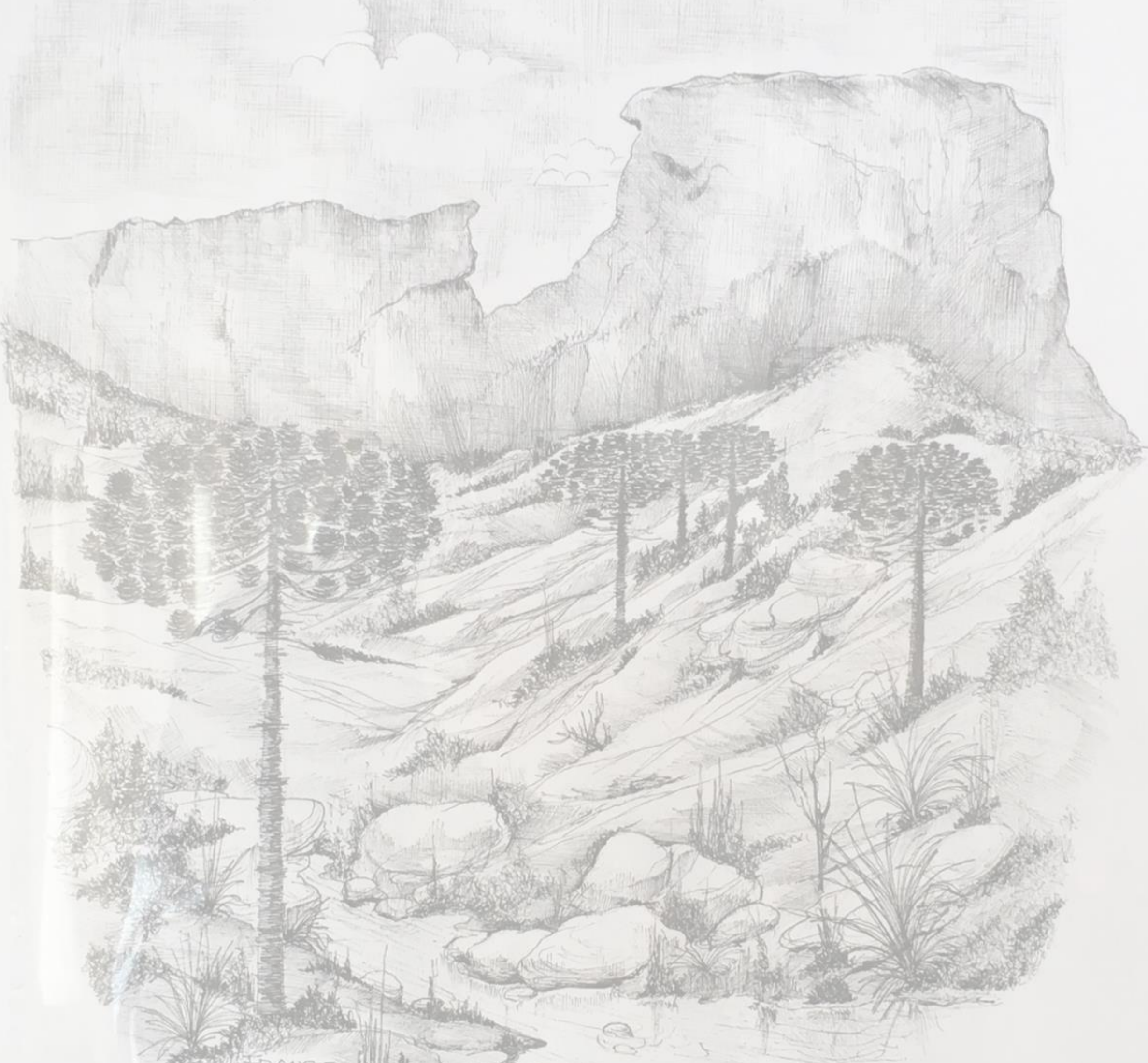
Managing the landscape across the Atlantic Forest to guarantee pollination service and biodiversity conservation



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São Paulo, 2022

UNIVERSIDADE DE SÃO PAULO

TESE DE DOUTORADO

Managing the landscape across the Atlantic Forest to guarantee pollination service and biodiversity conservation

Manejo da paisagem ao longo da Mata Atlântica para garantir o serviço de polinização e a conservação da biodiversidade

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Prof(a). Dr(a).	Prof(a). Dr(a).

Prof. Dr. Jean Paul Metzger
Orientador

Dedication

This thesis is dedicated to my parents, who once more taught me with their example than is never too late to start again, that the knowledge and experience acquired are some of the best tools to deal with uncertainties. I would also like to dedicate this work all living beings that have or will migrate at some point in their lives. May the wind provide the favorable conditions for a new beginning, and that patience makes the best while things get better.

Epigraph

“In the first years of your live, you live beneath the shadow of your past, too young to know what to do. In the last years, you find you are too old to understand the world coming at you from behind. In between there is a small and narrow beam of light that illuminates your life, that’s all you have. That little beam of light in which to create the full wonder of the unique human being and the challenge in life.

The ultimate creative challenge ...

...the ultimate creative challenge is to be the architect of your own life”.

shaman in Ecuador, from the book One River of Wade Davis.

Acknowledgements

I would like to first thank all the institutions that made this possible. This work was developed in the Ecology department in the Biosciences Institute of the University of São Paulo. The work was financed by the "Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001", and FAPESP projects 2013/23457-6 & 2017/19411-1; 2018/06330-6, crucial financial support that allowed for the fully time dedication to develop this work, destined to do research on key environmental and agronomic topics for Brazilian science with the intention to benefit Brazilian society hope to have benefits beyond its borders. The work greatly benefitted from an inspiring and creative environment, the one created and maintained by the professor and colleagues from the Ecology department and the Landscape and Conservation Ecology Lab (LEPaC). In the department several student initiatives occur were crucial, for experience exchange and more importantly is a welcoming environment in which I felt at home. Moreover, the staff and the commitment of the professors and students to create an amenable space for everybody, this was particularly evident during the pandemic which extended the PhD deadlines given the increasing uncertainties that arise.

I would like to give a special thanks to the student representative at that moment: Bruna and Julia who multiply to give attend newly demand from and unprecedented global quarantine. They articulate psychological support that led to conforming mindfulness support session and afterwards with the support from the ICB somatic experience group, that allow to stablish bond that still exist until these days. I most express a double thanks to Julia for her friendship, and partnership for the long hours on discussion shared in the lab and many more adventures and great moments in international events. The lab is also filled with great personalities most of which I'm profoundly thankful to

have met. Since I arrived in the LEPaC I was received with open arm, my ideas found a space to be expressed and were nurture and further expanded by the shared wish to find favorable conditions for us and the biodiversity we come from. A special shout out to current and former lab partners, Isabela, Larissa, Chico, Naty, Karine, Felipe, Catalina, Fernando, Melina, who soon became more than colleagues and were a family in which more than academics issues could be share. Also, to Marian Eiko, Douglas, Arthur, Sebastian, Clarice, Mila, Nataly, Paula, Victor, Mafe, Carito, Leandro and Mariana, always present to share laughter during the long lab hours and celebrate the small victories which were crucial to continue to the bigger goals partly express in this work.

The University is a beautiful place, not only for being a forest, highly diverse island within the largest south American city but also because the people that there arrive. In the Ecology department I had the luck to meet many great colleagues, must of which belonged to the LAGE collaboration space, where several great professor work, who also have a great institutional commitment that is both inspiring and empowering. I must send a huge hug to Andres with whom I have shared great moments and trips, but most importantly with whom the most intense part of the pandemic was lived. A special thanks to Soly, Renato, Gsus, Renan, Diana, Leticia, Pamela, Bruno, Luanne, Rodolfo, and the collegues from Bee Lab Liedson, Sheina, Rodolfo, Guaraci, Andre. I'm sure I'm forgetting many people who taught, encourage, and inspired me along this time. All crucial to keep going in the toughest moments, the same can be said for the institutional staff, Vera, Welintong, Shirlene, Erika, always there available to help with ease the struggles associated to the burocratic steps that never stop appearing.

I most thank the Argentinian family as well for making all more pleasant during my exchange period in the National University of Rio Negro at Bariloche. During the time in the Patagonian cold, I found much warmth in the house of Maxi and Jaqueline's family, with their wonderful three kids, Ana, Eliseo, and Juan. The mate, wines and long talk gave sense to live when the weather was too cloudy. Apart from their friendship, they were great landowner and neighbors while living in La Retaguardia, a shelter like house where every second lived felt like a dream came true. Special shout to the lab members of IRNAD, Matias, Pablo, Margarita, Fernanda, Facundo, and the Brazilian friends Dudu, Rafaela and Tati. I cannot leave out other biologists I met there, Cesar, Jimena and Juan.

This work greatly benefitted from the input and time of Cris Giannini, and Blande Viana from the companion committee. More importantly I was lucky to have three supervisors during the PhD. One of which is Lucas Garibaldi who acted as a supervisor during my time in Bariloche, who was also a friend who always treated me like equals, who welcomed me to his house and with whom great time was shared while driving too Yoga Classes. I have a keen interest in number and Lucas was a statistical sensei who prompted my confidence in the knowledge that have acquire, pushing me to be more confident on my work and to appropriate on was being develop. I'm deeply grateful for having the opportunity to go back to the Andes and get loosed in the valleys of the south American backbone, to have met that many great people in such intimate way. This experience greatly contributed to my maturity as a researcher, and it would have not been possible or as amazing as it was if it hadn't been for the institutional aid to undertake this academic endeavor. I was also very lucky that Luísa Carvalheiro accepted to be part of this project, she has an ease to share knowledge, provoke curiosity and improve the way to do science that always amazed me. The kindness with which she always did this was great, I would always look forward to seeing her comments and reviews as it always represented a new learning frontier.

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When things are on track one must be thankful, as thing don't last forever and during difficulties, we forget to appreciate what brought to us to this point. For great things to happen, some basic needs should be covered. The confidence to take on the challenge of making a PhD was not possible without the love of the family, their support was constant and always present despite the mile that separate us. I thanks to my brother her wonderful wife Danielle and my niece Clara Mei, always there with kind words and ready to make fun of me so that I don't take thing to seriously. My grandmother an inspiring woman, with whom I can share my love for the academic world and who always has a saying to continue my search. To my parents to whom the work is dedicated and their joyful spirit to take on live challenges. A deeply hearted thanks to Maria Paula who always has a smile, always there to give love and support on every aspect that my excited mine is willing to explore. Her partnership always felt present and help me to work within healthy hours to enjoy our time together. An extended thanks to Maria's family who more than one was there to create a warm environment for me to work on my thesis.

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Index

General Introduction

Biodiversity conservation is one of the most challenging tasks we face as humans. Probably the difficulty relays in the current western ways of life we lead, marked by the dominance of some individuals over others. What seems to be particular about us humans are the endless curiosity that has led us to pursue a lifestyle that controls the surroundings to generate the best conditions for ourselves and our society. Nonetheless, now more than ever is evident that to maintain our success as species, we need to secure the web of life we are part of. Hence, as a society, we find ourselves at a crossroads, wondering which lifestyle changes we can make to preserve that same biodiversity we rely upon. One of the most disruptive transformations we have made to the globe has been to transform the native vegetation for agricultural production. Today 40% of the terrestrial surface is farmland, with human and livestock biomass overwhelmingly surpassing the weight of wild mammals and birds (Bar-On et al., 2018).

Back in the 60ties, the late biologist Edwards Wilson and mathematician Robert McArthur contributed to synthesizing a theory that profoundly influenced biodiversity conservation and landscape planning. They described how large islands could maintain higher biodiversity communities allowing a more intricated web of interactions (mac Arthur & Wilson, 1967). The island biogeography theory grounded the design of conservation initiatives (Diamond, 1975), which was eventually challenged and led to viewing terrestrial fragments as part of a heterogeneous landscape (Haila, 2002). In the late 80s, another biologist, Monica Turner, helped redirect the attention to the interaction between ecological processes and observed patterns, more specifically towards understanding how the landscape patterns influence the biological process, which is the focus of the landscape ecology discipline (Turner, 1989). This discipline is at the core of the present work as we aim to understand how landscape management can enhance processes related to human well-being and the conservation of the web of life that we are part of.

Landscape ecology has helped guide conservation initiatives, biological invasion management, and ecological restoration, something so desperately needed in this time when zoonotic diseases have a global impact, despite existing regional evidence of landscape patterns influencing health issues (Crouzeilles & Curran, 2016; Didham et al., 2007; Ferreira et al., 2021; Prist et al., 2021; Ribeiro et al., 2019; Ribeiro Prist et al., 2022). This work aims to provide evidence and tools on where and how landscape management can contribute to finding synergies between native vegetation conservation and agricultural production, the most relevant factor threatening biological conservation (Hoang & Kanemoto, 2021).

Technological advances allow the transmission of human-induced or natural transformation almost simultaneously across the globe, such as a volcanic eruption in the middle of the Pacific Ocean (Tonga, January 2022) or detecting the location of large areas of the Amazon being cut down (MapbiomasAlert.org). Detrimental effects of landscape transformation on biodiversity loss have long been documented (Donaldson et al., 2016). The pressing need for pathways that contribute to reverting human-induced impacts on biodiversity demands evidence of more optimist realities, like where regenerating forests have more recovering success (Díaz et al., 2019) or where biodiversity contributes to agricultural production through pollination and pest control. They all share a governance limitation of articulating local-level actions with regional goals to safeguard the biodiversity that remains (Bennett et al., 2015; Isbell et al., 2017). To help guide local efforts that best contribute to achieving regional goals, we have focused on forest conservation contribution to crop yields.

Animal pollination is a vital ecosystem service that generates revenue from agricultural production while guaranteeing the production of many nutrients related to human well-being (Dicks et al., 2021; Potts et al., 2016). Multiple insect species pollinate most pollinator-dependent crops; thus, their fruit set relies on the flower visitors' abundance and diversity (Garibaldi et al., 2013; Garibaldi et al., 2016). Managed bee species like *Apis mellifera* have been used to increase the productivity of such crops. However, this species is only a suitable pollinator for some crop species (Giannini et al., 2014; Rader et al., 2015). Moreover, for most pollinator-dependent crops (Aizen & Harder, 2009), there is a need to maintain a higher diversity of flower visitors to increase temporal and spatial stability in flower visitation rate (Dainese et al., 2019; Klein et al., 2009). Conserving animal pollinators is thus crucial to account for the increasing animal pollination demands (Aizen et al., 2019). For instance, in Brazil, pollinators are estimated to contribute economically with around 30% of the annual agricultural income (Giannini et al., 2015, 2017), but this assumes that highly simplified landscapes still provide animal pollination.

A potential pollination service crisis can reduce agricultural production in Brazil by 16-51 million tons resulting in a loss of agricultural contribution to the Brazilian Gross Domestic Product (GDP) by 6% to 19% (Novais et al., 2016). Despite that, and neglecting suggestions made by previous studies (Carvalheiro et al., 2012; Garibaldi et al., 2014; Thomas & Kevan, 2012), the management of both bees and pollination services has not been a major target incorporated in conservation policies nor on crop management plans (but see http://www.operationpollinator.com/ from Syngenta). Probably because of the limited communication between academics and practitioners. However, it could also be attributed to a mismatch between the scale at which we understand biodiversity contribution to crop yields and the scale at which conservation initiatives are implemented (Isbell et al., 2017). Therefore, we aimed to relate landscape metrics known to affect biodiversity and service provision at a local scale with regional agricultural productivity to provide a spatial assessment of where pollination service could be boosted by landscape management (Breeze et al., 2016; Lautenbach et al., 2012).

There is a need to manage the land towards win-win scenarios by promoting both ecosystem service provision and biodiversity conservation (Senapathi et al., 2015). Achieving higher yields by enhancing biodiversity-based ecosystem services is at the core of the Sustainable Development Goals and nature-based solutions (Bommarco et al., 2013; DeClerck et al., 2016;

Escobedo et al., 2019; Garbach et al., 2016; Keesstra et al., 2018). Landscape management is among the most critical components of achieving ecological intensification (Bommarco et al., 2013) and can help maintain a high diversity of pollinators that could subsequently enhance productivity (Garibaldi et al., 2011; Mitchell et al., 2015; Ricketts et al., 2008). For instance, landscapes with less than 20 to 30% of natural vegetation have reduced community integrity (Banks-Leite et al., 2014). What remains to be tested is whether this biodiversity loss affects regional agricultural yields.

