration with agriculture production, restoration costs can be minimized (Brancalion et al. 2012), the pressure for more agricultural land can be mitigated (Latawiec et al. 2015), and the provision of ecosystem services improved (Brancalion et al. 2012; Uriarte & Chazdon 2016). Besides, forest-based production systems can increase landscape connectivity in degraded and deforested landscapes, benefiting biodiversity conservation (Bhagwat et al. 2008; Harvey et al. 2008; Uezu et al. 2008).

Agroforestry systems are among the most well-known production systems that integrate agriculture with environmental recovery (Lamb et al. 2005; Souza et al. 2016; Schulz & Schröder 2017; Harrison et al. 2018). These systems consist of land-uses where woody perennial plants are grown with agricultural crops or cattle pastures in a spatial arrangement or temporal sequence (Appanah et al. 2015; Hillbrand et al. 2017). Worldwide, agroforestry systems have been successfully used for agricultural production, especially in poor countries, where farmers have little access to resources for investing in external inputs (Besseau et al. 2018). High-diversity agroforestry has also been promoted as a cost-effective restoration approach (Ramos et al. 2009; Braga et al. 2018), which is more likely to be adopted by farmers (Souza et al. 2016; Besseau et al. 2018). Furthermore, some authors argue that agroforestry systems promote greater human involvement with forests, providing a sense of reconnection with nature that results in higher conservation outcomes (Miller 2005; Folke et al. 2011; Raymond et al. 2013).

Coffee agroforestry systems offer high potential for tropical forest restoration (Toledo & Moguel 2012; De Beenhouwer et al. 2013; Valencia et al. 2016; Irizarry et al. 2018). This production system is based on the use of shade trees, which can consist of several native species, and results in a well-developed forest structure (Braga et al. 2018), while coffee −a shade-tolerant small-tree− grows in the understory. Coffee agroforestry systems have been widely used in many regions around the world, and have been shown to yield high levels of both coffee production, and restoration and conservation outcomes (Perfecto et al. 2005; De Beenhouwer et al. 2013; Cerda et al. 2017; Nesper et al. 2017; Robusti et al. 2017).

Despite the environmental advantages of coffee agroforestry in comparison to traditional tree-less agricultural land uses, it is not clear whether these systems produce similar ecological outcomes as widely implemented active restoration approaches, and thus could be used even in contexts where restoration is mandatory. High-diversity restoration plantations have been widely used in the Atlantic Forest of southeastern Brazil to comply with the Forest Code, which mandates forest restoration in degraded landscapes (Rodrigues et al. 2011; Brancalion et al. 2016). Agroforestry could be used as a pathway for restoration in conjunction with restoration plantations and other strategies in a Forest and Landscape Restoration scenario, where the economic benefits of agroforestry could engage landowners in restoration that generates multiple benefits.

To investigate the potential of coffee agroforestry as a pathway for restoration in this context, we compared ecological outcomes among (1) 12-15 year old coffee agroforests established with several native shade trees, (2) 12-15 year old high-diversity native tree restoration plantations, established with no food production purposes, and (3) reference, old-growth forests, within a forest and landscape restoration project in the Pontal do Paranapanema region, in the Atlantic Forest of southeastern Brazil. We also identified landscape drivers of the attributes of these forests, in order to discuss general recommendations for both coffee agroforests and restoration plantations, aiming for FLR.

Methods

Study area and sites

The study was carried out in the Pontal do Paranapanema region (Fig. 1), municipalities of Teodoro Sampaio and Euclides da Cunha Paulista, São Paulo State, Southeast Brazil. The native vegetation in the region is classified as Seasonal Semi-deciduous Forest, which is one of the most threatened vegetation types within the Atlantic Forest hotspot for global biodiversity conservation (Ribeiro et al. 2009). The region has a tropical wet-dry climate (Alvares et al. 2013), with a hot and rainy season from October to March, and a dry period from April to September. Mean annual precipitation is 1,341 mm and mean annual temperature is 24.1°C. The elevation in the region varies from 265 m to 320 m, and predominant soil classes are the Ferrasols (Red Latosol) and Ultisols (Red-yellow Argisol) (Rossi 2017; Santos et al. 2018). The sandy soils of the region (Girardi et al. 2002) are especially vulnerable to erosion, which highlight the importance of regional restoration and more sustainable land uses (Ditt 2002).

Deforestation in the region peaked in mid-20th century for cattle production and coffee plantations (Leonidio 2009), and pasturelands on flat topography have been rapidly replaced by sugarcane plantations in the last decade. Land tenure in the region is heterogeneous, including land-reform settlements, small and large farms from private farmers and sugarcane mills, and protected areas (Valladares-Padua et al. 2002), such as the “Morro do Diabo” State Park, the second largest forest remnant (37,000 ha) of Seasonal Semi-deciduous Forest in the Brazilian Atlantic Forest (Uezu et al. 2008). Other forest fragments, with sizes ranging from 2 to 2,000 ha, are spread over several private properties and land-reform settlements (Cullen et al. 2005; Uezu et al. 2008). This region has one of the last populations of jaguar (*Panthera onca*) in the Atlantic Forest (Galetti et al. 2013) and is one of the last refugees of the endangered black lion tamarin (*Leontopithecus chrysopygus*), one of the rarest New World primates (Culot et al. 2015). During the last 15 years, the Brazilian NGO “Instituto de Pesquisas Ecológicas” (IPE) started restoration and agroforestry projects in the region in order to promote social development in land-reform settlements and conservation of the highly threatened species of the region (Cullen et al. 2005).

We selected 20 shaded-coffee agroforests (hereafter agroforests) established 12-15 years ago, four high-diversity restoration plantations with similar age as agroforests, and three reference, old-growth forests (hereafter reference) within the boundaries of the FLR program run by “Instituto de Pesquisas Ecológicas” in the region. All agroforests were about 1 ha in size, established in small farms within rural settlements (Fig. 1), and consisted essentially of two planting rows of coffee (*Coffea arabica* L., varieties Obatã and IPR 100) alternating with one row of Atlantic Forest native trees. These agroforests were established with the aim of increasing biodiversity conservation in the productive landscapes, through the creation of “stepping stones” between forest fragments. Because agroforests aimed to help restore native forest structure and diversity, they were implemented with about 20 or more native tree species, a particularity of these coffee agroforests compared to others in Brazil, which usually use a single shade tree species. Native trees species were randomly selected and planted in 4 m × 4 m spacing (625 trees.ha-^{1}), and initial spacing of coffee was about 1 m × 2.5 m (about 4,000 coffee plants.ha^{-1}). However, coffee abundance varied from site to site due to differences in the original abundance and post-planting survival of coffee shrubs. In some cases, farmers abandoned agroforests after the first few years and left the area only for forest protection, increasing mortality of coffee plants. In the productive sites, expected coffee production is 600 kg of processed coffee per hectare each year, with an income of up to USD 1000.ha^{-1}.year^{-1} for landowners. All agroforests were found within a radius of 40 km. Restoration plantations (Fig. 1) were more than 10 ha in area and were established within big farms, arranged as ecological corridors to increase connectivity between neighboring forest fragments. A 3 × 2 m spacing (1,667 trees.ha^{-1}) was employed, with 80-100 native tree species grouped into pioneers and non-pioneers, as typically done for forest restoration plantations in the Atlantic Forest (Rodrigues et al. 2009). Both agroforests and restoration plantations were fenced to prevent cattle invasion, and fertilized and weeded through mowing and/or glyphosate spraying in the first two years after planting. Some pioneer trees were pruned in the agroforestry plots after the second year after planting. Tree seedlings for both planted forests came from local community nurseries while coffee seedlings were obtained from comercial nurseries located in Paraná state, Brazil.