This work aims to generate knowledge that articulates local management practices and landscape composition and configuration at a larger scale to achieve pollination service provision and biodiversity conservation (e.g., the desired win-win situation) (Ekroos et al., 2016; Geertsema et al., 2016). We also aim to improve our ability to predict changes in **ecosystem service provision** by studying cropland productivity, which can help promote the development of incentives and policies that benefit forest conservation and pollination service management. We will evaluate synergies between forest conservation and agricultural productivity in one of the most diverse and threatened biomes in the world, the Brazilian Atlantic Forest. More specifically, we propose to answer three main questions:

(i) What is the relative importance of forest conservation compared to climatic conditions and management practices in predicting coffee productivity across the Atlantic Forest?

(ii) What is the relevance of mature forest conservation, and where are the best areas where forest regeneration can contribute to coffee productivity?

(iii) How does forest conservation contribute to temporal crop yield stability?

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Chapter 1

Positive forest cover effects on coffee yields are consistent across regions

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Abstract

1. Enhancing biodiversity-based ecosystem services can generate win-win opportunities for conservation and agricultural production. Pollination and pest control are two essential agricultural services provided by mobile organisms, many depending on native vegetation networks beyond the farm scale. Many studies have evaluated the effects of landscape changes on such services at small scales. However, several landscape management policies (e.g., selection of conservation sites) and associated funding allocation occur at much larger spatial scales (e.g., state or regional level). Therefore, it is essential to understand whether the links between landscape, ecosystem services, and crop yields are robust across broad and heterogeneous regional conditions.

2. Here, we used data from 610 Brazilian municipalities within the Atlantic Forest region (~50 Mha) and show that forest is a crucial factor affecting coffee yields, regardless of regional variations in soil, climate, and management practices. We found forest cover surrounding coffee fields was better at predicting coffee yields than forest cover at the municipality level. Moreover, the positive effect of forest cover on coffee yields was stronger for *Coffea canephora*, the species with higher pollinator dependence, than for *C. arabica*. Overall, coffee yields were highest when coffee fields were near to forest fragments, mostly in landscapes with intermediate to high forest cover (> 20%), above the biodiversity extinction threshold.

3. Coffee cover was the most relevant management practice associated with coffee yield prediction. An increase in crop area was associated with a higher yield, but mostly in high forest covers municipalities. Other localized management practices like irrigation, pesticide use, organic manure, and honey-bee density had little importance in predicting coffee yields than landscape structure parameters. Neither the climatic or topographic variables were as relevant as forest cover at predicting coffee yields.

4. *Synthesis and application.* Our work provides evidence that landscape relationships with ecosystem service provision are consistent across regions with different agricultural practices and environmental conditions. These results provide a way in which landscape management can articulate small landscape management with regional conservation goals. Policies directed towards increasing landscape interspersion of coffee fields with forest remnants favor spillover process and can thus benefit the provision of biodiversity-based ecosystem services, increasing agricultural productivity. Such interventions can generate win-win situations favoring biodiversity conservation and increased crop yields across large regions.

Keywords: Pollination service, landscape configuration, ecosystem service supply and demand, coffee production, pest control, forest cover, multi-scale analysis, Stingless bees.

Introduction

The increase in agricultural production, mainly through conventional intensification and continuous transformation of native vegetation into cropland while relying on the use of external inputs (fertilizers, pesticides, irrigation, and tillage), continues to be the current major threat to biodiversity (Tilman et al. 2011; Hunter et al. 2017; Ramankutty et al. 2018; Curtis et al. 2018). The imbalance between achieving higher productivity and conserving biodiversity could be solved by enhancing local biodiversity contributions in agricultural landscapes (L. A. Garibaldi et al., 2019). In this sense, robust evidence shows that wild mobile organisms, which directly support crop production through pollination and pest control, depend on the extent of the native vegetation and its proximity to productive areas (Dainese et al. 2019). Unfortunately, along with biodiversity decline, evidence indicates that services are also being eroded globally (Brauman et al. 2020). Thus, it is crucial to align local and regional targets that contribute to increased crop yield through ecosystem services provision and biodiversity conservation (Senapathi et al. 2015; Isbell et al. 2017).

The capacity of a given patch of natural habitat to supply mobile organisms that provided services depends on the overall habitat amount at larger landscape scales (Batáry et al. 2011; Fahrig 2013). Hence enhancing biodiversity in specific cropland depends on the remaining natural vegetation in the landscape that should be above the extinction threshold (Banks-Leite et al. 2014; Boesing et al. 2018a). Simultaneously, the agricultural landscapes' heterogeneity will affect biodiversity and consequently service provision (Sirami et al. 2019; Dainese et al. 2019). For instance, increasing the amount of a specific crop cover will determine the ecosystem service demand while affecting organism mobility's permeability (Holzschuh et al. 2016; Rusch et al. 2016). Therefore, landscape features directly affect ecosystem service supply and demand and the flow between those areas (Mitchell et al. 2015b; Metzger et al. 2020).

Improving our understanding on the effects of land-use changes on ecosystem service and crop yield, especially across larger spatial regions, it is essential to better inform policy and conservation practitioners (Isbell et al. 2017). For instance, researchers advocate for establishing ambitious goals, proposing to restore or conserve landscape or even the entire globe with more than 40% of natural habitat (Watson and Venter 2017; Arroyo-Rodríguez et al. 2020a). Nonetheless, Earth's biome has already been heavily transformed, and environmental policies commonly require no more than 5% of the agricultural landscape to be preserved for most countries, despite the evidence that a regional increase of native vegetation up to 30% could reduce biodiversity extinction risk by 50% (L. A. Garibaldi et al., 2020; Hannah et al., 2020). Such policies are primarily established for conservation proposes only, which might constrain farmers' acceptance. In Brazil, for example, there have been considerable efforts to soften those laws, further threatening biodiversity (Metzger et al. 2019). Hence, there is a need to frame such conservation policies together with societies' benefits drawn from them to engage synergies (Fischer et al. 2017).

Evidence showing that the positive landscape effects on biodiversity and ecosystem service cascade down to crop yields have recently started to emerge (Dainese et al. 2019). Nonetheless, most come from studies executed at small scales, generally smaller than two kilometers radius circular landscapes (Chaplin-Kramer et al. 2011; Motzke et al. 2016). The few studies that evaluate pest control and pollination at larger regional scales estimate the proportion of regional production that can be attributed to these regulating services, by assuming that mobile organism are either fully present or absent in crop fields across large regions (Losey and Vaughn 2006; Naranjo et al. 2015; Breeze et al. 2016). Hence, there is an urge to assess whether we can predict regional or national yields using the habitat amount around crop fields'. Moreover, such assessment across large regions would allow understanding whether landscape context can replace, complement, or interact with localized agricultural management practices to predict regional yields, as ecosystem effects on yield depend on management practices (Gagic et al. 2017; Liere et al. 2017).

Brazilian coffee production more than doubled between 1996 and 2010 through conventional intensification, with only a 12% increase in coffee area (Jha et al. 2014), which indicates that land productivity per unit area increased. Yet, since coffee production benefits from pest control and pollination services (Chain-Guadarrama et al. 2019), it is likely that land productivity is below its potential. Brazil is the primary producer of the two most traded coffee species, *Coffea arabica* and *C. canephora*. Consequently, the reduction or suppression of native vegetation should result in lower crop yield (Karp et al. 2013), especially for the high pollinator-dependent coffee species (*C. canephora*) when compared to *C. arabica*, which modesty benefits from pollination services (Klein et al. 2003). Here we use land cover maps to test if 20% of the world coffee production associates with forest cover around the coffee fields. We intend to assess the potential of using landscape spatial management in agriculture by testing whether the landscape context surrounding coffee fields is more relevant than management practices across large variety of environmental conditions.

Using open data sources (from government and ONGs) from Brazil we can assess which scale does forest cover most contributes to increasing municipality productivity across the whole Atlantic Forest Biome (Objective 1). We incorporated biological information of coffee species dependency on pollination to evaluate if forest contribution varies accordingly to pollinators demand (Objective 2). Moreover, by comparing management practices, climatic and topographic information, we were able to test the relevancy of landscape structure parameters at predicting coffee yields (Objective 3). We expect that small scale forest cover (at the surrounding coffee fields), which are known to affect biodiversity-based ecosystem services like pest control and pollination, are best at predicting coffee yield than the amount of forest cover in the municipality. We expect that municipalities with higher pollination dependency would be more affected by forest cover changes, as natives' bees (the main coffee pollinator) are known to respond to forest cover changes. Finally, we expect that landscape parameters (forest and coffee cover) are equally relevant to climatic variables and management practices crucial for achieving high productivity, as the spatial relationship between areas that supply, and demand service determines biodiversity contribution to productivity.

Materials and Methods

Study area and focal crop species

Coffee production is distributed widely across the tropics, and within Brazil, it ranges from subtropics nearly to the Equator, presenting broad environmental plasticity. Nonetheless, each of the two coffee species produced occupies a different niche. Arabica coffee (*C. arabica*) is mainly produced in the southeast Brazilian region, where mean annual temperatures range from 18 to 23°C. In contrast, Robusta coffee (*C. canephora*) is mainly cultivated in the lowlands of the states of Espírito Santo and Rondônia, where the annual mean temperature is higher than in the southeastern of Brazil (22 to 26 °C, (Bunn, Läderach, Ovalle Rivera, & Kirschke, 2015).

For this study, we gathered information from 1.3 Mha destined for coffee production from the 610 municipalities that planted more than 50 ha of coffee each year between 2006 and 2012 (Fig. 1). In the Atlantic biome the production is concentrated in 5 states, Bahia (n=37), Espírito Santo (n=64), Minas Gerais (n=264), Paraná (n=146) and Sao Paulo state (n=99). Using data from the Brazilian Institute of Geography and Statistics (IBGE, http://www.ibge.gov.br/), we calculated coffee yield (productivity) for each year per municipality by dividing the total production (tons) by the total coffee area (ha) planted per municipality per year. Mean coffee yields were calculated from three consecutive years for each municipality. The years considered for each municipality depended on data availability of the coffee fields' maps, which was different for each state (see Table S1 *in Supporting Information*). The three-year window selected for yield data corresponded to the year that coffee fields were mapped plus the year before and after. Little spatial variation within the three-year window is expected, as coffee is a perennial crop that might be thinned every 7-8 year. We transformed the yield (kg/ha) values to the number of coffee bags (of 60 kg) per hectare, a frequently used unit among coffee farmers and trade agencies.

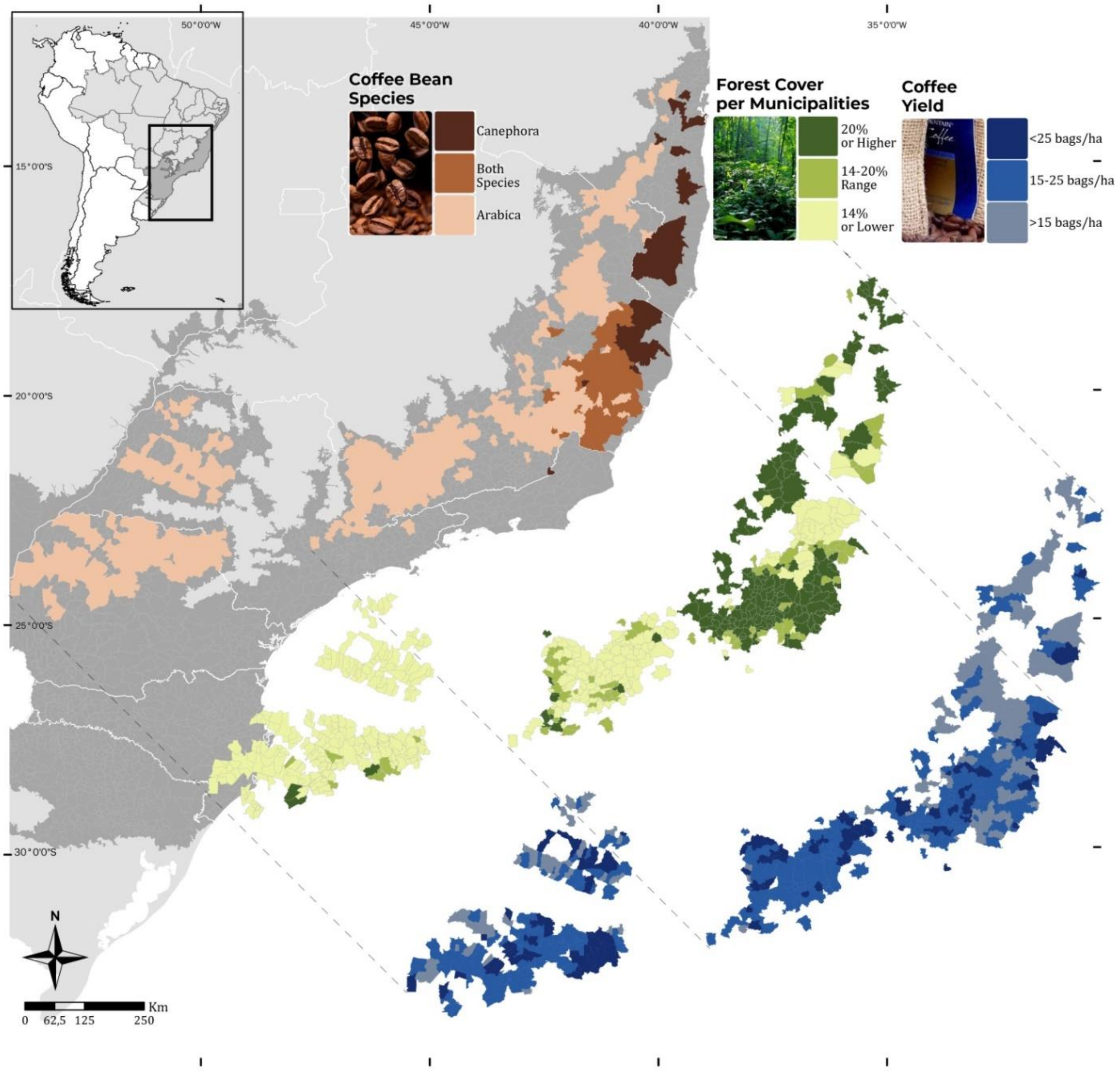

Figure 1: Study region within the Atlantic forest, the different shades of brown indicate the species planted in the municipality. Average forest cover surrounding coffee fields within 2 km radius per municipality are in green and subdivided into three categories: 1) In dark green municipalities with more than 20% surrounding coffee fields within 2km radius (green), 2) in green municipalities with forest cover between 14%, and 20% and 3) in light green municipalities with less than 14%. Those forest cover categories are associated to restoration success probability (Crouzeilles & Curran, 2016). The color blue indicates the productivity levels of each municipality, also subdivided into three levels.

Pollination service demand

To evaluate if the effect of forest cover on coffee yields varies with the animal pollination demand, we calculated the pollinator dependence per municipality according to the proportion of the area planted with each coffee species (the pollinator dependency). Using the IBGE data set, we calculated the pollinator dependency (PD) of the coffee produced in each municipality using the following equation:

$$PD = \left(\frac{Area_{arabica}}{Area_{coffee}} * 0.3\right) + \left(\frac{Area_{canephora}}{Area_{coffee}} * 1\right)$$

$Area_{arabica}$ corresponds to the municipality area planted with *C. arabica*, $Area_{canephora}$, the area planted with *C. canephora,* and $Area_{coffee}$, the total area planted with coffee in the municipality. The coefficients 0.3 and 1 correspond to the level of pollinators' contributions associated with each crop species. *C. canephora* dependence ratio is equal to 1, while the modest pollinator-dependent *C. arabica* has a ratio equal to 0.3 (Klein et al. 2003). The municipality *pollinator demand* varies between 0.3 and 1.0 according to the area destined to each coffee species; a municipality with half of the planted area of each coffee species had values equal to 0.65. The majority of the municipalities (91 %) planted one species only (44 municipalities with *C. canephora* and 509 with *C. arabica*).

Landscape structure parameters

To determine forest cover surrounding coffee plantations, we used coffee maps from the National Company of supply (CONAB, http://www.conab.gov.br/), which compiled maps from the five leading coffee producing states within the Atlantic forest. Additionally, we used annual forest remnants maps from MapBiomas (Project of annual mapping of land-use and land-cover of Brazil, http://mapbiomas.org/), both with a resolution of 30x30 m. The year of forest cover maps was selected according to the coffee field maps, matching the coffee yield data years. For each coffee pixel (30 x 30 m), we calculated forest and coffee cover in circular areas at different scales (2 km, 1 km, and 500 m radius), as the scales of effects have been shown to vary according to the mobile organism functional characteristics (Greenleaf et al. 2007; Chaplin-Kramer et al. 2011). We calculated the mean values of forest and coffee cover surrounding coffee fields per municipality for each scale.

Moreover, we calculated the amount of forest and coffee cover at the municipality level to compare with the means obtained with the circular buffers (around focal coffee pixels). Forest cover (at all scales) was calculated for each of the three consecutive years, and mean values were calculated accordingly to the year of coffee maps. We obtained the mean distance of coffee fields to the nearest forest fragment, by measuring the minimum distance pixel of coffee and forest and then obtaining the coffee fields' mean distance per municipality. We calculated the number and density of forest fragments and forest edge density per municipality, with the forest remnant maps. Similarly, we measured coffee cover (at different scales) and the number and density of coffee patches in the municipality.

Environmental and farm management factors

Temperature, humidity, and soil condition are known to affect coffee yields (DaMatta 2004). Moreover, management practices and socioeconomic characteristics also influence yield outcomes (Hipólito et al. 2016). Therefore to assess the relative impact that forest cover can have on coffee yield, we gathered 19 bioclimatic variables (source: www.chelsa-climate.org) from the same year of coffee production considered in the analyses, 12 soil properties variables (physical and chemical) based on 2017 model (www.soilgrids.org), and 9 farm management variables. Environmental variables were extracted using the coffee fields' shapefiles, and we calculated mean values for each municipality. The management factors resulted from mean values between the data available from the closest annual data obtainable from national survey carried twice by IBGE (2006 and 2017) which contains municipalities' data (see *Appendix S1*).

Statistical Analysis

First, we tested whether the spatial structure contributed significantly to the variation in coffee yield (log-transformed) by incorporating the centroid's coordinate of every municipality in the models. We used linear mixed models (LMM) to compare the full model with and without the residual spatial correlation structure, linear and different equations function were considered as suggested in the statistic literature (Crawley 2007; Zuur et al. 2009) (Fig. S6 & Table S5). The exponential spatial correlation was considered in all the following model comparisons. Two model comparisons were made, one to select the scale for forest and coffee cover that best explained coffee yields (table S2), and a second comparison to select the bests fixed structure among the landscape, management and climatic variables. We included municipalities' mesoregions nested within the state as a random structure in all models, allowing the intercept to vary according to the geopolitical mesoregions within the state that each municipality belongs to. This nested structure is essential because there is an inherent variation in the socioeconomic and agronomic practices that affect coffee productivity across the main producing regions within each state of Brazil (Bliska *et al.,* 2009).

We selected which landscape variable of forest and coffee cover at 500 m, 2 km radius, or at the municipality level best predicted coffee yields by creating 15 models, in which only additive effects were considered between coffee and forest at each scale (Table S2). Forest and coffee covers were not correlated, but forest cover at different scales were correlated (as well as coffee covers), reason why we avoid including the same variable at different scales in the same model. We compared all combinations using a multi-model inference approach based on information theory using Akaike Criterion Information (AIC) (Burnham and Anderson 2002). Forest cover at smaller scales were consistently better, so we maintained the 2 km scale for the rest of the analysis (Table S2), as local scales are known to affect biodiversity and ecosystem services. We considered the 2 km scale for coffee and forest to create the full models to test our hypothesis.

To test whether 1) forest cover predicts coffee productivity (yield) better than management practices or climatic variables, and 2) whether forest contribution to coffee productivity varies accordingly to the pollination dependency of the crops, we created a full model with 16 fixed-effect variables, considering only two-way interactions between either forest or pollinator dependency (PD) and each one of the other fixed-effect variables (table 1 & Fig. 1c). The 16 fixed-effect variables considered in the full model are a subset of all 60 variables gathered, selected after checking for correlation to avoid multicollinearity, by excluding variables with Pearson correlation coefficient higher than 0.4 (Fig S1, see Appendix S1 for more information on the data gathered).

Table 1: The predictive variables included in the full model, with a short description, average, and range values. The data came from different sources, we calculated the variables using data from: $^{+1}$ MapBiomas and; $^{+2}$ CONAB; $^{+3}$ variables came from IBGE database, and $^{+4}$ and $^{+5}$ from Worldclim and soil Grid respectively.

Factor	Variable	Description	Average	Range
Landscape	Forest Cover*	Mean value of the forest cover at 2 km surrounding each coffee pixel (%) $^{+1}$	16	0.6 – 81
	Forest Patch Density	Density of forest patches divided by the total area of the municipality (n° patches/hectares x10^{6}) $^{+1}$	2.2	0.25 – 4.9
	Coffee Cover	Mean value of coffee cover at 2 km surrounding each coffee pixel (%) per municipality $^{+2}$	9	0.02 – 49.3
	Land Use diversity	Shannon index of agricultural land uses considering the area of each crop $^{+3}$	1.1	0.08 – 2.2
	Mean coffee field size	Coffee area divided by the number of coffee farms (ha) +3	16	0.7 – 268
Ecosystem service	Pollinator dependency	Proportionality of each coffee species planted per municipality, based upon the dependency on pollinator of each coffee species	0.65	0.3 - 1
Infrastructure	GDP	Gross domestic product (R$x1000000) $^{+3}$	355	14.8 – 36,688
	Honey production	Total honey production in kilograms $^{+3}$	3,832	0 – 108,193
Management	Family agriculture	Family coffee farms (%) of the total of coffee farms $^{+3}$	74	0 – 100
	Irrigation	coffee farms that use irrigation (%) of the total of coffee farms $^{+3}$	6.6	0 – 100
	Organic fertilizer	Coffee farms that use organic manure (%) of the total of coffee farms $^{+3}$	8.3	0 – 66.7
	Use of Agrotoxic	Coffee farms that use agro toxics (%) of the total of coffee farms $^{+3}$	36	0 – 100
Climatic	Precipitation	Mean annual precipitation (mm) $^{+4}$	1339	748 – 1823
	Precipitation of the driest month	Precipitation of the driest month (mm) $^{+4}$	34	6.3 – 117
	Wind	Wind speed (m/s) $^{+4}$	1.9	1 – 2.6
Soil	Coarse fraction	Soil volumetric coarse fraction (%) $^{+5}$	1.1	0 – 10.4

We compared all possible combinations derived from the full model, including a model without fixed effects (null model), using a multi-model inference approach based on information theory using Akaike Criterion Information (AIC) (Burnham and Anderson 2002). For defining the scale, we also used LMM with Gaussian error distribution to predict the variability of coffee yield (60 bags per hectare) (log-transformed). The best models (all with ΔAIC <2) were selected from comparing all the possible combinations of the full model (Fig. 2c) using the "dredge" function of the MuMIn package in R (Barton 2015). For the best-fitting models (i.e., lowest AIC), we tested the Gaussian and homoscedasticity assumptions for the standardized residuals. To calculate each variable's importance at predicting coffee productivity, we used the sum model weights of all models, including each explanatory variable (Barton 2015). For example, variables presented in all best models have relative importance close to 100%. We assess the strength of effect among the best fitting model's selected variables by comparing the standardized estimate.

Results

On average, the Atlantic Forest biome produced 28.5 million coffee bags (60 kg bags) per year in 1.3 Mha, representing 81% of all coffee produced in Brazil (Fig. 1, Fig. S5). For one-third of the coffee municipalities, coffee plantations represented more than 10% of the land, with coffee cover extending up to 21,600 hectares in total. On average, forest cover surrounding coffee fields (within 2 km circular landscapes) ranged from 0.6% to 81% (Table 1). The average forest cover for municipalities that produce either *C. arabica* or *C. canephora* was 14% and 30%, respectively. Nonetheless, most of the coffee fields of the species that rely entirely on pollinators (C. canephora) have less than 20% of the forest in their surroundings. Most coffee production occurs in family farms (74% of the municipalities' farms), with the mean coffee fields size close to 16 hectares.

The best-fitting models explained 81% of the variation in coffee yields, with forest effects at smaller scales (average cover at 2 km or 500 m radius around the coffee fields) predicting better than total cover at the municipality level (Table S2). Forest cover at smaller scales (from here forth forest cover) was the most important variables predicting coffee yields, with an overall positive effect (Fig. 2). Moreover, forest cover effects were higher in the municipalities that planted more *C. canephora,* which is fully dependent on pollinators, but for *C. arabica*, yields tend to stabilize above ~16% of forest cover (Fig. 3). Increasing coffee cover had a positive effect on yields, but only for *C. canephora* and when forest cover was intermediate or high (>20%) (Fig. 4). None of the management practices or the climatic variables were among the best fitting models (Fig. 2 & S4).

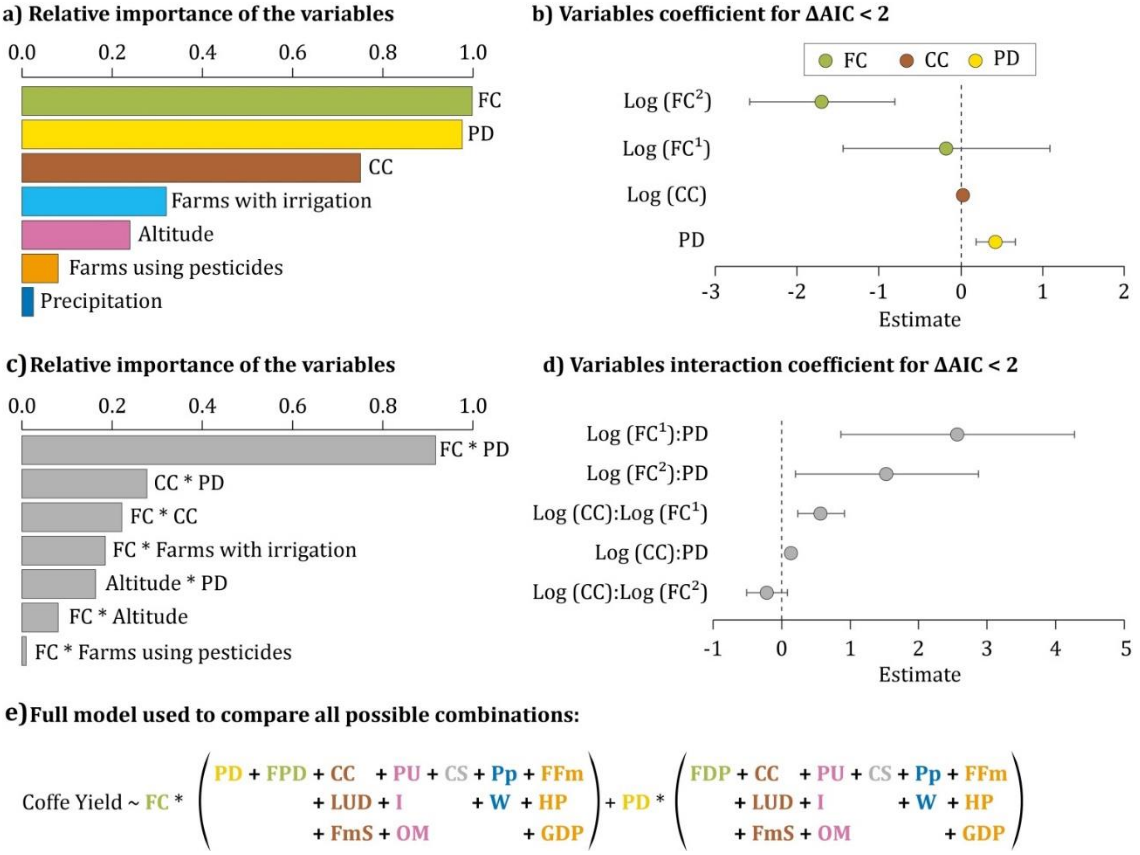

Figure 2: a) Relative importance of the single variables based upon the AIC weight considering all the possible fixed-effects combinations resulting from the full model to predict coffee yield per municipality. b) Variables coefficient estimated and their standard error from all the models with ΔAIC lower than 2. c) Relative importance of the interactions between the variables considered. d) The coefficient estimated for each of the two way interaction of the models with ΔAIC lower than 2. e) The full model for which we tested all possible combinations. The variables are listed in table 1, and are abbreviated as follows: FC = forest cover at 2 km scale; PD = pollinator dependency; CC = coffee cover at 2 km scale; LUD = land-use diversity; FmS = mean farm size; PU = pesticide use; I = irrigation; OM = organic manure; CS = Soil Coarse Fraction(%); Pp = mean annual precipitation; W = mean wind speed; FFm = family farms; HP = honey production; GDP = gross domestic product. See supplementary material (Table S4) for the first 20 models rank according to AIC, only the first four models presented ΔAIC lower than 2.

The landscapes that benefited most from the presence of forest cover were those with a more interspersed configuration between forest fragments and coffee fields (Fig. S1a & S1b). The forest and coffee cover increments in the municipalities are related to higher fragmentation and closer proximity between forest patches and coffee fields, as forest fragmentation was highest at intermediate forest cover (20 to 40%; Fig. S2). The coffee field's spatial arrangement was more fragmented as coffee cover increased (up to 50%) (Fig. S3). In such landscapes dominated by coffee fields and forest, where coffee productivity was higher, coffee was closer than 200 m from any forest fragment (Fig. S3).

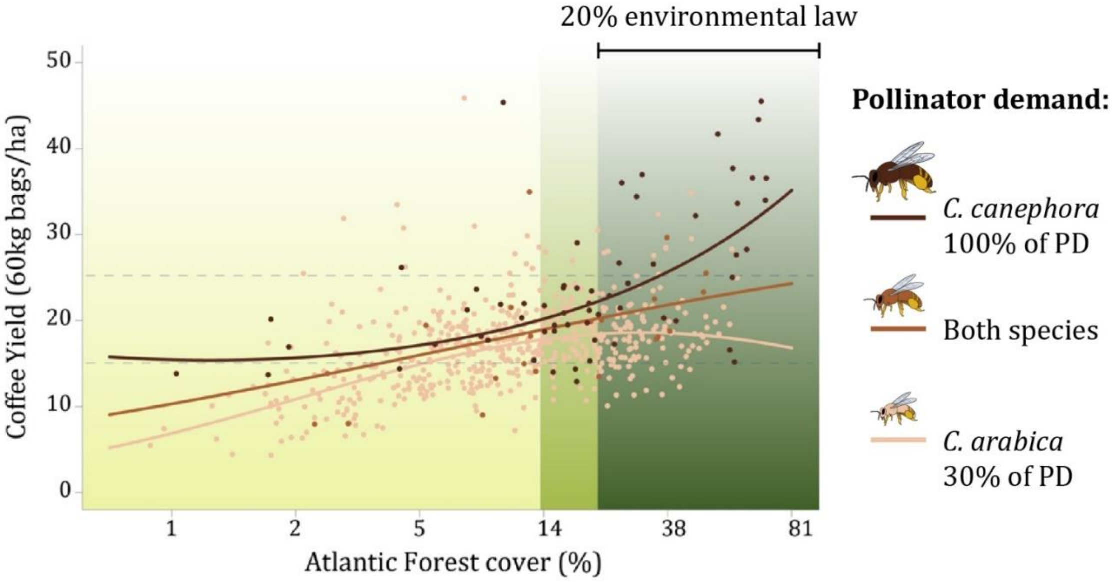

Figure 3: Relation between coffee yields (bags/ha) and forest cover (2 km radius) across the Brazilian Atlantic Forest. Light brown dots represent municipalities that produce *C. arabica* (30% of pollinator demand), and dark brown dots correspond to municipalities that produce *C. canephora* (100% of pollinator demand), brown dots represent municipalities that produce both coffee species. The symbol of the bees' size represents the percentage of bee contribution to coffee productivity for each species. The continuous lines represent the predicted relationship according to the selected model. Dark green shade represents the 20% threshold that environmental law in Brazil requires farmers to preserve with their farm, lighter green shade is associated to the categories from figure 1.