We selected three old-growth, well-conserved forest patches (Fig. 1) which form part of the National Ecological Stations of the Black Lion Tamarin as reference ecosystems and were no more than 15 km away from the restoration sites we sampled. Although reference plots were installed 50 m from forest edge, forest structure was heterogeneous, with some areas of discontinuous and/or low canopy, probably due to pervasive edge effects that may go beyond the 50 m buffer (Barlow et al. 2016). Thus, structure and diversity values of our reference forests may be lower than similar old-growth forests in the literature, but since all restoration plantations and agroforests sampled in this study are near a forest edge, we still consider such forests as valid references for interpretation of our results.

Data collection

We sampled trees in 24 plots of 25 ×16 m (400 m^2) in the 20 agroforests, 14 plots in the four restoration plantations, and eight plots in the three reference forests, totaling 27 sites and 46 plots. In the reference forests, plots were at least 100 m apart from each other, whereas the minimum distance for restoration and agroforestry plots was 50 m. We sampled all restoration plantations in the selected landscape. But, because there was a low number of them with similar age to agroforests, we sampled fewer plots in restoration plantations than agroforests. Within each plot we identified and measured diameter at breast height (DBH) and height of all living trees with DBH ≥ 5 cm. Additionally, we installed two 4 × 25 m subplots inside each sample plot to assess canopy cover, and abundance and species richness of spontaneously regenerating saplings (with height ≥ 0.5 m and DBH < 5 cm). Canopy cover was estimated by an adaptation of the line interception method (Viani et al. 2018). A 25-m line was placed in the forest floor and the portions of this line covered by the vertical projection of tree crowns (including those of coffee plants) were measured and converted in percentage. Using secondary data, all identified species were classified into seed dispersion syndromes as animal-dispersed or abiotic-dispersed (Embrapa 2011; Silva 2012; Zama et al. 2012; Barbosa et al. 2017).

Data analysis

First, we calculated abundance and number of species per plot, separately for trees with DBH ≥ 5 cm and for regenerating saplings. We estimated tree aboveground biomass (AGB) of each stem based on the allometric equation developed by Chave et al. (2014) for plots in the reference ecosystem, and by Ferez et al. (2015) for restoration plantations and agroforests. Data on wood density for the sampled tree species were obtained from Global Wood Density Data Base (Chave et al. 2009). For unidentified trees (27 from 1,327 individuals), we estimated wood density as the average density for the plot. Then, abundance, canopy cover, mean species density per plot and AGB were compared among agroforests, restoration plantations and references using ANOVA followed by the Tukey test for mean post-hoc comparison ($\alpha = 0.05$) when data were normally distributed. When data were non-normally distributed, we compared by Kruskal-Wallis followed by the Wilcoxon test for mean comparison ($\alpha = 0.05$). We used R 3.5.1 for all analysis (R Core Team 2018).

To compare tree and regenerating saplings species richness, we generated species rarefaction curves with individuals identified to species level, using the rarify function in the R package ‘vegan’ (Oksanen et al. 2018). To compare species composition among restoration strategies and reference ecosystems, we calculated Chao-Jaccard dissimilarity index (Chao et al. 2004) between each plot and created a graph using nonmetric multidimensional scaling to visualize dissimilarity among plots using the “mds” function. Exotic species (6.9%, 16 from 216) were excluded from richness analyses. Finally, we compared values for regenerating sapling richness and abundance, and for canopy cover with reference values (prescribed as adequate, minimum or critical according to the thresholds) used to assess trajectory of mandatory ecological restoration in São Paulo state, Brazil (Chaves et al. 2015). Abandoned and productive agroforests were grouped into a single category for all the comparisons, because a preliminary analysis showed no difference between them for ecological indicators (Fig. S1).

We used generalized linear models to identify landscape drivers of four forest attributes related to ecological outcomes and carbon sequestration in agroforests and restoration plantations. The four forest attributes analyzed were: i) biomass; regenerating saplings ii) abundance, iii) richness, and iv) proportion of animal-dispersed individuals. We considered as drivers i) old-growth forest cover in a 1-km buffer around the plot (Sloan et al. 2016); ii) plot distance from old-growth forests; and iii) plot distance from all forests, including any agroforest and restoration planting.

We checked for variable inflation and removed variables that could compromise the models. When data fitted normal distribution, we developed models using the Gaussian distribution. For each forest attribute, we generated all possible models plus a null model using the R package MuMIn (Barton 2016) and calculated the sum of squares for each model, selecting models with ΔAICc ≤ 2. If the null model was among the best models, we considered that the drivers were uninformative for the given attribute. We found no spatial autocorrelation of our data through the Mantel Test using packages "ade4" (Dray & Dufour 2007) and "geoR" (Ribeiro Junior & Diggle 2018).

Results

Ecological outcomes of agroforests and restoration plantations

Reference forests had a much higher abundance of trees and regenerating saplings than agroforests and restoration plantations (Fig. 2, Table S1). Although agroforests and restoration plantations did not differ in tree abundance, agroforests had higher sapling abundance and canopy cover (Fig. 2). According to local quality standards to assess forest restoration legal compliance, the average abundance of regenerating saplings and canopy cover of agroforests were minimum (intermediate level) and adequate (top level), respectively, while restoration plantations were critical (low level) for both indicators (Fig. 2b,d; and Table S1).

Reference forests had higher species density of trees and saplings per plot, whereas mean number of tree species per plot did not differ between agroforests and restoration plantations (Fig. 3). No differences in the proportion of animal-dispersed tree species (DBH $\geq$ 5 cm) were found among forest types (Fig. 3). However, both species density and proportion of animal-dispersed sapling species were higher in agroforests compared to restoration plantations. Rarefied species richness curves confirmed the higher richness of native trees and saplings in agroforests compared to restoration plantations (Fig. 4). Tree species composition was markedly different in reference sites and similar in agroforests and restoration plantations, whereas sapling composition was similar in all forest types (Fig. 4).

The number of native woody species regenerating in agroforests varied from 3 to 21 species per site. When we counted number of species per site, we found that seven out of the 20 agroforest sites had 15 or more species, the minimum legal threshold for forest restoration in São Paulo state, but only four of 20 reached the adequate levels of regenerating sapling richness in the understory (Table S1). Half of the restoration plantations (two out of four) had more naturally regenerating species than the minimum legal threshold (Table S1). All the species sampled are listed in Table S2).

The abundance of regenerating saplings is related to the density of coffee plants in the agroforests (Fig. 5). According to our model, 15-yr-old agroforests would have to have between 1,600 and 1,100 coffee plants per hectare to support regenerating saplings abundance within the minimum and adequate reference values, respectively, according to the legal quality standards for ecological restoration in the State of São Paulo (Fig. 5).

Four of the five agroforests with more than 2,500 regenerating saplings per hectare were abandoned and only one is productive (Fig.5).

Landscape drivers of forest attributes

Most drivers of forest attributes had low r-squared values (< 0.5) for the linear models applied, therefore some results show weak trends and should be interpreted with caution. Distance from native forests was a key landscape driver of forest attributes mainly for restoration plantings (Table 1). Restoration plantings had higher biomass, and regenerating saplings richness and proportion of animal dispersed individuals when closer to native forests. On the other hand, agroforests showed lower abundance of regenerating saplings when closer to old-growth forests. The complete list of the models generated is in Table S3.

Discussion

In agricultural landscapes, where farmers heavily rely on land use for their wellbeing, and where needs for productive land uses present conflicts for establishing restoration plantations, we found that coffee agroforestry is a promising component of FLR contributing to both tree diversity and bio-economy. Coffee agroforestry may have equivalent (or better) ecological outcomes than conventional restoration plantations for tropical forest restoration in the studied agricultural landscape. In addition, most of the coffee agroforestry sites we evaluated achieved the regional quality standards for canopy cover and abundance of regenerating saplings suggesting that forest restoration is following a desirable trajectory.

While the restoration type was a significant determinant of forest attributes 12-15 years after implementation - with agroforests having higher abundance, richness, and proportion of animal-dispersed species of regenerating saplings than restoration plantations – more isolated restoration plantings showed lower regenerating sapling abundance and richness, indicating the relevance of landscape considerations such as spatial arrangement of interventions for ecological restoration. As expected, compared to reference forests, both restoration treatments showed lower tree and regenerating saplings abundances and species richness.

Even though agroforests were initially implemented with lower tree densities, they showed higher AGB – especially when it contained more tree species – probably because landowners are more likely to tend for these systems on the long term for their direct benefits (Viera et al. 2009) and because they are closer to their residences. Nevertheless, results varied among forests. Surprisingly, reference forests presented high plot variation in AGB, probably because some of them are near (~50 m) to forest edges, and changes in microclimate conditions and human-mediated disturbances associated with this environment may have also reduced reference forest AGB (Magnago et al. 2016). As both agroforests and restoration plantations are usually carried out in areas < 50 m from edge, the references selected are valuable guidelines for restoration in the region.

At the landscape scale, isolation was an important factor in defining regenerating sapling proportion of animal-dispersed individuals and tree AGB in restoration plantings. Other studies have reported limited regeneration of native woody species in isolated ~10 year old restoration plantations in the Atlantic Forest region (César et al. 2018), yet older plantations can have a high abundance and richness of regenerating plants (Bertacchi et al. 2016).

Periodically cleaning the understory by weeding is a common practice to favor coffee plants in agroforestry systems (Boreux et al. 2016). This may explain the limited richness of regenerating saplings in the agroforests understory, which was farther than other ecological indicators to achieving the values attesting forest restoration compliance in São Paulo State, Brazil. However, we found more abundant and diversified native woody species regenerating in the understory of agroforests than in restoration plantations. Possibly, this is caused by greater attraction of seed dispersers (Viani et al. 2015), because this system provides better habitat for vertebrates (Perfecto et al. 2003; Komar 2006; Caudill et al. 2015). In addtion, the greater abundance of natural regeneration may be related to the higher canopy cover in agroforests, which may provide a more favourable habitat to seedling establishment by supressing invasive grasses. Regardless results reinforce the high ecological restoration value of high-diversity agroforests in some agricultural landscapes. High-diversity restoration plantations have been successfully used for decades in the Atlantic Forest region (Rodrigues et al. 2009), and there are many sites with biomass stocks and tree species richness with comparable levels to old-growth forests (Garcia et al. 2016). However, restoration plantations require intensive labor and high financial investments for at least two-three years after implementation to succeed (Ferez et al. 2015; Brancalion et al. 2019). Besides, young restoration plantations do not provide direct financial benefits to farmers, who are often unable to invest sufficient resources to support the development of successful restoration trajectories in native tree plantations. In other cases, farmers may find alternative ways to profit from restoration plantations, like cutting fences for allowing cattle grazing in plantation understory, a common problem in the region especially in the dry season, when pastures are dry and farmers have to complement cattle feeding. In extreme cases, young second-growth forests are re-cut to use the land for agriculture (Reid et al. 2019). In this context, agroforests can be considered a garden for farmers, who manage and produce several other products besides coffee (i.e. timber, fruits, honey), thus maintaining and protecting these forest patches (de Oliveira & Carvalhaes 2016; Souza et al. 2016). It is necessary to investigate more deeply the social and economic factors that motivate landowners'to carefully manage the forest type under restoration. Our results corroborate the idea that more constant monitoring and maintenance carried out by farmers may be an advantage and the main cause for the higher ecological outcomes of agroforests than conventional forest restoration plantations in the study region (Vieira et al. 2009; Brancalion et al. 2012).

In the study region, costs for establishing agroforestry and restoration plantations are around US$3,000 and US$4,800 per hectare, respectively (L. Cullen, 2019, Institute of Ecological Research - IPE, Brazil, personal communication). Thus, agroforestry can be a cost-effective pathway for restoration that provides direct economic benefits for farmers, especially in the early years. However, managing coffee agroforests for restoration may require navigating complex trade-offs between natural regeneration and coffee production, as the abundance of regenerating saplings was negatively associated with the abundance of coffee plants. For instance, we found that coffee abundance should be, in general, lower than 1,600 individuals per hectare to support the minimum legally accepted understory recolonization by native plants at the age of 15. This is a low density of coffee plants for shade systems (Baggio et al. 1997; Soto-Pinto et al. 2000), which in turn could make shade coffee production no longer attractive to landowners. We found an exception of a productive coffee agroforest with almost 2,000 coffee plants per hectare harboring more than 3,000 native regenerating saplings per hectare. It suggests that it is somehow possible to keep good levels of native tree species recruitment with higher densities of coffee plants. Thus, we suggest that further studies investigate which cropping and restoration practices may lead to these results.

One alternative to be tested would be to plant high abundance of coffee at the moment of agroforestry implementation, and manage it in the first years, when higher light availability may allow for good coffee yields in the shade of developing native plants, as is frequently done in some regions in Brazil (Baggio et al. 1997, Campanha et al. 2004). After this period, the density of coffee plants would be reduced or the system could be abandoned for forest recovery. In this context, high-diversity coffee agroforests would be a pathway for restoration – a transient land use used to facilitate native forest recovery while providing income for landowners for a few years (Vieira et al. 2009). Also, pruning and thinning native trees may thus be necessary to maintain coffee production (van Oijen et al. 2010) during restoration development. While the impacts of these practices require further studies, it may in fact benefit forest restoration (Swinfield et al. 2016). We are neither advocating for the sole use of agroforestry systems for forest restoration nor that coffee agroforesty systems will always have better outcomes than high-diverse restoration plantations, especially in the long term. We argue instead that managing agroforests for restoration requires looking at the landscape level and integrating ecological and production data, as well as the perception of farmers on the pros and cons of these systems, in order to achieve both socio-economic and environmental benefits through forest restoration.

Acknowledgements

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001, by WeForest Asbl/Vzw and was supported by the Institute of Ecological Research (IPE), to whom we thank Laury Cullen and the staff of the Pontal Project. The authors also would like to thank Vanessa Erler Sontag (Illus) for the support with the figures, the volunteers during field work and the landowners that allowed forest sampling in their properties. PHSB thanks the National Council for Scientific and Technological Development of Brazil (CNPq) (grant #304817/2015-5).