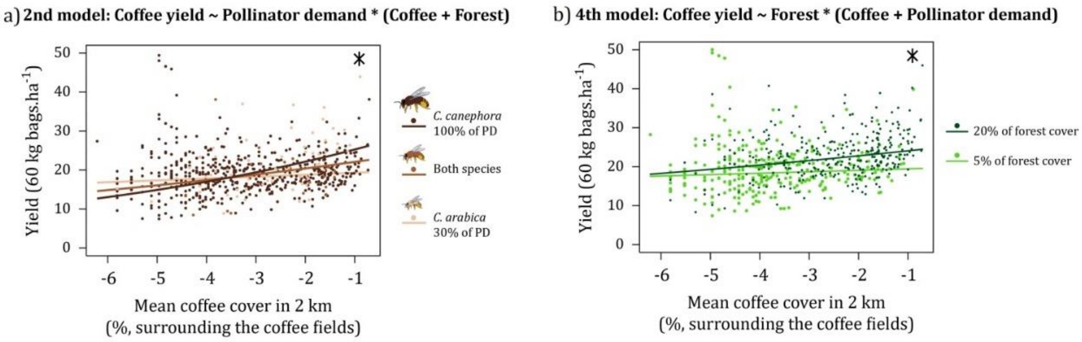

Figure 4: The relation between coffee cover, and coffee yields depending on: a) the pollinator dependency of the coffee planted in the municipality (brown = *fully dependent*, red= *intermediate* and yellow = *modest* benefited); and b) depending on the amount of forest cover in the landscape (low forest cover = light green - 5% and intermediate forest cover = dark green - 20%), model predicted was plotted considering the effect on the fully dependent coffee species. Each graph is the result of the model selected in which coffee effect interacts with another variable (see Table S4).

Discussion

Conservation and agriculture policy decisions occur at large scales (i.e., municipality or state levels) where governments are interested in stimulating and implementing practices that enhance the gross internal product while complying with environmental legislation (Metzger et al. 2019). Until now, it was unclear whether the benefits previously detected at smaller landscape scales would also be evident at larger scales since regional differences in climate, soil type, or even agricultural practices could alter the relationship obtained at the landscape scale. Here we detected that the amount of forest in the surrounding coffee fields was a major predictor of coffee productivity throughout the whole Atlantic Forest region, representing 20% of the world's coffee production. Forest cover was a more relevant predictor than management practices (i.e., agrochemicals, irrigation) and environmental conditions (i.e., rain, altitude), which affect coffee production. Our results suggest that the benefits crop production draws from natural vegetation are mediated by changes in ecosystem service provision (Martin et al. 2019; Sirami et al. 2019) and thus indirectly by biodiversity, as yields are higher in landscapes known to enhance functional and taxonomic biodiversity (Boesing et al. 2018a). Especially, pollination service seems to be an essential ecosystem service enhancing productivity.

Increments in forest cover had more substantial productivity effects on the coffee species with the highest pollinator dependency (*C. canephora*).

Ecosystem services contribute to regional coffee yields

Each coffee species' different responses to the amount of forest cover were under our expectations related to different levels of pollinator dependence (Klein et al., 2003). Forest cover contributes to higher coffee fruit set by enhancing bee visitations (Saturni et al. 2016; Hipólito et al. 2018; González-Chaves et al. 2020), and we have found that municipalities with coffee fields surrounded by 20% of forest or more were more productive, especially for the coffee species which entirely rely on animal pollination. Together our findings reinforce that loss of biodiversity results in lower coffee yields, as landscapes with less than 20% of forest cover tend to present an abrupt loss of species richness in coffee landscapes (Banks-Leite et al. 2014; Boesing et al. 2018a). Although we did not assess direct evidence of pollination services, literature shows that pollination dependency is a crucial feature to predict pollen limitation related to yield stability at a national level across the world (Deguines et al., 2014; L. a Garibaldi, Aizen, Klein, Cunningham, & Harder, 2011).

Alternatively, the effect of pollination dependency in our model could be due to differences in each species' productivity not necessarily associated with pollination service. For instance, *C. canephora* is more resistant to disease, higher temperatures, and water scarcity than *C. arabica* (DaMatta 2004). Although we found that each coffee species responded differently to other variables (coffee cover, irrigation, altitude, and pesticide use, *see* Fig. S4), none of the variables were more robust than forest cover. Hence, our results further reinforce that the difference between coffee species is not related to pest resistance or climatic variables but instead due to pollination service. Nonetheless, our results do not rule out that forest cover contributes to coffee production through other biodiversity mediated ecosystem services. As local landscapes with more than 20% of forest cover are known to favor spillover of birds, bats, and invertebrates that contribute with reducing pest incidence (e.g., coffee berry borer and leaf miners) and positively affecting coffee yields (Librán-Embid et al. 2017; Boesing et al. 2018a; Aristizábal and Metzger 2019). Moreover, forests are known to contribute to water availability, probably reducing landscape temperature and enhancing evapotranspiration and moisture, therefore, the need for irrigation (Ellison et al. 2017; Mendes and Prevedello 2020).

Landscape features that favor pollinators and pest enemy's spillover towards crop fields

Landscape simplification negatively affects biodiversity and ecosystem service provision (Sirami et al. 2019; Dainese et al. 2019). On the other hand, landscapes with more interspersed configuration between coffee fields and forest fragments were proven, at a smaller scales, to have higher bee diversity and crop pest control, which contribute to coffee yields (Saturni et al. 2016; Librán-Embid et al. 2017; Hipólito et al. 2018; Medeiros et al. 2019; Aristizábal and Metzger 2019). Our work shows that such relationships can be upscale to the municipality level and across large regions, as it seems that the amount of forest in the municipality reflects the amount of forest surrounding the coffee fields. Moreover, we found that in the Atlantic forest, coffee plantations are located on average at less than 200 m from a forest patch in landscapes with more than 20% of forest, distance above which pollination is highly restricted (González-Chaves et al. 2020). Furthermore, distances greater than 1 km are reported to reduce biodiversity by half (Ricketts et al. 2008). Together, all this evidence reinforces that coffee landscape arrangement in relationship to forest patches can enhance biodiversity-based ecosystem services and that the negative effects of landscape simplification occurs across large regional areas (Martin et al. 2019; Sirami et al. 2019; Dainese et al. 2019).

Implications for local and regional policies

Increasing tropical forest cover is a goal for the 2020-2030 decade, but it might still be unappealing for farmers (Burton et al. 2008; Brancalion et al. 2019). Here we present strong evidence that managing cropland configuration within landscapes with intermediate habitat can enhance farmers' revenue and national income, specifically for coffee fields located nearby forest remnants. By doing a cross-regional study, we were able to compare the effects of landscape variables, agricultural practices, and environmental variables like soil, climatic factors to directly estimate the relative importance of landscape parameters on crop yields, which generally is done through controlled experiments (Liere et al. 2017) or by inferring effects on yields (Letourneau and Bothwell 2008; Chaplin-Kramer et al. 2011). Hence, we suggest tying together restoration/conservation goals with regional agricultural productivity by integrating governmental yield and management data with forest remnants' spatial information at different scales (from farm to municipalities), following recommendations that landscape should be managed at multiple spatial scales (Ekroos et al. 2016). After all, we reinforce the positive economic revenue for farmers that would result from landscape restoration initiatives (Morandin et al. 2016), which depend on incorporating natives plants (Carvalheiro et al. 2012; Albrecht et al. 2020). Municipality forest cover and coffee cover in the surrounding coffee field should guide restoration efforts within the Atlantic Forest by providing landscape strategies for coffee producers, which can potentiate their productivity by enhancing biodiversity-based ecosystem services.

Our results suggest that maintaining at least 20% of forest cover at the municipality level, preferentially with an interspersed configuration of forest fragments with coffee fields, could increase national income associated with coffee production. Currently, less than a third of municipalities (n=170) are above the 20% threshold. Hence, our model predicts that restoration of up to 20%, targeted at maintaining proximity between forest fragments and coffee fields, would result in an annual increase of 50 thousand tons of coffee (842 thousand bags), which could be equivalent to 84 million dollars. Nonetheless, it is noteworthy that 39% of the coffee produced in the Atlantic Forest is undoubtedly benefiting from ecosystem service, as the few municipalities with forest cover above the 20% threshold concentrate the majority of the coffee production (Fig. S5a). Moreover, municipalities that produce *C. canephora* have a higher potential to benefit from forest restoration, as the majority (79%) of the fields from this highly pollinator dependent coffee species has low forest cover in their surroundings (Fig.1 & S5).

Currently, Brazilian environmental law requires medium and large farms to set-aside 20% of their farms for conservation as native vegetation and restores the land if the necessary area was deforested in the past. Alternatively, the equivalent area can be compensated elsewhere (e.g. buying from landowners with forest surplus). Consequently, those farmers who chose to compensate elsewhere are least prone to benefit from ecosystem service. The same might occur with small farmers without forest, who are not required to set aside land for conservation, at least when they do not have riparian buffer zones or mountain tops. These law features do not embrace coffee farmers to benefit from conservation and ecosystem service, hence missing the opportunity to achieve higher productivity, especially for small farmers for whom pollination has the most significant impact (Brancalion et al., 2019; L. A. Garibaldi et al., 2016; Metzger et al., 2019).

Final remarks

We present evidence that it is possible to coordinate local landscape efforts with regional planning, for instance, by identifying municipalities in which restoration efforts could enhance productivity. Therefore, cross-scale management of the restored areas and coffee fields' spatial arrangement can favor local landowners to comply with the law while benefitting through increments in crop productivity. Furthermore, we present evidence that by monitoring forest cover over large regions, we can also predict ecosystem service provision, as local landscape effects of native vegetation on service provision are consistent across larger regions, regardless of environmental and social variations. Therefore, managing landscape for conservation purposes across biomes can be coordinated with agricultural goals, facilitating the generation of win-win scenarios for economic development and species conservation.

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Conflict of Interest

All authors contributed writing the manuscript, approved the version to be published and declare the absence of any conflicts of interest.

Authors’ contributions

AGCh, LGC, LAG, and JPM conceived the project and wrote the manuscript. AGCh and JPM obtained funding. AGCh collected the data. AGCh and LAG analysed the data. AGCh wrote the first manuscript.

Data Availability Statement

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.612jm644g (González-Chaves et al., 2021)

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Supplementary Information

Methods

To define the final subset of 16 variables, we classified the 60 variables gathered in four dimensions or classes (landscape, soil, climatic, and management). Within each dimension, we analyzed correlation matrices to check for redundant variables (Fig. S1). To further ensure that other dimensions did not confound landscape dimension variables, we ran a non-metric multidimensional scaling analysis to look for associations between the landscape variables and the different variables selected from the environmental and management variables.

Environmental factors

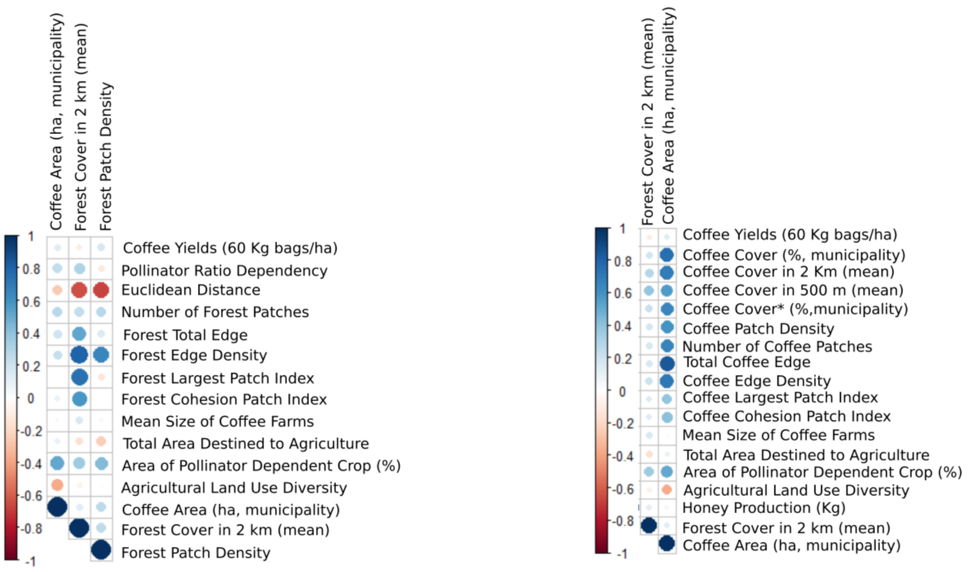
Temperature, humidity, and soil condition are known to affect coffee yields (DaMatta, 2004), therefore to assess the relative impact that forest cover can have on coffee yield, we gathered

19 bioclimatic variables from the Worldclim 30 seconds resolution database (www.worldclim.org). We calculated the mean values per municipality by extracting the climatic values from the coffee field maps. The bioclimatic variables include annual mean temperature and precipitation, and extreme or limiting factors relevant to coffee production (Table S1). Regarding soil properties, we obtained physical (bulk density, clay coarse and silt content at different depths) and chemical (cation exchange capacity, soil organic carbon content and soil pH) data from SoilGrids at 250 m (www.soilgrids.org), and then extracted mean values for the coffee fields at the municipality level (Fig. S1).

Socio-Economic factors

Coffee agricultural management practices are from the IBGE database, based on a field survey done in 2006 and 2017 that assessed the number of coffee farms under a particular management practice. We considered variables associated with management intensity and calculated the percentage of farms that use: irrigation, mechanical harvest, organic or chemical manure, and pesticides. Additionally, we also calculated the percentage of organic farms within each municipality. Moreover, because enhancing flower visitor abundance, specifically with *A. mellifera*, is a common practice to guarantee coffee pollination, we obtained information from the IBGE on the total honey produced per municipality as a proxy of the density of managed *A. mellifera* hives. Considering that smallholders benefit more from pollination service (Garibaldi et al., 2016), we calculated two variables: the municipality coffee area divided by the number of coffee farms, as a proxy of mean-field size; and the percentage of farms classified as family farms within the municipality of the total amount of farms in the municipality. According to the Brazilian legislation, a family farm is one with farms between 20 to 400 ha, depending on the municipality.