Literature cited

Adams C, Rodrigues ST, Calmon M, Kumar C (2016) Impacts of large-scale forest restoration on socioeconomic status and local livelihoods: what we know and do not know. Biotropica 48:731-744

Alvares CA, Stape JL, Sentelhas PC, de Moraes Gonçalves JL, Sparovek G (2013) Koppen's climate classification map for Brazil. Meteorologische Zeitschrift 22:711–728

Appanah S, Shono K, Durst PB (2015) Restoration of forests and degraded lands in Southeast Asia. Unasylva 66:52–63

Báez S, Ambrose K, Hofstede R (2011) Ecological and social bases for the restoration of a High Andean cloud forest: preliminary results and lessons from a case study in northern Ecuador. Pages 628–643 In: Juvik J, Scatena S, Bruijnzel, S Hamilton, L (eds) Tropical Montane Cloud Forests: Science for Conservation and Management. Hawaii University Press, Honolulu, Hawaii

Baggio AJ, Caramori PH, Androcioli Filho A, Montoya L (1997) Productivity of Southern Brazilian coffee plantations shaded by different stockings of Grevillea robusta. Agroforestry systems 37:11-120

Barbosa LM, Shirasuna RT, Lima FC, Ortiz PRT, Barbosa KC, Barbosa TC (2017) Lista de espécies indicadas para Restauração Ecológica para diversas regiões do Estado de São Paulo. Governo do Estado de São Paulo/Secretaria do Meio Ambiente/Instituto de Botânica, São Paulo, Brazil

Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, Mac Nally R, Thomson JR, Ferraz SF, Louzada J, Oliveira VH, Parry L, Solar RR, Vieira IC, Aragão LE, Begotti RA, Braga RF, Cardoso TM, de Oliveira RC Jr, Souza CM Jr, Moura NG, Nunes SS, Siqueira JV, Pardini R, Silveira JM, Vaz-de-Mello FZ, Veiga RC, Venturieri A, Gardner TA (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535:144–147

Barton K (2016) MuMIn: multi-model inference

Bertacchi MIF, Amazonas NT, Brancalion PHS, Brondani GE, Oliveira ACS, Pascoa MAR, Rodrigues RR (2016) Establishment of tree seedlings in the understory of restoration plantations: Natural regeneration and enrichment plantings. Restoration Ecology 24:100–108

Besseau P, Graham S, Christophersen T (2018) Restoring forests and landscapes: the key to a sustainable future. Global Partnership on Forest and Landscape Restoration, Vienna, Austria

Bhagwat SA, Willis KJ, Birks HJ, Whittaker RJ (2008) Agroforestry: a refuge for tropical biodiversity? Trends in Ecology and Evolution 23:261–267

Birch JC, Newton AC, Aquino CA, Cantarello E, Echeverría C, Kitzberger T, Schiappacasse I, Garavito NT (2010) Cost-effectiveness of dryland forest restoration evaluated by spatial analysis of ecosystem services. Proceedings of the National Academy of Sciences 107:21925–21930

Boreux V, Vaast P, Madappa LP, Cheppudira KG, Garcia C, Ghazoul J (2016) Agroforestry coffee production increased by native shade trees, irrigation, and liming. Agronomy for Sustainable Development 36:42

Braga DP, Domene F, Gandara FB (2018) Shade trees composition and diversity in cacao agroforestry systems of southern Pará, Brazilian Amazon. Agroforestry Systems 93:1409-1421

Brancalion PHS, Campoe O, Mendes JCT, Noel C, Moreira GG, van Melis J, Stape JL, Guillemot J (2019) Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. Ecological Aplications 29(2):e01847

Brancalion PHS, Cardozo IV, Camatta A, Aronson J, Rodrigues RR (2014) Cultural ecosystem services and popular perceptions of the benefits of an ecological restoration project in the Brazilian Atlantic Forest. Restoration Ecology 22:65–71

Brancalion PHS, Chazdon RL (2017) Beyond hectares: four principles to guide reforestation in the context of tropical forest and landscape restoration. Restoration Ecology 25:491-492

Brancalion PHS, Schweizer D, Gaudare U, Mangueira JR, Lamonato F, Farah FT, Nave AG, Rodrigues RR (2016) Balancing economic costs and ecological outcomes of passive and active restoration in agricultural landscapes: the case of Brazil. Biotropica 48:856–867

Brancalion PHS, Viani RAG, Strassburg BBN, Rodrigues, RR (2012) Finding the money for tropical forest restoration. Unasylva 63:25–34

Campanha MM, Santos RHS, Martinez HEP, Garcia SLR, Finger FL (2004) Growth and yield of coffee plants in agroforestry and monoculture systems in Minas Gerais, Brazil. Agroforestry systems 63:75-82

Caudill SA, Declerck FJA, Husband TP (2015) Connecting sustainable agriculture and wildlife conservation: Does shade coffee provide habitat for mammals? Agriculture, Ecosystems and Environment 199:85–93

Cerda R, Allinne C, Gary C, Tixier P, Harvey CA, Krolczyk L, Mathiot C, Clément E, Aubertot JN, Avelino J (2017) Effects of shade, altitude and management on multiple ecosystem services in coffee agroecosystems. European Journal of Agronomy 82:308–319

César RG et al. Moreno VS, Coletta GD, Chazdon RL, Ferraz SFB, de Almeida DRA, Brancalion PHS (2018) Early ecological outcomes of natural regeneration and tree plantations for restoring agricultural landscapes. Ecological Applications 28:373–384

Chao A, Chazdon RL, Colwell RK, Shen T (2004) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8:148–159

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman RC, Henry M, Martínez-Yrízar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Pélissier E, Casey PP, Ryan M, Saldarriaga JG, Vieilledent G (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biology 20:3177–3190

Chaves RB, Durigan G, Brancalion PHS, Durigan G, Aronson J (2015) On the need of legal frameworks for assessing restoration projects success : new perspectives from São Paulo state (Brazil). Restoration Ecology 23:754–759

Cullen L, Alger K, Rambaldi DM (2005) Land reform and biodiversity conservation in Brazil in the 1990s: conflict and the articulation of mutual interests. Conservation Biology 19:747–755

Culot L, Griese J, Knogge C, Tonini M, dos Santos MM, Estevam CG, Lopes BP, da Cunha BM, Silva AB, do Prado BHS, Garcia F, Fonseca RCB, Port-Carvalho M (2015) New records, reconfirmed sites and proposals for the conservation of Black Lion Tamarin (Leontopithecus chrysopygus) in the middle and upper Paranapanema. Neotropical Primates 22:32-39

Dray S, Dufour A (2007) The ade4 Package: Implementing the Duality Diagram for Ecologists. Journal of Statistical Software 22(4):1-20De Beenhouwer M, Aerts R, Honnay O (2013) A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. Agriculture, Ecosystems and Environment 175:1–7

de Oliveira RE, Carvalhaes MA (2016) Agroforestry as a tool for restoration in Atlantic Forest: Can we find multi-purpose species? Oecologia Australis 20:425–435

Ditt EH (2002) Fragmentos florestais no Pontal do Paranapanema. Annablume, São Paulo, Brazil.

Embrapa (2011) Lista das Famílias e Espécies nativas encontradas na regeneração natural de plantios de Eucalyptus do Brasil. Embrapa, Campinas, Brasil

Ferez APC, Campoe C, Mendes JCT, Stape JL (2015) Silvicultural opportunities for increasing carbon stock in restoration of Atlantic forests in Brazil. Forest Ecology and Management 350:40–45

Folke C, Jansson A, Rockstrom J, Olsson P, Carpenter SR, ChapinIII FS, Crépin AS, Daily G, Danell K, Ebbesson J, Elmqvist T, Galaz V, Moberg F, Nilsson M, Österblom H, Ostrom E, Persson A, Peterson G, Polasky S, Steffen W, Walker B, Westley F (2011) Reconnecting to the Biosphere. AMBIO 40:719–738

Galetti M, Eizirik E, Beisiegel B, Ferraz K, Cavalcanti S, Srbek-Araujo AC, Crawshaw P, Paviolo A, Galetti Jr. PM, Jorge, ML, Marinho-Filho J, Vercillo U, Morato R (2013) Atlantic rainforest's jaguars in decline. Science 342:930–933

Garcia LC, Hobbs RJ, Ribeiro DB, Tamashiro JY, Santos FAM, Rodrigues RR (2016) Restoration over time: is it possible to restore trees and non-trees in high-diversity forests? Applied Vegetation Science 19:655–666

Garrity D, Okono A, Grayson M, Parrott S (2006) World Agroforestry into the Future. World Agroforesty Centre, Nairobi, Kenia

Girardi E, Meneguette A, Girardi EP (2002) Atlas Interativo da bacia hidrográfica do Rio Santo Anastácio: Implementação E Disponibilização Em Cd-Rom E Na Www. Simpósio Brasileiro de Geomática, Presidente Prudente, 9-13 July 2002

Harrison R, Miccolis A (2018). The critical role of agroforestry in forest and landscape restoration. Current Conservation 12:8–12

Harvey CA, Komar O, Chazdon R, Ferguson Bg, Finegan B, Griffith DM, Martínez-Ramos M, Morales H, Nigh R, Soto-Pinto L, van Br eugel M, Wishnie M (2008)

Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. Conservation Biology 22:8–15

Hillbrand A, Borelli S, Conigliaro M, Olivier E (2017) Agroforestry for landscape restoration Exploring the potential of agroforestry to enhance the sustainability and resilience of degraded landscapes. FAO, Food and Agriculture Organization of the United Nations, Rome, Italy

Irizarry AD, Collazo JA, Pacifici K, Reich BJ, Battle KE (2018) Avian response to shade-layer restoration in coffee plantations in Puerto Rico. Restoration Ecology 26(6):1212–1220

Komar O (2006) Priority Contribution Ecology and conservation of birds in coffee plantations: a critical review. Bird Conservation International 1:1–23

Kremen C, Merenlender AM (2018) Landscapes that work for biodiversity and people. Science 362:304

Lamb D, Erskine P, Parrotta J (2005) Restoration of Degraded Tropical Forest Landscapes. Science 310:1628–1632

Latawiec AE, Crouzeilles R, Brancalion PHS, Rodrigues RR, Sansevero JB, dos Santos JS, Mills M, Nave AG, Strassburg BB (2016) Natural regeneration and biodiversity: a global meta-analysis and implications for spatial planning. Biotropica 48:844–855

Leonidio A (2009) Violências fundadoras: o Pontal do Paranapanema entre 1850 e 1930. Ambiente & Sociedade 12:37–48

Magnago LFS, Magrach A, Barlow J, Schaefer CEGR, Laurance WF, Martins SV, Edwards DP (2016) Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? Functional Ecology 13:542–552Mansourian S, Vallauri D, Dudley N (2005) Forest restoration in landscapes: beyond planting trees. Springer, New York.

Mercer DE (2004) Adoption of agroforestry innovations in the tropics: A review. Agroforestry Systems 61:311–328

Miller JR (2005) Biodiversity conservation and the extinction of experience. Trends in Ecology and Evolution 20:430–434

Moguel P, Toledo VM (1999) Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology 13(1):11–21

Molin PG, Chazdon R, Ferraz SFB, Brancalion PHS (2018) A landscape approach for cost-effective large-scale forest restoration. Journal of Applied Ecology 55:2767–2778

Muler AE, Prieto PV, Richards RC, Brancalion PHS (2018) Ecological outcomes and popular perceptions of urban restored forests in Rio de Janeiro, Brazil. Environmental Conservation 45:155–162

Oksanen J , Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) Vegan: Community Ecology Package. R package version 2.5-2.

Perfecto I, Mas A, Dietsch T, Vandermeer J (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation 12:1239–1252

Perfecto I, Vandermeer J, Mas A, Pinto L S (2005) Biodiversity, yield, and shade coffee certification. Ecological Economics 54(4): 435-446

R Core Team (2018) R: A language and environment for statistical computing.

Ramos SF, Chabaribery D, Monteiro AVVM, Silva JR (2009) Sistemas Agroflorestais: estratégia para a preservação ambiental e geração de renda aos agricultores familiares. Informações Econômicas 39:37–48

Raymond CM, Singh GG, Benessaiah K, Bernhardt JR, Levine J, Nelson H, Turner NJ, Norton B, Tam J, Chan KMA (2013) Ecosystem Services and Beyond: Using Multiple Metaphors to Understand Human–Environment Relationships. BioScience 63:536–546

Reid JL, Fagan ME, Lucas J, Slaughter J, Zahawi RA (2019) The ephemerality of secondary forests in southern Costa Rica. Conservation Letters 1–7

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141–1153

Ribeiro Junior, Diggle PJ (2018) geoR: Analysis of Geostatistical Data. R package. Version 1.7-5.2.1

Robusti EA, Zapparoli ID, Santoro PH (2017) Café arborizado no estado do Paraná, Brasil: Indicadores financeiros e interferências ambientais. Agroalimentaria 23:79–91

Rodrigues RR, Gandolfi S, Nave AG, AronsoN J, Barreto TE, Vidal CY, Brancalion PHS (2011) Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. Forest Ecology and Management 261:1605–1613

Rodrigues RR, Lima RAF, Gandolfi S, Nave AG (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. Biological Conservation 142:1242–1251

Rossi M (2017) Mapa Pedológico do Estado de São Paulo: revisado e ampliado. Instituto Florestal, São Paulo, Brazil

Santos HG dos, Jacomine PKT, Anjos LHC, Oliveira VA, Lumbreras JF, Coelho MR, Almeida JA, Araujo filho JC, Oliveira JB, Cunha TJF (2018) Brazilian Soil Classification System. Embrapa, Brasília, Brazil

Schulz JJ, Schröder B (2017) Identifying suitable multifunctional restoration areas for Forest Landscape Restoration in Central Chile. Ecosphere 8:e1644

Silva JM da (2012) Floresta urbana: síndrome de dispersão e grupos ecológicos de espécies do sub-bosque. Boletim de Geografia 31:135–144

Sloan S, Goosem M, Laurance, SG (2016). Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region. Landscape Ecology 31:601–618.

Soto-Pinto L, Perfecto I, Castillo-Hernandez J, Caballero-Nieto J. (2000). Shade effect on coffee production at the northern Tzeltal zone of the state of Chiapas, Mexico. Agriculture, Ecosystems & Environment 80:61-69

Souza SEXF, Vidal E, Chagas GF, Elgar AT, Brancalion PHS (2016) Ecological outcomes and livelihood benefits of community-managed agroforests and second growth forests in Southeast Brazil. Biotropica 48:868–881

Swinfield T, Afriandi R, Antoni F, Harrison RD (2016) Accelerating tropical forest restoration through the selective removal of pioneer species. Forest Ecology and Management 381:209–216

Toledo VM, Moguel P (2012) Coffee and sustainability: The multiple values of traditional shaded coffee. Journal of Sustainable Agriculture 36:353–377

Uezu A, Beyer DD, Metzger JP (2008) Can agroforest woodlots work as stepping stones for birds in the Atlantic forest region? Biodiversity and Conservation 17:1907–1922

Uriarte M, Chazdon RL (2016) Incorporating natural regeneration in forest landscape restoration in tropical regions: synthesis and key research gaps. Biotropica 48:915–924