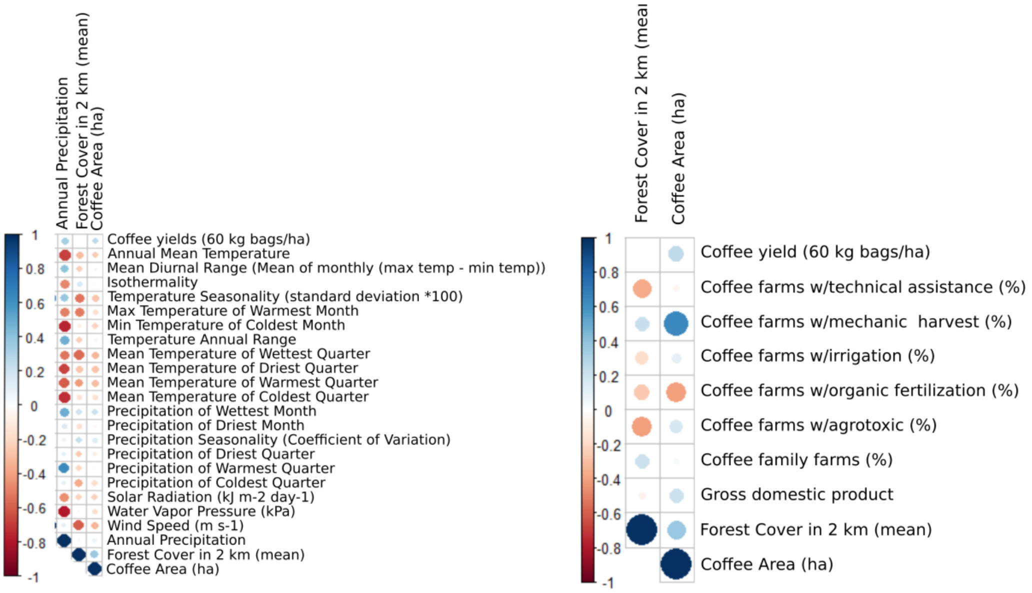
Figures



a) Forest Cover Variables

b) Coffee Cover Variables

Figure S1: Correlation of the main explanatory variables for each group of factors: a) Forest landscape variables associated with service supply; b) Coffee landscape variables associated with demand variables; c) climatic variables; c) Socio-economic variables. The color represents the direction of the correlation, whether it is negative (red) or positive (blue), and the size of the circle indicates the absolute value (the largest circle corresponds to correlation equal to 1). *Continues*



c) Climatic Variables

d) Socio Economic Variables

Figure S1: Correlation of the main explanatory variables for each group of factors: a) Forest landscape variables associated with service supply; b) Coffee landscape variables associated with demand variables; c) climatic variables; c) Socio-economic variables. The color represents the direction of the correlation, whether it is negative (red) or positive (blue), and the size of the circle indicates the absolute value (the largest circle corresponds to correlation equal to 1). *Continuation*

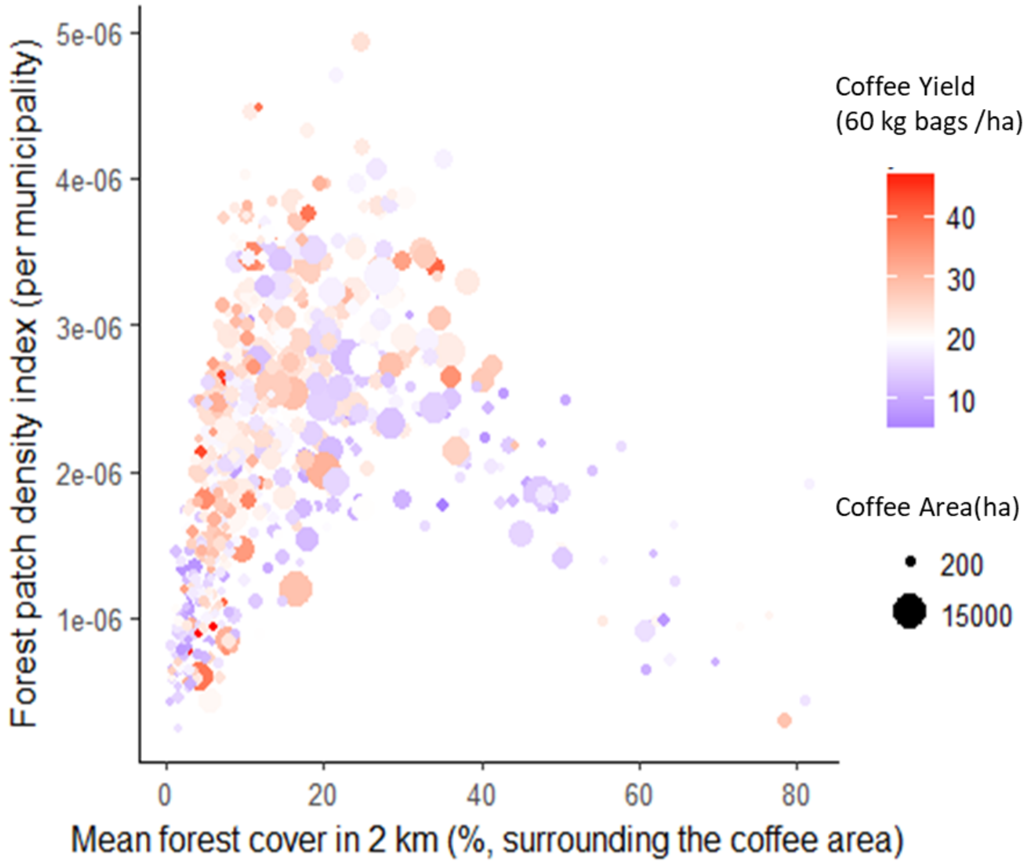


Figure S2: Forest cover (composition variable) and forest patch density (configuration variable) relationship with coffee yields. Each dot represents a coffee-producing municipality varying in color accordingly to its coffee productivity (yield) measured in 60 kg bags per hectare. The size of the dot is related to coffee cover per municipalities: smaller points have less than 200 ha; bigger points have more than 15000 ha; medium points are in between those values.

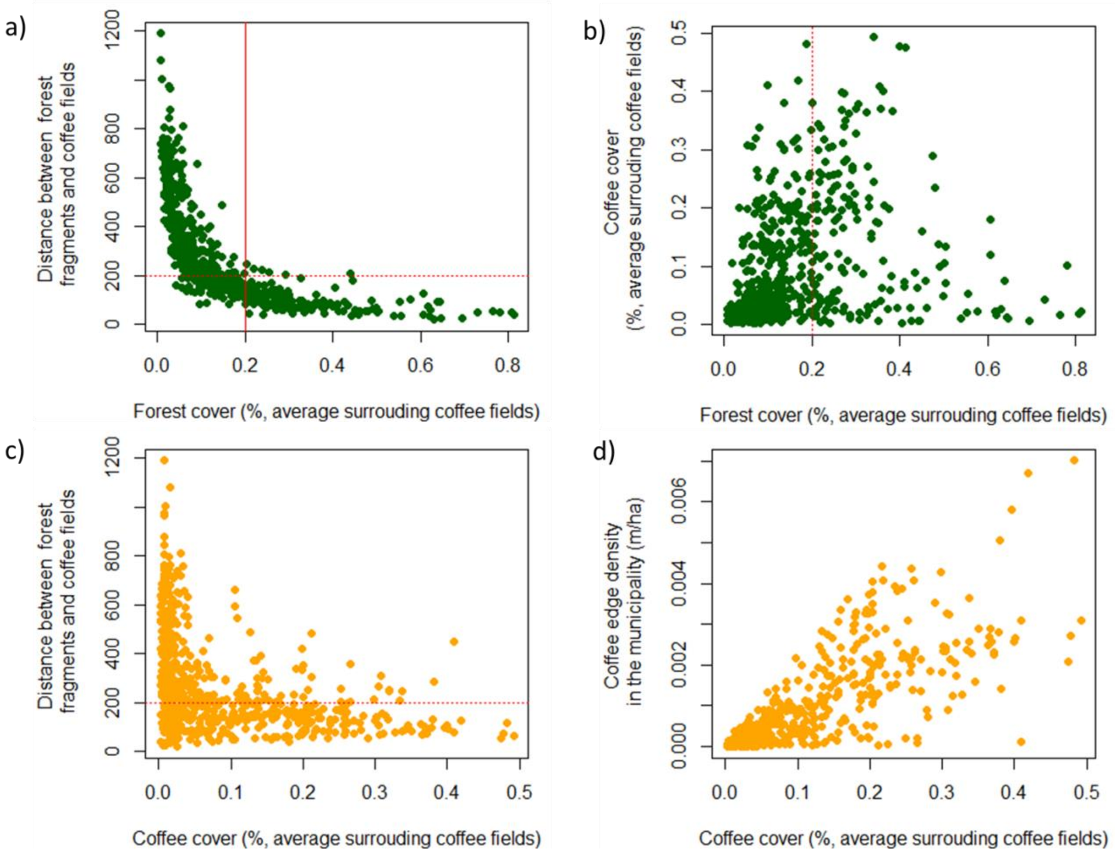


Figure S3: Association between forest cover (a & b) and coffee cover (b, c & d). a) show the relationship between Euclidean distance and forest cover, which are highly correlated. In red two threshold are presented: dotted line to represent the 200m threshold at which bee diversity has been shown to decrease (González-Chaves *et al.* 2020); and the solid line showing the 20% threshold below which biodiversity composition drastically decreases (Banks-Leite *et al.* 2014). b) Shows the relation between forest cover and coffee cover at the same scales, which are not correlated (r < 0.4). c) Showing coffee cover with Euclidean distance between coffee field and forest fragments. d) Relationship between coffee cover (at 2km radius landscapes) with the edge density of coffee fields in the municipality, showing coffee fields fragmentation along with coffee cover.

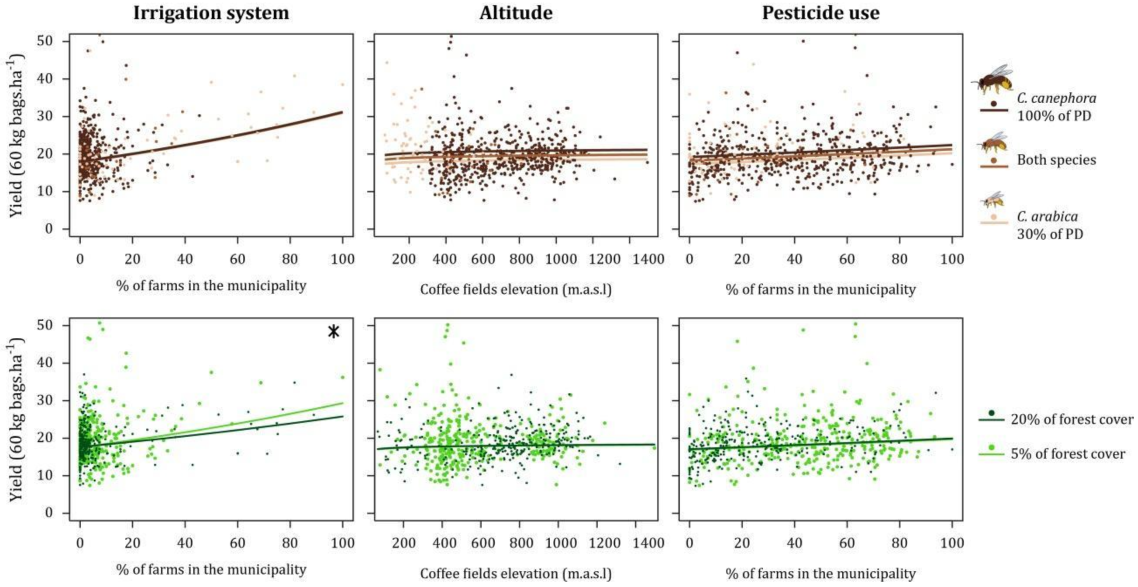


Figure S4: The management practice (a-Irrigation and c-pesticide) and topographic (b – altitude) effect on coffee productivity, in relationship with the coffee pollinator demand and the amount of forest cover in the coffee fields' surroundings. Using the coefficients of the models that includes them variables with the lowest delta AIC (see table S4), models 5, 10 and 13 respectively.

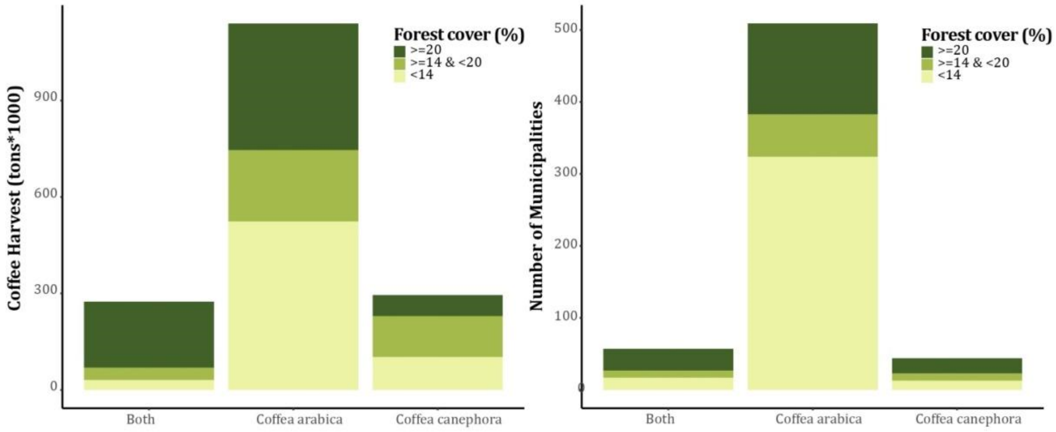


Figure S5: a) Coffee production (1000* tons) produced and the nmber of municipalities in which each coffee species (and municipalities that produce both of them) according to the amount of forest surrounding coffee fields in each municipality.

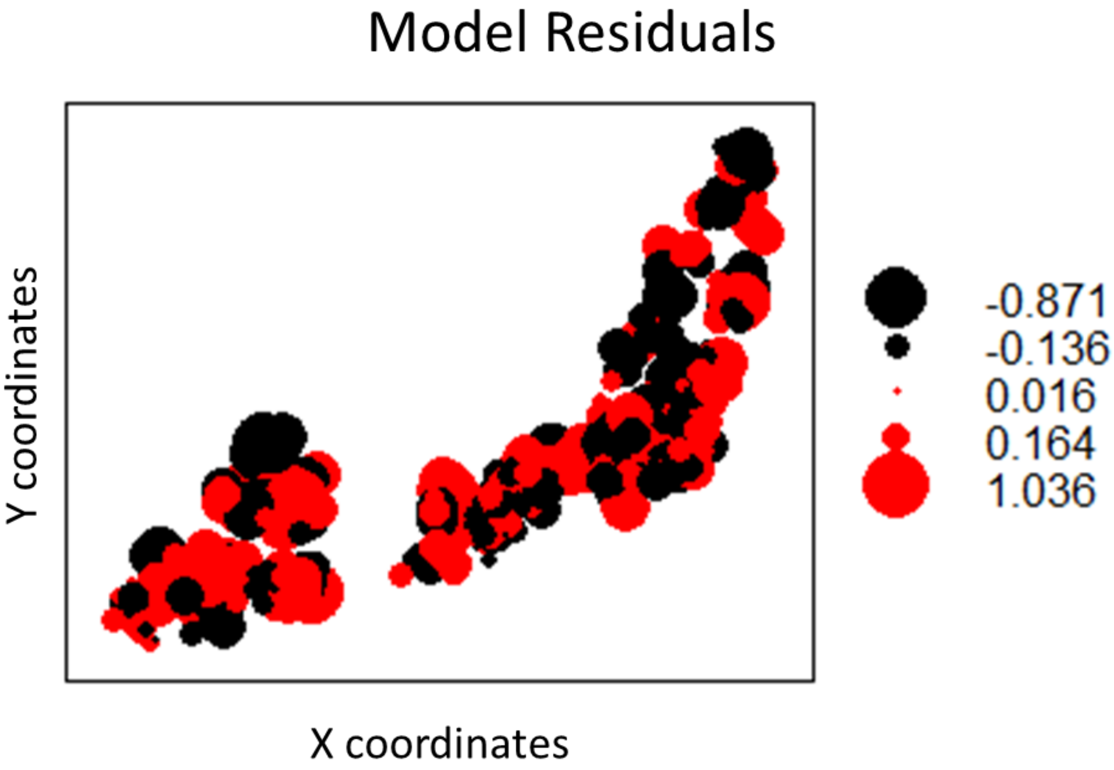


Figure S6: Model residuals associated to the coordinates of the centroid of each municipality of the first model of the model selection (Table S4 – *see below*). The model includes the exponential relationship between the centroids of the municipalities.

Tables

Table S1: Year for which coffee maps were available and the corresponding forest cover maps and coffee yields data used for each state. * We considered a three-year interval to calculate mean values, using maps from the three previous years. ** for coffee yields, we used a year difference with the forest maps as coffee harvest occurs nine months after (May –July) the blooming period occurs.

State	Coffee	Forest *	Yields**
Bahia	2009	2007 – 2009	2008 - 2010
Espirito Santo	2007-2008	2006 – 2008	2007 - 2009
Minas Gerais	2012	2010 – 2012	2011 – 2012
Paraná	2011	2009 – 2011	2011 - 2013
São Paulo	2010	2008 – 2010	2009 - 2011

Table S2: Summary of the model selection performed to compare different scales for each of the landscape variables (coffee and forest cover). Every model included the exponential relationship between municipality centroid coordinated, and the nested random structure of the meso-region within the state that each municipality belong to.