Valencia V, Naeem S, García-Barrios L, West P, Sterling EJ (2016) Conservation of tree species of late succession and conservation concern in coffee agroforestry systems. Agriculture, ecosystems & environment 219:32–41

Valladares-Padua C, Padua SM, Cullen L (2002) Within and surrounding the Morro do Diabo State Park: biological value, conflicts, mitigation and sustainable development alternatives. Environmental Science & Policy 5:69–78

van Oijen M, Dauzat J, Harmand JM, Lawson G, Vaast P (2010). Coffee agroforestry systems in Central America: II. Development of a simple process-based model and preliminary results Agroforestry systems 80: 361–378

Viani RAG, Barreto TE, Farah FT, Rodrigues RR, Brancalion PHS (2018) Monitoring Young Tropical Forest Restoration Sites: How Much to Measure? Tropical Conservation Science 11:1–9

Viani RAG, Vidas NB, Pardi MM, Castro DCV, Gusson E, Brancalion PHS (2015) Animal-dispersed pioneer trees enhance the early regeneration in Atlantic Forest restoration plantations. Natureza & Conservação 13:41–46

Vieira DLM, Holl KD, Peneireiro FM (2009) Agro-Successional Restoration as a Strategy to Facilitate Tropical Forest Recovery. Restoration Ecology 17:451–459

Zama MY, Bovolenta YR, Carvalho ES, Rodrigues DR, Araujo CG, Sorace MAF, Luz DG (2012) Florística e síndromes de dispersão de espécies arbustivo-arbóreas no Parque Estadual Mata São Francisco, PR, Brasil. Hoehnea 39:369–378

Table 1. Models ΔAICc<2 for the landscape drivers of forest and natural regeneration attributes of coffee agroforests and restoration plantations in Pontal do Paranapanema region, Southeast Brazil. LAND.COVER: proportion of old-growth forest cover in a 1-km buffer around the plot; DIST.ALL: distance from the nearest forest (including agroforests or restoration sites); DIST.OG: distance from old-growth forests.

Coffee agroforestry systems			
Attribute	**Best models**	**ΔAICc**	**R^2**
Biomass	NULL*	0.00	0.00
	LAND.COVER	0.95	0.06
	DIST.OG	1.45	0.05
Regenerating saplings abundance	DIST.OG	0.00	0.19
Regenerating saplings richness	DIST.ALL	0.00	0.12
	NULL*	0.66	0.00
Regenerating saplings proportion of animal dispersed individuals	DIST.OG	0.00	0.14
	NULL*	1.17	0.00
	DIST.ALL + DIST.OG	1.71	0.17
Restoration plantations			
Attribute	**Best models**	**ΔAICc**	**R^2**
Biomass	DIST.ALL + DIST.OG	0.00	0.49
	DIST.OG	0.52	0.34
	DIST.ALL + LAND.COVER	0.59	0.47
	DIST.ALL + DIST.OG + LAND.COVER	1.78	0.57
Regenerating saplings abundance	NULL*	0.00	0.00
Regenerating saplings richness	DIST.ALL	0.00	0.33
Regenerating saplings proportion of animal dispersed individuals	DIST.ALL + DIST.OG	0.00	0.48
	DIST.ALL	0.32	0.33

*No relevant drivers, since the null model is among the best models.

Figure 1. Locations of the study sites in the Pontal do Paranapanema landscape, São Paulo state, Brazil. Each black marker (star, square, triangle) represent a 400 m² study plot.

Figure 2. Abundance of trees (DBH ≥ 5 cm; A) and regenerating saplings (height ≥ 50 cm, DBH < 5 cm; B), aboveground biomass (AGB; C), and canopy cover (D) in reference forests, coffee agroforests, and restoration plantations in the Pontal do Paranapanema landscape, São Paulo state, Brazil. Different letters above the boxplots indicate significant differences (Tukey test for A, C-D; Wilcoxon test for B; $p < 0.05$). Values above the dotted line are considered adequate, between the dotted and continuous lines are considered minimum, and below the continuous line are considered critical according to the legal ecological standards of São Paulo State to attest forest restoration compliance.

Figure 3. Mean species richness for trees (DBH ≥ 5 cm; A) and regenerating saplings (height ≥ 50 cm cm, DBH < 5 cm; B), and proportion of animal-dispersed trees (C) and regenerating saplings (D) in reference forests, coffee agroforests, and restoration plantations in the Pontal do Paranapanema landscape, São Paulo state, Brazil. Different letters above the boxplots indicate significant differences (Tukey test for A, C-D; Wilcoxon test for B; $p < 0.05$).

Figure 4. Rarefied species richness of trees (DBH $\geq$ 5 cm; A) and regenerating saplings (height $\geq$ 50 cm cm, DBH < 5 cm; B), and two-dimensional nonmetric dimensional scaling plots of Chao-Jaccard dissimilarity index for trees (C) and regenerating saplings (D) in reference forests, coffee agroforests, and restoration plantations in the Pontal do Paranapanema landscape, São Paulo state, Brazil. Dotted lines represent one standard deviation from the mean number of species in graphs A and B.

Figure 5. Negative binomial generalized linear model between the density of regenerating saplings and the coffee abundance in abandoned (red points) and productive (blue points) coffee agroforestry systems at Pontal do Paranapanema landscape, São Paulo, Brazil. Values above the continuous line are considered adequate, and below the dotted line are considered critical according to the legal ecological standards of São Paulo State to attest forest restoration compliance.

Fig. 1

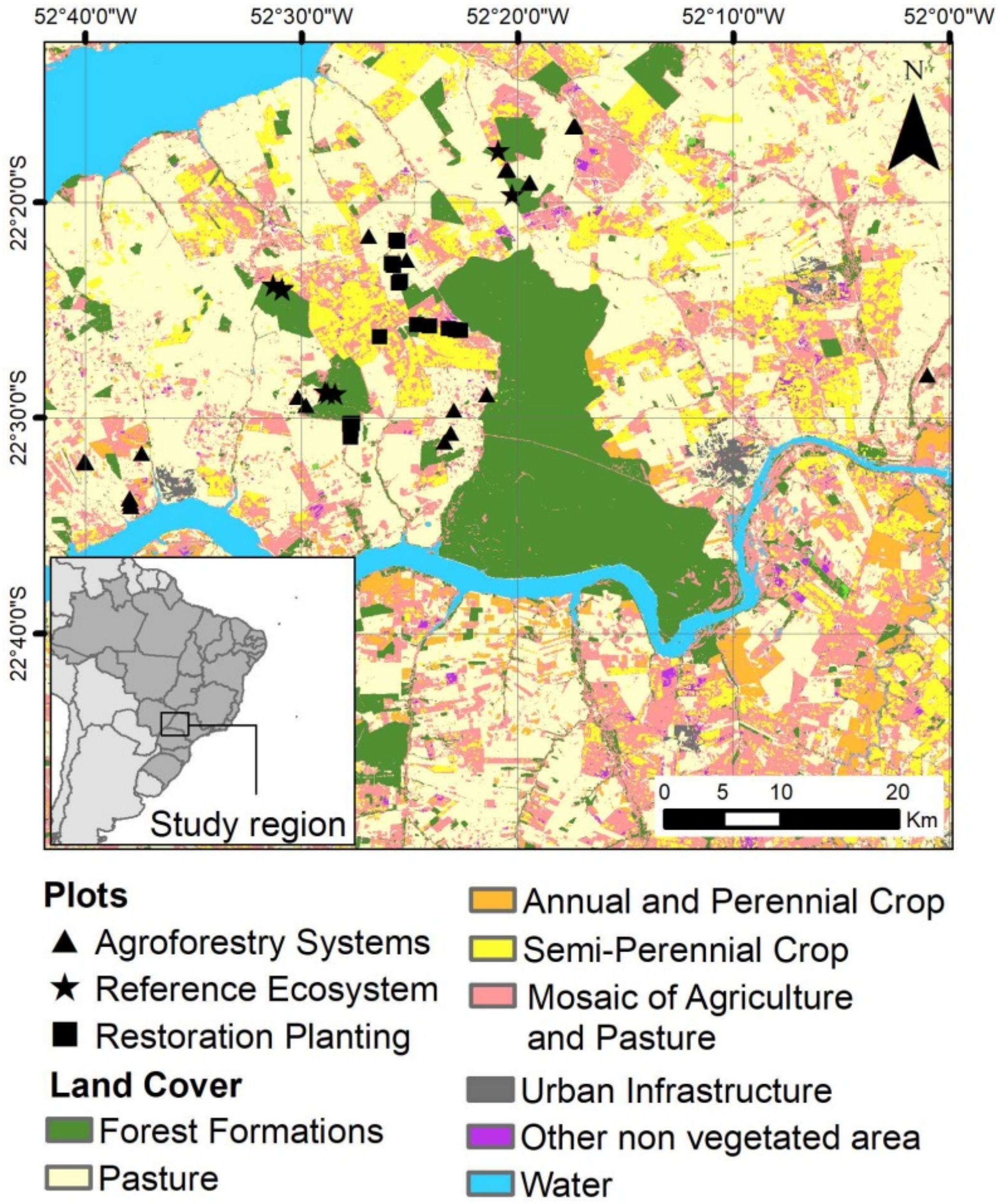
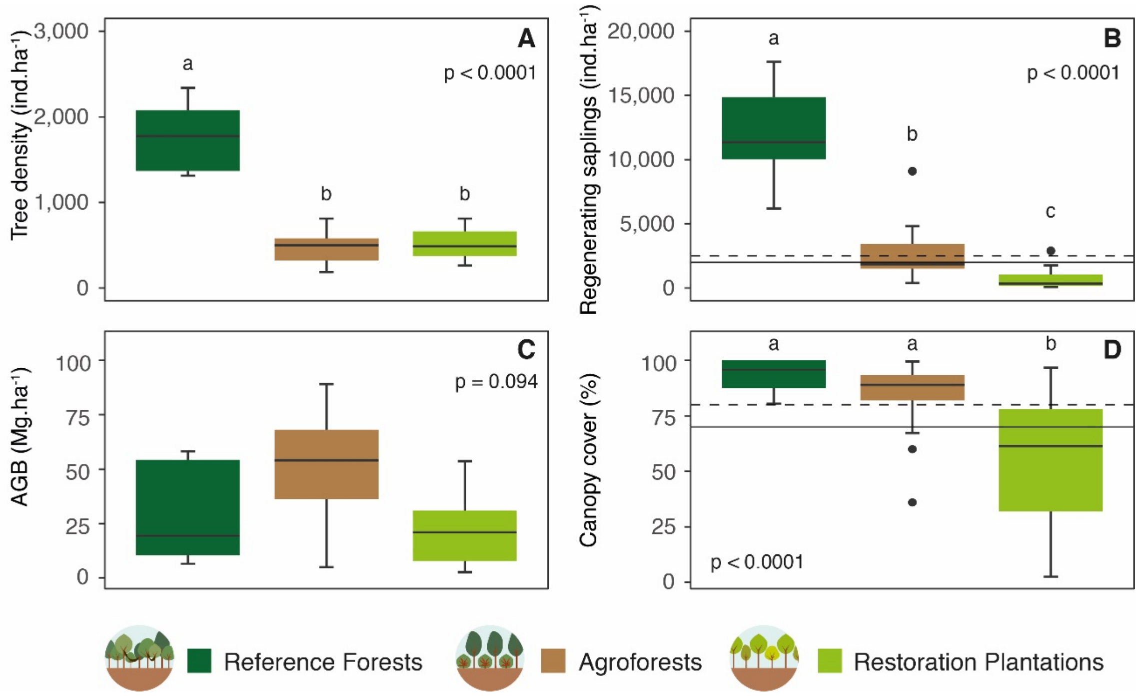
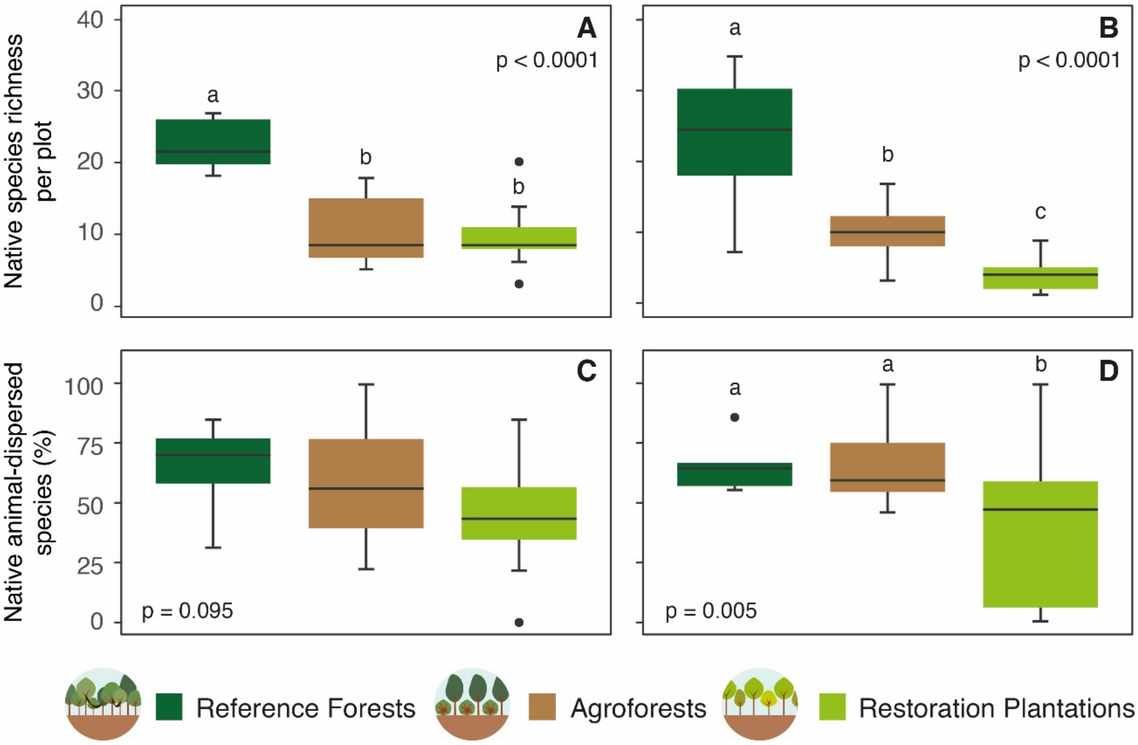

52°40'0"W
52°30'0"W
52°20'0"W
52°10'0"W
52°0'0"W
22°20'0"S
22°30'0"S
22°40'0"S
N
Study region
0 5 10 20
Km
Plots
Agroforestry Systems
Reference Ecosystem
Restoration Planting
Land Cover
Forest Formations
Pasture
Annual and Perennial Crop
Semi-Perennial Crop
Mosaic of Agriculture and Pasture
Urban Infrastructure
Other non vegetated area
Water