Response	Predictors	AIC	ΔAIC	Weight
Coffee yield	Coffee municipality + Forest at 2km	137.5	0.00	0.507
	Coffee municipality + Forest at 500m	138.0	0.46	0.403
	Coffee municipality	142.9	5.35	0.035
	Coffee 2km + Forest at 500 m	144.7	7.22	0.014
	Coffee 2km + Forest at 2 km	145.4	7.88	0.010
	Forest cover at 2 km	145.4	7.92	0.010
	Forest cover at 500 m	145.4	7.93	0.010
	Coffee in the municipality + Forest in the municipality	146.8	9.24	0.005
	Coffee 500 m+ Forest at 500 m	147.2	9.64	0.004
	Coffee 500 m+ Forest at 2 km	148.3	10.75	0.002
	Coffee cover at 2 km	159.8	13.28	0.001
	null	154.6	16.82	0.000

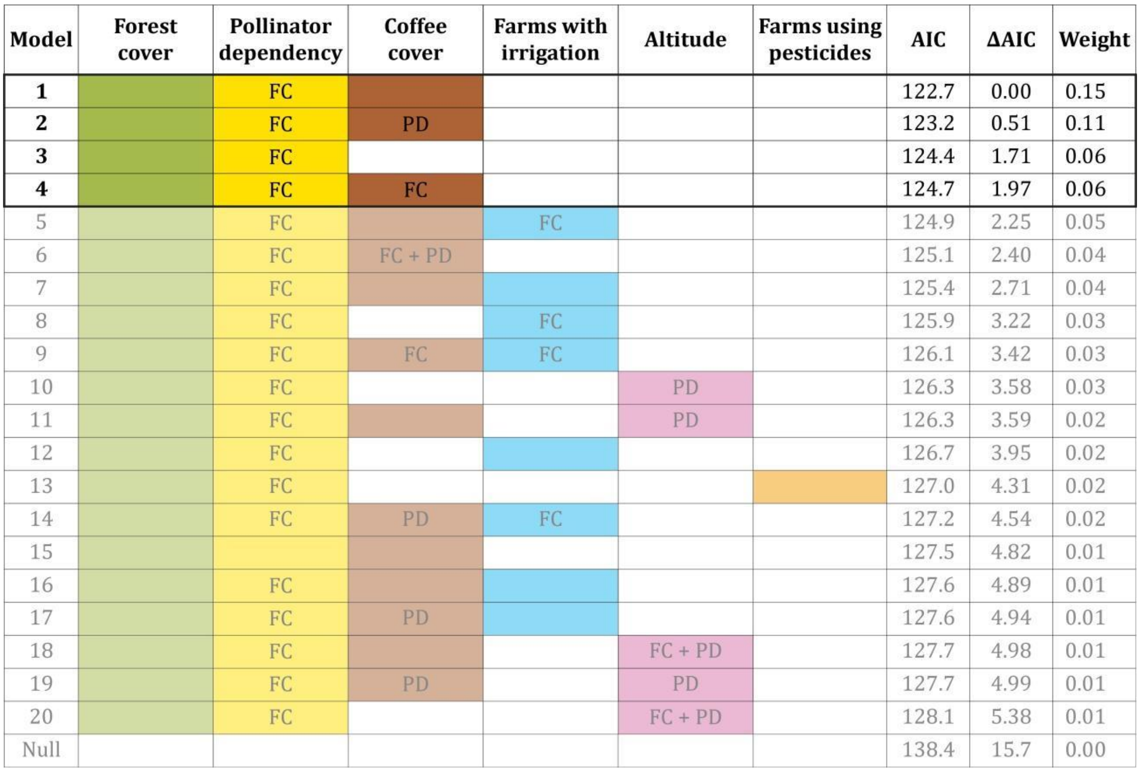
Non-linear relationship between forest cover and coffee yield

Given that forest cover could be related to biodiversity, and thus to pollination service, in a non-linear way, we tested if incorporating the quadratic term on the forest cover variable would alter (reduce/increase) the model fit. Furthermore, models assuming a quadratic effect of forest cover explained better the variability in coffee production than a model assuming a linear effect of forest cover. Therefore, we calculate for which forest values coffee achieved the highest yields for each species using the parabola equation and the mean values of the co-variables of the model selected.

Table S3: Summary of the model selection performed to compare the quadratic effect of coffee cover. All models had as a random effect different intercepts according to the state and sub-region that each municipality belongs to.

Response	Predictors	AIC	ΔAIC	Weight
Coffee yield (60 kg bags ha^{-1})	poly(Forest cover) *(all variables)	208.0	0.00	1
	Forest cover * (all variables)	255	47.24	0

Table S4: Summary of the model selection performed to compare different variable combination from the full model (figure 2e). Models with ΔAIC < 2 were considered equally plausible. The color of each cell corresponds to the dimension of each variable and indicates whether the variable is present in the model or not (blank). The letters within each cell indicate whether the interaction is present in the model. Every model included the exponential relationship between municipality centroid coordinated, and the nested random structure of the meso-region within the state that each municipality belong to.



Model	Forest cover	Pollinator dependency	Coffee cover	Farms with irrigation	Altitude	Farms using pesticides	AIC	ΔAIC	Weight
1	🟩	FC	🟫				122.7	0.00	0.15
2	🟩	FC	PD				123.2	0.51	0.11
3	🟩	FC					124.4	1.71	0.06
4	🟩	FC	FC				124.7	1.97	0.06
5	🟩	FC	🟫	FC			124.9	2.25	0.05
6	🟩	FC	FC + PD				125.1	2.40	0.04
7	🟩	FC	🟫	🟦			125.4	2.71	0.04
8	🟩	FC		FC			125.9	3.22	0.03
9	🟩	FC	FC	FC			126.1	3.42	0.03
10	🟩	FC			PD		126.3	3.58	0.03
11	🟩	FC	🟫		PD		126.3	3.59	0.02
12	🟩	FC		🟦			126.7	3.95	0.02
13	🟩	FC				🟧	127.0	4.31	0.02
14	🟩	FC	PD	FC			127.2	4.54	0.02
15	🟩	🟨	🟫				127.5	4.82	0.01
16	🟩	FC	🟫	🟦			127.6	4.89	0.01
17	🟩	FC	PD	🟦			127.6	4.94	0.01
18	🟩	FC	🟫		FC + PD		127.7	4.98	0.01
19	🟩	FC	PD		PD		127.7	4.99	0.01
20	🟩	FC			FC + PD		128.1	5.38	0.01
Null							138.4	15.7	0.00

Table S5: Summary of model selection performed to compare the best spatial correlation structure. Model 1 with exponential spatial structure out performed all the other correlation structure as well as the models without spatial structure (model 4). The fix variables considered for the first six models are the same full model as the one presented in figure 2e (*see table 24.1 from* Crawley, 2007).

Chapter 2

Time lag evidence of regenerating tropical forest ability to contribute to coffee yields

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Abstract

Conservation and restoration of native tropical forests is crucial for the protection of biodiversity and ecosystem functions, such as carbon stock capacity. Little is known on the contribution of early regenerating forests for the provision of ecosystem services driven by mobile agents such as pollination service and pest control. Using data from 610 municipalities along the Brazilian Atlantic Forest, we evaluated the contribution of young regenerating forest (with less than 20 years of age) to coffee yield and if such contribution depended on the amount of preserved forest in the surroundings of the coffee fields, considering a spatial resolution of 30 m. We found that while coffee yield increases are mainly associated with total forest cover, increasing young regenerating forest (within a 500 m buffer) can result in higher coffee yields, especially when the amount of total forest in a 2 km buffer is above a 20% threshold. These results suggest that older preserved forests are essential to sustain populations of pollinators and pest enemies, but regenerating fragments contribute to increase connectivity between such forest and crop fields in landscapes with a minimum (20%) amount of forest. These results highlight a potential debt of at least 20 years in the ability of regenerating forests to provide coffee pollination service. Our study emphasizes, the need to implement actions and public policies that not only promote regeneration but also guarantee the permanence of these new forests over time.

Introduction

Most of the landscape across the globe have been transformed to varying degrees with less of 20% considered as *wildlands*, without clear intervention of human impact (Ellis et al. 2021). In tropical regions, a large part of the remaining native vegetation is within private lands (Ribeiro et al. 2009; Watson and Venter 2017). Agricultural fields are the major land use responsible for the clearance of tropical native vegetation (Gibbs et al. 2010). Thus, identifying strategies to increase agricultural production through biodiversity conservation in working landscape, are crucial to align food system transformation with an effective post-2020 biodiversity conservation strategy (Leclère et al. 2020; dos Santos et al. 2020).

An intertwined approach on forest and landscape restoration is gaining momentum, aiming to achieve both agricultural production and conservation goals (Brancalion et al. 2019; Arroyo-Rodríguez et al. 2020). However, many agricultural landscapes have been severely simplified, dedicate to one specific land use, with little habitat remaining, and thus trespassing their capacity to retain biodiversity and provide ecosystem service(Benayas et al. 2009; Arroyo-

Rodríguez et al. 2020). In such cases, native vegetation regeneration is among the most cost-effective ecological restoration management action and is considered the cornerstone for achieving forest restoration goals (Crouzeilles et al. 2020). Despite the evidence that regenerating forests partially recovers its biodiversity and the capacity stock carbon (Barlow et al. 2007; Poorter et al. 2016; Rozendaal et al. 2019), evidence regarding their capacity to locally contribute to agriculture through the provision of ecosystem services (e.g. Pollination and pest control) is still scarce.

Most of the restoration initiative are expected to occur in agricultural landscapes (Erbaugh et al. 2020). For instance, iIn the Brazilian Atlantic Forest, a restoration hotspot (Brancalion et al. 2019), the legislation requires farmers to hold a minimum of 20% forest cover within their land; when below this threshold, farmers must restore (or compensate elsewhere within the biome) (Soares-filho et al. 2014; Metzger et al. 2019; d'Albertas et al. 2021). In such cases, trade-offs between agricultural production and conservation might be unavoidable when agricultural interests are not aligning with biodiversity conservation goals (Metzger et al. 2019). Therefore, assessing whether regenerating forests will result in immediate productivity gains is crucial to back up the economic viability of forest restoration, which can hold farmers to comply with restoration goals within their farms (Wainaina et al. 2020; d'Albertas et al. 2021). To reduce these trade-offs Assessing where restoration of biodiversity is likely to benefit agricultural production and increase economic net-gains is essential.

Assessing whether landscape restoration would overcome implementation costs, resulting from the enhanced pollination and pest control, is crucial to also understand the temporal ecological delays that result from habitat restoration (Lira et al., 2019). Biodiversity takes time to respond to changes in habitat amount, hence ecosystem services should also have a delayed response to land use changes (Lira et al. 2019; Poorter et al. 2021). For instance, previous studies have shown that secondary forest takes almost 30 years to recover their biodiversity and their ability to stock carbon and to improve soil properties (Gageler et al. 2014; Poorter et al. 2016). For pollinators and other small mobile agents' recovery might start sooner, but it will still take a few years for economic benefits to be noticeable (Blaauw and Isaacs 2014). Whether forest restoration contributes to crop yields through the provision of ecosystem services across large scales remains to be tested.

Landscape structure can also affect the success of local restoration practices, as well as ecosystem service provision (Crouzeilles and Curran 2016; Metzger et al. 2021). Thus, we expect that the ability of regenerating patches to act as a source of pollinators will depend on the amount of habitat present in the landscape. Conversely, regenerating forest will be less prone to provide ecosystem services in highly transformed landscapes (M'gonigle et al. 2015). Here, we tested whether young regenerating forest recovered its ability to contribute to coffee yield across the whole Brazilian Atlantic Forest region. We expect that greater amount of forest, particularly of older forest fragments, should be associated to higher coffee yields due to their ability to contribute with ecosystem services.

Methods

Study area and focal crop species

The study focused on the coffee cultivation areas within the Brazilian Atlantic Forest. One of the most common and economically important land-use in the region, which is also widely distributed across the tropics. Locally, coffee has been shown to benefit from pollination and pest control associated to forest conservation (Saturni et al. 2016; Chain-Guadarrama et al. 2019; Medeiros et al. 2019; González-Chaves et al. 2020). Across larger regions, forest in the surroundings coffee fields has been more relevant at predicting yields than management practices, climatic variables, and soil characteristics (González-Chaves et al., 2021). In the Atlantic Forest the two most traded coffee species (*Coffea arabica* and *C. canephora*) are produced. The two crops' species differ in pollinators demand, which influences the benefits that coffee yields draw from forest (González-Chaves et al. 2022). Furthermore, the Atlantic Forest region has seen a steady increase in forest cover, mostly associated to second growth regeneration (Rosa et al. 2021).

Coffee production and spatial distribution

We gathered data on crop productivity from the Brazilian Institute of Geography and Statistics (IBGE, http://www.ibge.gov.br/)-, corresponding to 1.3 Mha destined to coffee production within 610 municipalities in the Atlantic Forest. Most of the municipalities produce *C. arabica* (509), and a small proportion cultivates either *C. canephora* (44) or both species (57). We specified the coffee species planted in each municipality by using a pollinator demand index (PD), which considers the benefits known to draw from pollination weighted by the area destined to each species considering (Klein et al 2003; González-Chaves et al 2021). We calculated the mean coffee yields (number of 60 kg bags per hectare) from three consecutive years for each municipality, accordingly to the coffee field maps available for each of the five Brazilian States where coffee is produced within the Atlantic Forest (Figure 1; Table S1). The year of the coffee field maps ranges between 2008 and 2012, as they were independently done by initiatives in each State and brought together by the National Supply Company (CONAB in Portuguese, https://www.conab.gov.br/) who shared the data.

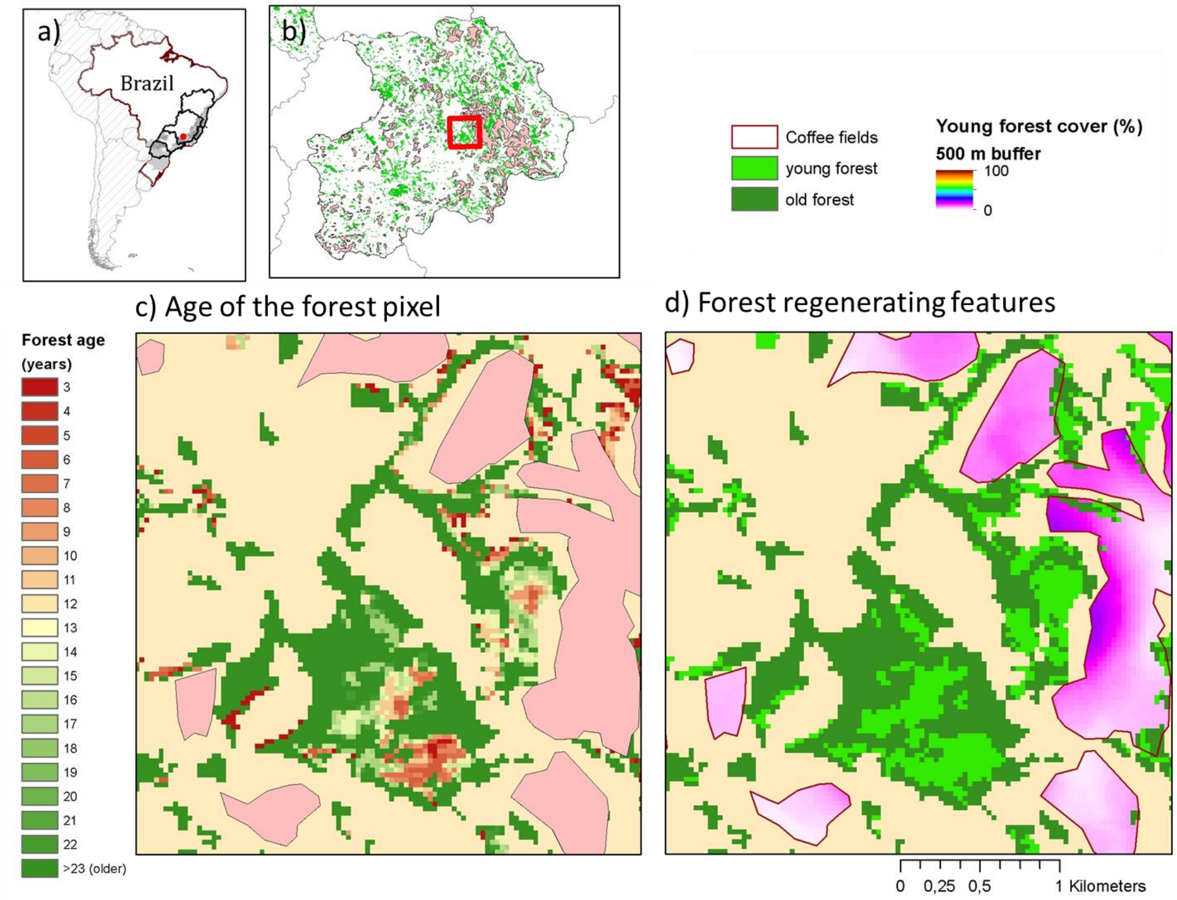


Figure 1: a) Map showing the location of the Atlantic Forest region in gray, and highlight the major States involved in the production of *C arabica* and *C. canephora*(in black). b) Detail illustrating the land use and land cover map in one of the 610 municipalities. c) Further detail highlighting forest age. d) Reclassification of the forest into young regenerating forest (light green) and older forest (darker green). The shades of purple represent the young regenerating forest cover in 500 m buffer for each coffee pixel. Forest related layer are from Mapbiomas.org, while coffee fields maps were obtained from CONAB.

Regenerating forest age stages

We estimated the age of each native forest pixel surrounding coffee fields using the annual land-use cover maps from the MapBiomas collection 5.0 based on Landsat imagery with a spatial resolution of 30 m from 1985 to 2019 (Souza et al. 2020). We developed a forest age map for each of the five states included in the analysis based on the years of available coffee field maps (Figure 1c, Table S1). First, we mapped native forest cover that was present since 1985 (older forest), which is the first year of the Mapbiomas time series. We then identified regenerating forests as forest pixels that were classified either as cropland or pasture for at least three years and remained as forest until the correspondent year from the coffee reference map, considering a minimum of 3 years as forest (Rosa et al. 2021). The age of regeneration was calculated as the number of years between the regeneration event and the coffee reference map for each state.

The regenerated forests are still a small fraction of the forest cover in the regions. Most patches are below 5 years of age or above 18 years old, given the dynamic resulting from forest clearance (Rosa et al. 2021). Thus, subdivided the Atlantic Forest fragments from our study region into two groups: those with less than 20 years of age (hereafter young regenerating forest, YRF) and those with 20 or more years, older forest (see Fig. 1d). The 20 years age threshold was established due to limitation in our data, as the Mapbiomas time series started in 1985 and the oldest coffee map available for Espirito Santo state was 2008, thus 20 years is the oldest age available for all municipalities (Souza et al. 2020; Rosa et al. 2021). Therefore, the forest age is unknown for forest already present before 1985. We did not consider any threshold for younger forest fragments as secondary forests are highly dynamic in Latin America (including the Atlantic Forest) and forest fragments with less than 10 years of age are more commonly cleared (Chazdon et al. 2016; Rosa et al. 2021). Moreover, biodiversity can partially recover after 20 years of age (Barlow et al. 2007; Poorter et al. 2016), as well as the reproductive functional traits of trees (Romanowski et al. 2021). We ended up with three forest features: *i)* young regenerating forest (YFR) under twenty years of age, *ii)* forest with more than twenty years of age and *iii)* overall forest cover disregarding forest age.

We calculated the percentage of young regenerating forest and older forest surrounding of coffee fields by using a moving window analysis for each coffee pixel at 2 km and 500 m buffer radius, with the raster package using R 4.1 (R Development Core Team 2021). The spatial scales were considered based on studies showing that above and below ground biodiversity responds to those scale in human modified landscapes (le Provost et al., 2021), as well as pollination and pest control services benefitting coffee production (Aristizábal and Metzger, 2019; González-Chaves et al., 2020; Librán-Embid et al., 2017; Saturni et al., 2016) . Moreover, regeneration is also known to respond to landscape at similar scales (Crouzeilles and Curran 2016). Coffee yield data was available at the municipality level, a scale at which forest cover has been monitored to reduce deforestation (Koch et al. 2019). Thus, apart from calculating mean values of the percentage of forest surrounding coffee fields for each municipality, we also calculate the percentage of each forest feature at the municipality level. Therefore, we evaluated the three forests categories, at the three different scales (500 m, 2 km and municipality level).

Statistical Analysis

To relate coffee yield with forest features, we used a model from a previous study comparing the relative effect of management practice, climatic features, soil characteristics and topography for predicting coffee yield(González-Chaves et al. 2022) . According to the model coffee yield increases with the overall forest cover, the benefits being higher for municipalities with the highest pollinator demand (ex, those producing C. canephora), and the amount of coffee cover has an additive positive effect on coffee yields. We used this model as a starting point to compare the predictability between the different regeneration age stages. However, instead of only considering forest cover we created alternative models with: 1) older forest cover, 2) young regenerating forest cover (YFR), in addition to the former model with the 3) overall forest cover. Therefore, first, we compared the 3 models by replacing the overall forest cover variable with each of the forest age features (YRF and older forest), and for each forest variable we also create a model for the three study scales (Table 1). Additionally, we tested if the amount of young regenerating forest modulates the effect of overall forest cover or older forest cover, thus we included a fourth model with the interaction term between young regenerating forest and older forests. Moreover, we created a full model with all possible two-way interactions between young regenerating forest and the rest of the variables (pollinator dependency index, coffee cover, and forest cover), to test if the amount of young regenerating forest modulated the effects on any of the known previous fixed effect variables described to predict coffee yields (Table S2).

All model comparison were done using a multi-model inference approach based on information theory using Akaike Information Criterion (AIC) (Burnham and Anderson 2002). We used linear mixed-effect models as the log-transformed response variable (coffee yield) presented a Gaussian distribution. We included municipalities' mesoregions (group of municipalities with similar geographic and social characteristics, as defined by the IBGE) nested within the state as a random structure in all models, allowing the intercept to vary accordingly. This nested structure is essential because there is an inherent variation in the socioeconomic and agronomic practices that affect coffee productivity across the main producing mesoregions within each state of Brazil (Bliska *et al.* 2009). Moreover, as spatial correlation had been previously detected (using the DHARMa package in R), we included in all the models the exponential relationship between yields of the municipalities related to the geographical distance between the centroids of each municipality as a covariable of the models. All models with ΔAIC lower than 2 were considered equally plausible. Finally, we checked the Gaussian and homoscedasticity assumptions for the standardized residuals.

Results

Coffee yield varied greatly across the municipalities, between 4.7 and 47.3 coffee bags per hectare, and with a mean and median value of 20 bags/ha. Total forest cover surrounding coffee fields also varied greatly, between 0.4% and 91% on average (Fig 2), with less than half (45%) of the municipalities having more than 20% of forest cover within a 2 km radius, which was the best scale to explain coffee yields (Table 1). Most of the forest cover was composed by forest older than 20 years, the reason why we found that old forest cover was highly correlated with overall forest cover (Fig 2). Almost a quarter (23.6%) of the municipalities had less than 1% of young regenerating forest cover. Nonetheless, for 14% of the municipalities', young regenerating forests comprise more than half of the forest cover surrounding of coffee fields at 500 m radius (Fig 2a), which was the best scale relating young regenerating forest with coffee yield (Table 1 & 2).

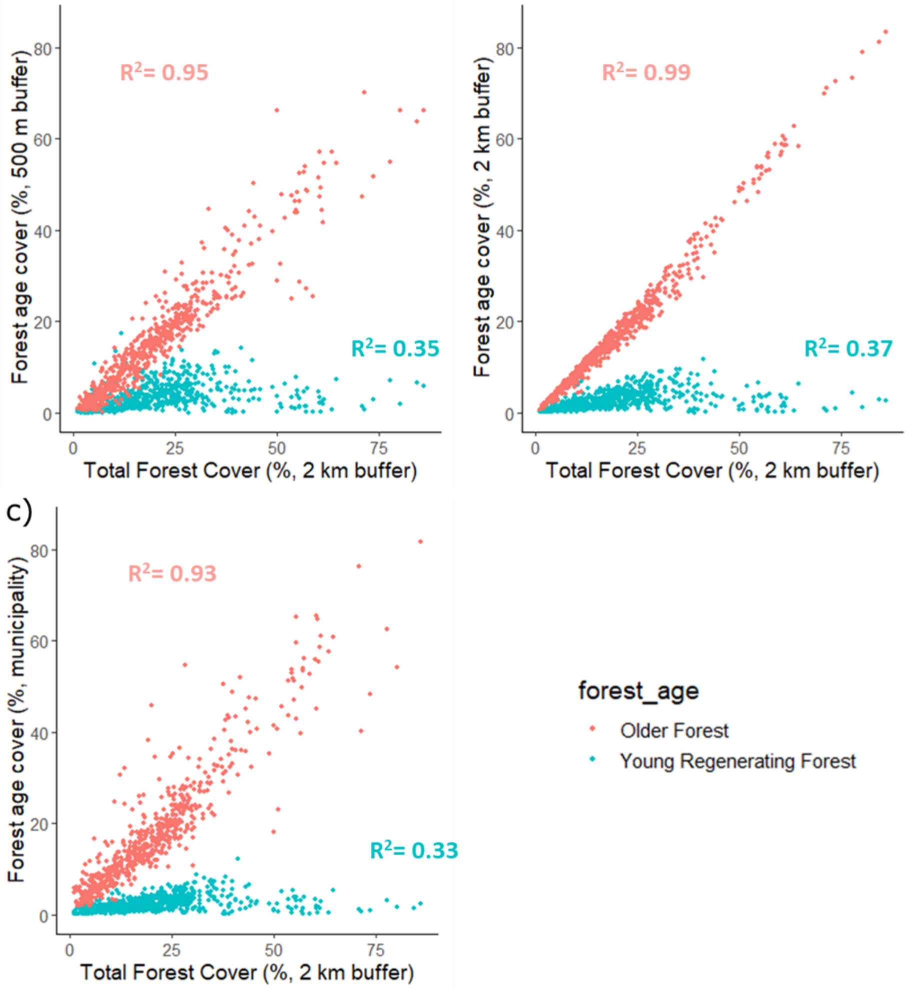
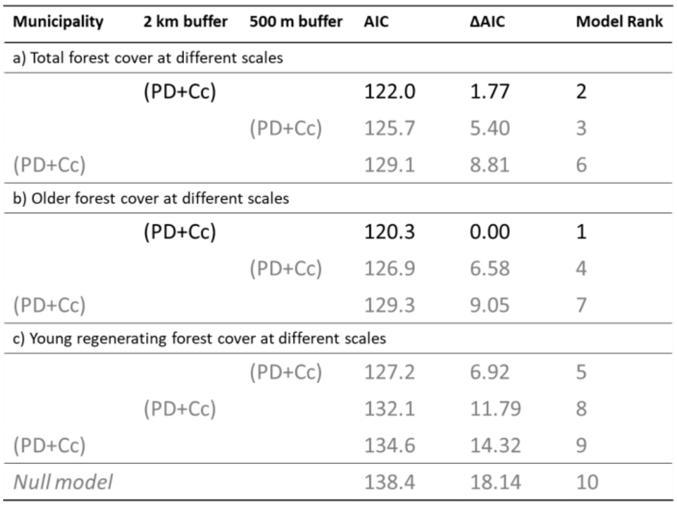


Figure 2: Relationship between total forest cover in at 2 km buffer radius with older and younger forest cover at different scales: a) 500 m buffer surrounding coffee fields, b) 2 km buffer, and c) at the municipality scale. Values of R^2 for Spearman correlation are presented for each relationship (Forest age feature vs. total forest cover at 2 km buffers).

Table 1: Model performance predicting coffee yields at different scales (500 m, 2km, and municipality) as a function of each of the following forest covers: a) total forest cover, b) older forest cover (fragments with more than 20 years), and c) young regenerating forest (<20 years). All models were compared and ranked according to the ΔAIC value. All the models also included the interaction between the forest cover and the pollinator dependence (PD) plus the additive effect with the coffee cover (Cc).



Municipality	2 km buffer	500 m buffer	AIC	ΔAIC	Model Rank
a) Total forest cover at different scales					
	(PD+Cc)		122.0	1.77	2
		(PD+Cc)	125.7	5.40	3
(PD+Cc)			129.1	8.81	6
b) Older forest cover at different scales					
	(PD+Cc)		120.3	0.00	1
		(PD+Cc)	126.9	6.58	4
(PD+Cc)			129.3	9.05	7
c) Young regenerating forest cover at different scales					
		(PD+Cc)	127.2	6.92	5
	(PD+Cc)		132.1	11.79	8
(PD+Cc)			134.6	14.32	9
Null model			138.4	18.14	10

Older forests were equally as good as overall forest cover to explain coffee yield variations, which was expected given the high correlation between both variables (Table 1 & 2, Figure 2). Hence, from here forth we will focus on the older forest cover effect. On the other hand, young regenerating forests alone did not contribute explaining the variations in coffee productivity (table 1). However, the interaction of young regenerating forest with older forest cover was important to explain variations in coffee yield (Table 2). This effect occurred on a particular combination of scales, with young regenerating contributing at a smaller scale, 500 m, while total or older forest cover contribute at 2 km buffer (Table 1, 2).

Table 2: Model performance predicting coffee yield which also considers the interaction between young forest fragment and older forest cover. The different scales were tested for young regenerating forest while we maintained constant the 2km buffer scale for the old forest cover. All the models also considered the interaction between the forest features and the pollinator dependence (PD) and the additive effect with the coffee cover (Cc).

Municipality	2 km buffer	500 m buffer	AIC	ΔAIC	R^2m / R^2c	Model Rank
		(YRF+PD+Cc)	111.2	0.00	0.10 / 0.56	1
	(YRF+PD+Cc)		126.9	14.7	0.09 / 0.55	2
(YRF+PD+Cc)			129.3	17.1	0.09 / 0.55	3
Null model			138.4	26.2	0.00 / 0.34	4

More specifically, the effect of young regenerating forest cover varies according to the amount of total forest cover in the 2 km landscape (Figure 2). When total forest cover is above 20% increasing young regenerating forest cover has a positive effect on coffee yield, contrary to what happens in landscapes with less than 20% of forest cover (Figure 2). Landscapes with low forest cover dominated by young regenerating forest at the local 500 m scale, are thus associated with low coffee yields. Finally, neither pollinator dependency nor coffee cover were affected by the amount of young regenerating forest (Table 2, table S2), but they were relevant for explaining coffee yield (Table 1, 2).

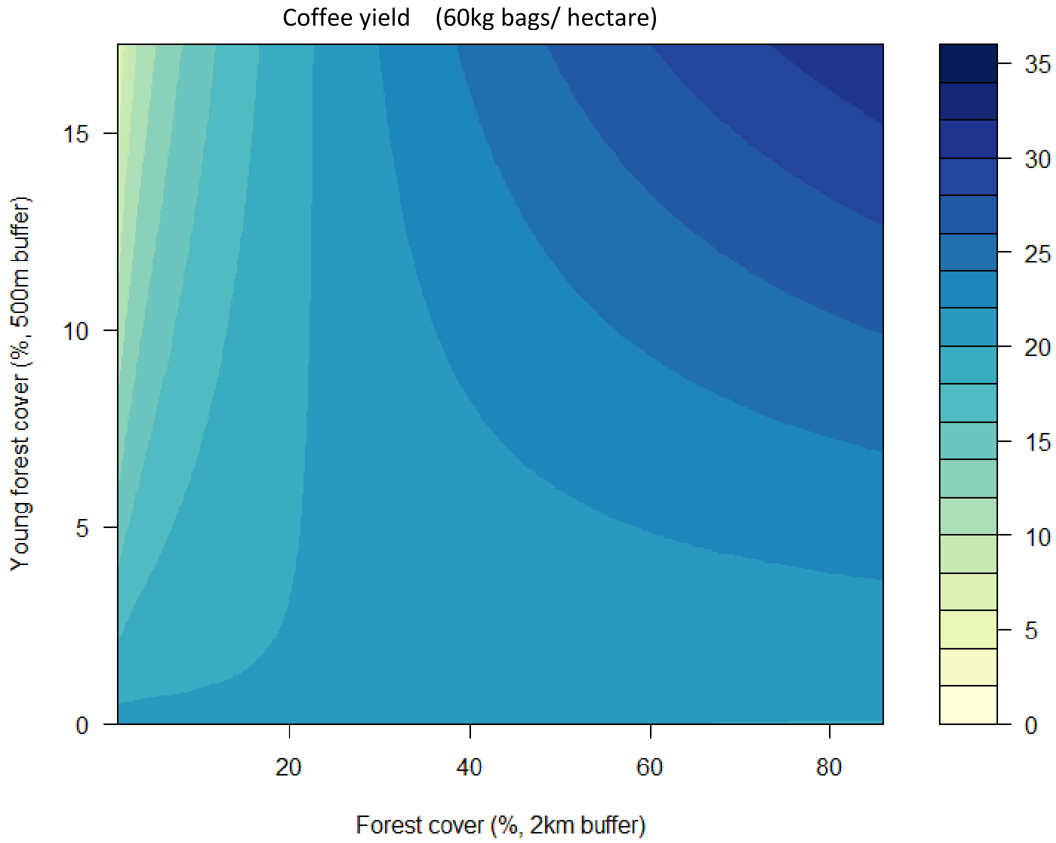


Figure 2: Coffee yield response to the effect of forest cover at 2 km buffer interacting with young regenerating forest cover at 500 m buffer. Darker color represents higher coffee yields represented in number of coffee bags of 60 kg per hectare, for which the range is presented on the right.