Fig. 2



A
p < 0.0001
Tree density (ind.ha⁻¹)
3,000
2,000
1,000
0
a
b
b
B
p < 0.0001
Regenerating saplings (ind.ha⁻¹)
20,000
15,000
10,000
5,000
0
a
b
c
C
p = 0.094
AGB (Mg.ha⁻¹)
100
75
50
25
0
D
p < 0.0001
Canopy cover (%)
100
75
50
25
0
a
a
b
Reference Forests
Agroforests
Restoration Plantations

Fig. 3



A
p < 0.0001
B
p < 0.0001
C
p = 0.095
D
p = 0.005
Native species richness per plot
Native animal-dispersed species (%)
a
b
b
a
b
c
a
a
b
40
30
20
10
0
100
75
50
25
0
Reference Forests
Agroforests
Restoration Plantations

Fig. 4

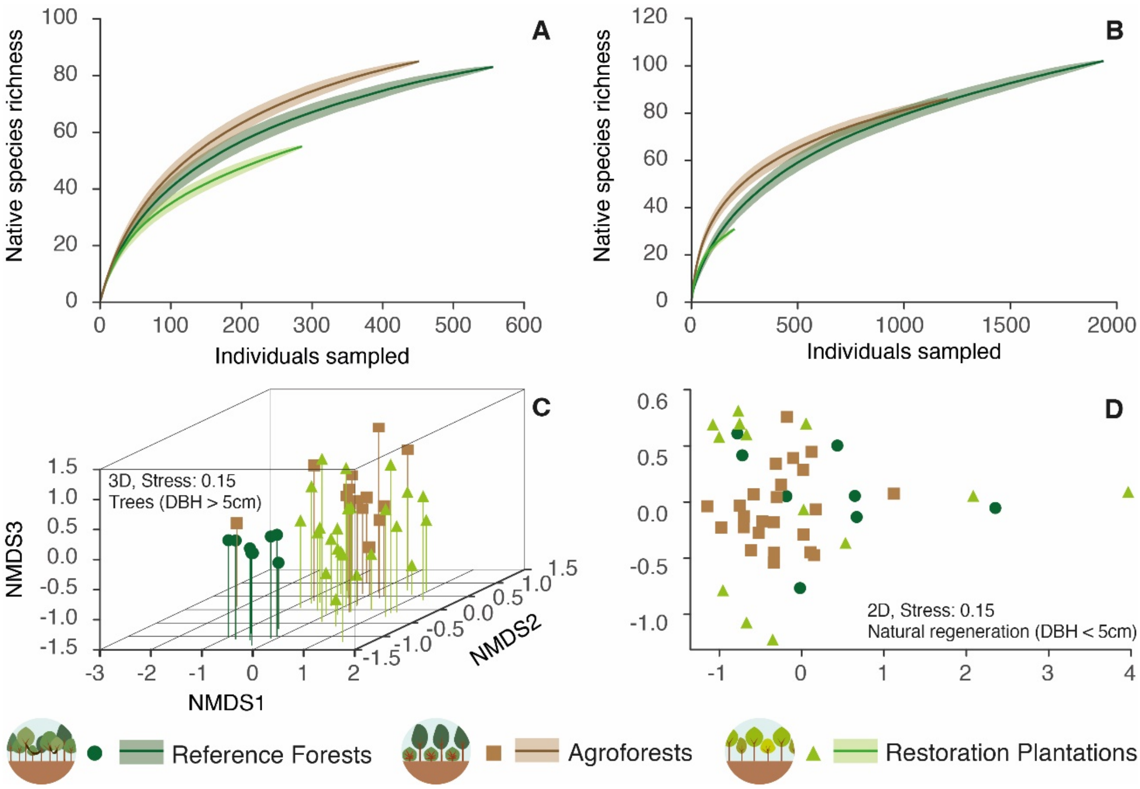
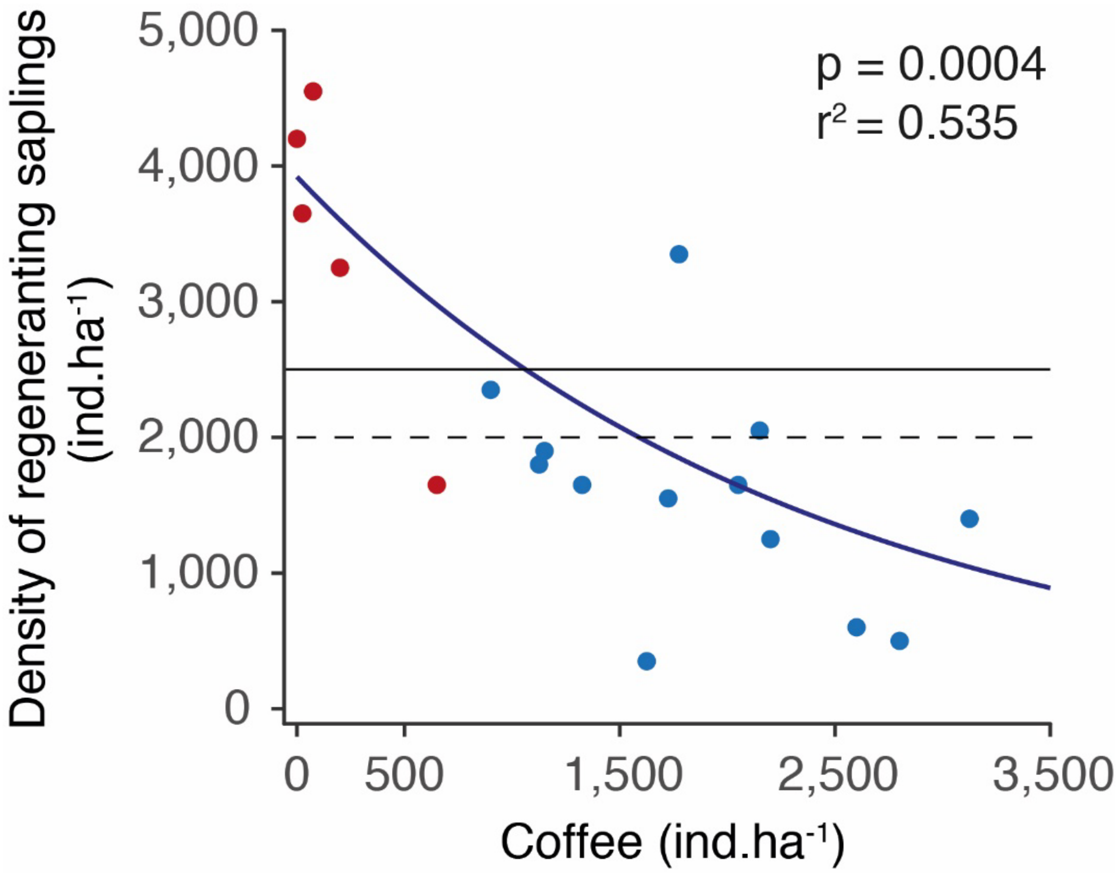

A
B
C
D
Native species richness
Individuals sampled
NMDS1
NMDS2
NMDS3
3D, Stress: 0.15
Trees (DBH > 5cm)
2D, Stress: 0.15
Natural regeneration (DBH < 5cm)
Reference Forests
Agroforests
Restoration Plantations

Fig. 5



p = 0.0004
r2 = 0.535
Density of regeneranting saplings (ind.ha-1)
5,000
4,000
3,000
2,000
1,000
0
0
500
1,500
2,500
3,500
Coffee (ind.ha-1)