Discussion

Considering the need to restoration to be upscaled, mainly within working landscapes we present evidence of where forest regeneration has contributed to increase agricultural productivity. Our results suggest that young regenerating forest do not contribute directly to increase coffee productivity once landscapes dominated by young regenerating forest (with less than 20 years) were associated with lower productivity. However, those young forest seems to provide resources that enhance landscape biodiversity, which associated with the presence of more than 20% of older forest can further enhance pollinators and pest enemies known as that contribute with higher coffee yields. All these results indicate important temporal and spatial limitations to the contribution of regenerating forest to the increase in coffee productivity, which should be considered when implementing public policies that promote or regulate forest restoration.

Temporal dynamics

First, there seems to be a temporal limitation in the ability of young regenerating forest to contribute to agricultural production. Young regenerating forests alone cannot sustain the biodiversity associated with pollination and pest control, probably because early forest succession stages lack the nesting and feeding resource for the establishment of populations capable of meeting ecosystem services demand (Cockle et al. 2010; Styring et al. 2011; Sobreiro et al. 2021). For instance, the forest ability to harbor more diverse bee communities might be limited to higher carbon stocks from more mature forest, as many of the bee taxa visiting coffee flowers depend on tree trunks to build their nest (Cockle et al. 2010; Silva et al. 2013; González-Chaves et al. 2020). Besides in landscapes dominated by young regenerating forests, where coffee productivity is lower, the impoverished diversity may not sustain large population of pest enemies, more likely acting as serving as reservoirs for pest population which negatively affect coffee yield (Blitzer et al., 2012).

It is expected that the biodiversity present in the landscape would benefit from forest regrowth, given the evidence that the incremented light availability at early stages of forest succession, might lead to longer flowering periods and, increase floral resources (Kang and Bawa 2003). Nonetheless, in highly degraded landscapes the higher abundant flower resources are associated with lower plant diversity (Liow et al. 2001), which will host less diverse pollinators and pest enemies' communities, composed of super generalist species (Jaffé et al. 2015; Giannini et al. 2015), whose interaction might result in low pollination service (González-Chaves et al. 2020).

Alternatively, highly productive municipalities occurred where the habitat amount was above 20% of older forest, precisely the habitat amount above which biodiversity extinctions are less likely to occur (Keitt 2009; Banks-Leite et al. 2014; Boesing et al. 2018). Where the diversity of arthropods that contribute with ecosystem service are also expected to be enhanced (Martin et al. 2016; Dainese et al. 2019), especially the bees of the Meliponini tribe, the main coffee flower visitors, which are also known to be associated with more develop vegetation along a successional gradient of tropical forest (Ramalho 2004; Ramos-Fabiel et al. 2019). Besides, recent studies have shown that pollination service stability has been related to wild insect biodiversity, especially across large regions (Winfree et al. 2018; Senapathi et al. 2021). Hence the delayed ability of young regenerating forest to recover biodiversity when isolated from mature forest might be hampering the capacity of young forest to provide ecosystem services that benefit agricultural production.

Spatial Dynamics

Landscape with intermediate forest cover amount between (20% to 40%) have spatial arrangements that expected to favor the spill-over of pollinator and pest enemies towards crop fields, but also to favor the arrival of seeds needed for natural regrowth (Villard and Metzger 2014; Mitchell et al. 2015). Therefore, the proximity between regenerating fragment and older fragments mediates the landscape regenerating capacity to recover its biodiversity (Crouzeilles et al. 2020). Further explaining why in highly degraded landscape the ability of young forest to contribute with coffee yields is also hampered.

In landscape that favor biodiversity integrity, young regenerating forest are likely occurring in the proximity of older fragments and will further decrease the distance between forest and coffee fields facilitate forest connectivity and making the landscape more permeable to pollinators and pest enemies (González-Chaves et al. 2022). Hence, we would expect that these spatial dynamics will favor biodiversity recovery, and as regenerating forests fragments get older, they might start providing nesting resources and become a source of pollinators and pest enemies by favoring the establishment of more diverse communities rather than just enhancing the population of the communities present in the landscapes(M'gonigle et al. 2015; Woodard and Jha 2017; Iles et al. 2018).

Implications for the search of synergies between conservation and agriculture

In our study we argue that young regenerating forests can enhance the flowers resources on which pollinators and pest enemies rely, however, the ability to potentiate ecosystem services will rely on the community present in the landscape, as we found that the lower coffee yields occurred in highly degraded landscape with only young regeneration forest (Poorter et al. 2021). This suggests that for the half of the municipalities where most of the Atlantic Forest has been cleared, the regeneration might be missing the opportunity to enhance coffee productivity and assisted forest regrowth might be needed to avoid overloading the burdens of restoration on famers (Gastauer et al. 2021). Spatial planning of forest restoration is crucial to avoid discouraging a widely uptake by farmers in regions where restoration is most needed. Therefore, apart from the opportunity cost associated with setting land aside for forest regeneration, the restoration initiatives will also have to look for economic opportunities to help engage farmers to invest in landscape restoration as the benefits expected from ecosystem services to crop production will take time to be perceived.

Our work further reinforces the importance of implementing policies that help to guarantee the permanence of regenerating natural forest for achieving restoration goals, besides guaranteeing that at least 20% of natural habitat remain as an active part of agricultural landscapes. This is especially relevant in tropical regions, older forests are constantly being cut down and replaced by younger forest, a hidden factor affecting biodiversity and carbon stock capacity (Chazdon et al. 2016; Rosa et al. 2021; Piffer et al. 2022) Secondary forest might partly recover the richness of several taxa and the ability to sequester carbon in a short period of time (Barlow et al. 2007; Poorter et al. 2016, 2021), but here we show that the ability of secondary forests to contribute directly to crop productivity relays on landscape that are above the biodiversity extinction threshold. Given that most of the landscape have been severely transformed, economic incentive and building capacity will be crucial for farmers to engage in farmland restoration.

Conclusion

Ecological restoration is becoming mainstream and can greatly benefit from understanding the economical outcomes across large regions (Strassburg et al. 2019). Here we provide evidence that mature Atlantic Forest conservation contributes to coffee yields and identified where short-term conservation of young regenerating forest will have the largest potential to increase crop revenue. Despite the evidence showing that restoration is economically viable, the temporal delay of ecological recovery in highly simplified landscapes needs to be considered when implementing forest restoration and analyzing the revenue of restoring biodiversity within the farm. An economic alternative to undertake forest restoration, is incorporating, along with the native trees, cash crop and fruit trees in the beginning of the forest succession that would provide revenue for farmer until forest maturity is achieved. With such practices the time-lag associated with forest biodiversity recovery in highly simplified landscaped can be compensated by direct income of cash crop associated to forest regeneration (Melo et al. 2021). Socio-economic studies of forest restoration have suggest that the greatest potential for natural regeneration to occur is in small rural properties (Gastauer et al. 2021), precisely those which would benefit more from pollination service (Garibaldi et al. 2016), thus we strongly encourage to consider the delayed enhanced economic revenue from ecosystem services to agriculture when planning restoration initiatives.

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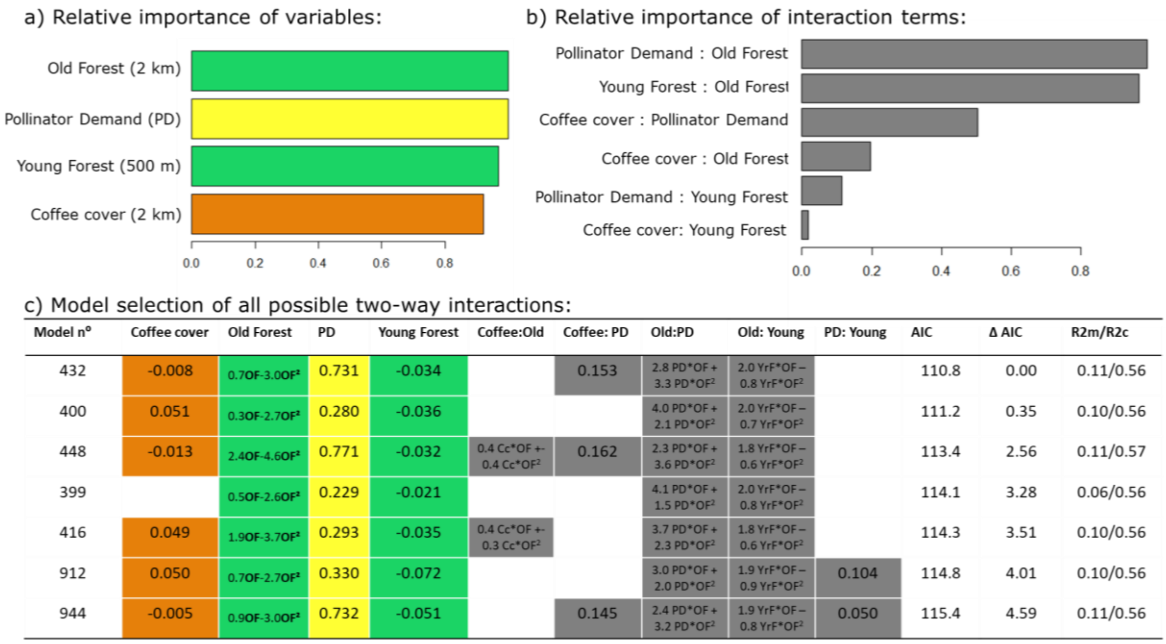
Supplementary Information

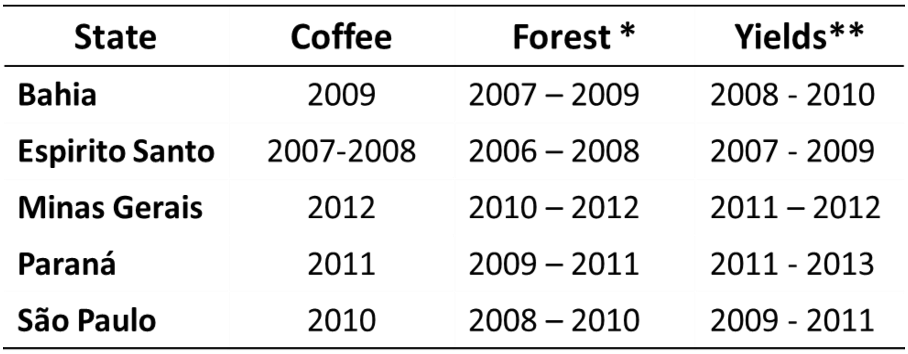


c) Model selection of all possible two-way interactions:

Model n°	Coffee cover	Old Forest	PD	Young Forest	Coffee:Old	Coffee: PD	Old:PD	Old: Young	PD: Young	AIC	Δ AIC	R2m/R2c
432	-0.008	0.7OF-3.0OF^2	0.731	-0.034		0.153	2.8 PD*OF + 3.3 PD*OF^2	2.0 YrF*OF – 0.8 YrF*OF^2		110.8	0.00	0.11/0.56
400	0.051	0.3OF-2.7OF^2	0.280	-0.036			4.0 PD*OF + 2.1 PD*OF^2	2.0 YrF*OF – 0.7 YrF*OF^2		111.2	0.35	0.10/0.56
448	-0.013	2.4OF-4.6OF^2	0.771	-0.032	0.4 Cc*OF +- 0.4 Cc*OF^2	0.162	2.3 PD*OF + 3.6 PD*OF^2	1.8 YrF*OF – 0.6 YrF*OF^2		113.4	2.56	0.11/0.57
399		0.5OF-2.6OF^2	0.229	-0.021			4.1 PD*OF + 1.5 PD*OF^2	2.0 YrF*OF – 0.8 YrF*OF^2		114.1	3.28	0.06/0.56
416	0.049	1.9OF-3.7OF^2	0.293	-0.035	0.4 Cc*OF +- 0.3 Cc*OF^2		3.7 PD*OF + 2.3 PD*OF^2	1.8 YrF*OF – 0.6 YrF*OF^2		114.3	3.51	0.10/0.56
912	0.050	0.7OF-2.7OF^2	0.330	-0.072			3.0 PD*OF + 2.0 PD*OF^2	1.9 YrF*OF – 0.9 YrF*OF^2	0.104	114.8	4.01	0.10/0.56
944	-0.005	0.9OF-3.0OF^2	0.732	-0.051		0.145	2.4 PD*OF + 3.2 PD*OF^2	1.9 YrF*OF – 0.8 YrF*OF^2	0.050	115.4	4.59	0.11/0.56

Figure S1: Complementary model selection results of all possible combination considering a full model with all the two-way interaction possible among the three landscape variables (Old Forest cover, young regenerating forest cover and coffee cover) and the pollinator demand index (PD). In a) the relative importance of all the variables after running the dredge function with the full model; in b) the relative importance of the interaction terms are presented, in which is confirm that the only relevant interaction with young regenerating forest is with old forest. In c) the model selection with the coefficients of each term or interaction, all model with delta AIC lower than 6 are presented. The two first models are equally plausible and only differ in incorporating the interaction between coffee cover and pollinator demand, this interaction term was previously discussed in a former study (González-Chaves et al. 2022) and is not a novelty result of this current research.

Table S1: Year for which coffee maps were available and the corresponding forest cover maps and coffee yields data used for each state. * We considered a three-year interval to calculate mean values, using maps from the three previous years. ** for coffee yields, we used a year difference with the forest maps as coffee harvest occurs nine months after (May –July) the blooming period occurs.



State	Coffee	Forest *	Yields**
Bahia	2009	2007 – 2009	2008 - 2010
Espirito Santo	2007-2008	2006 – 2008	2007 - 2009
Minas Gerais	2012	2010 – 2012	2011 – 2012
Paraná	2011	2009 – 2011	2011 - 2013
São Paulo	2010	2008 – 2010	2009 - 2011

Chapter 3

Forest fragmentation can contribute to the temporal stability of crop yields

Adrian González-Chaves, Lucas A. Garibaldi; Luísa G. Carvalheiro, Tereza C. Gianini & Jean P. Metzger

Abstract

Pollinators' visitation to crop and crop yields vary across space depending on the amount and spatial arrangement of native vegetation and their interspersion with crop fields. Such landscape features influencing spillover of pollinators and pest enemies from habitats towards crop fields may also affect the stability of these ecosystem services over time. However, little is known about yield temporal variability. Here we analyzed data on 16 crops distributed across ~1700 Brazilian municipalities located in the Atlantic Forest temporal region to evaluate the effect of natural habitat cover and configuration on crop stability. We compare these effects with the ones of climatic variability and soil nutrient availability gradients, always considering crops pollinators' dependency. Landscape features were as relevant to the temporal yields' stability of crops as precipitation variability. Forests contributed to yield stability, especially when the density of forest patches in the municipality is high. Forest patch density enhanced more the temporal stability of crops that are highly dependent on pollinators than those that do not depend on pollination service (e.g., maize, sugarcane), with the effects being particularly strong when forest cover is approximately 20%. Crop productivity in municipalities with lower diversity of crops were more stable across time, but only when forest patch density is high. Since greater forest fragmentation, and thus interspersion with crops areas helps stabilizing pollination service provision, by facilitating pollinators spillover from natural to agricultural areas, our results give further strength to the idea that investing in native forest conservation and promoting the proximity to cultivated areas in the proximity is crucial for guarantee temporal stability in crop productivity. Forest fragmentation can thus by promote synergies between biodiversity conservation and agricultural production, especially when forest cover is greater than 20%.

Introduction

Agricultural production is a major driver of climate change, contributing both directly through greenhouse gas emission and indirectly due to resulting substitution of natural habitats by crops (del Grosso & Cavigelli, 2012). Conversely, conserving and restoring biodiversity's ability to stabilize ecosystem functions and associated services in working landscapes can help mitigate climate change impacts by stocking carbon and avoiding further biodiversity loss (Chazdon et al. 2016; García-Palacios et al. 2018). Moreover, climate change poses a further threat to the temporal stability of agricultural production either by changing the climatic distribution of crops due to extreme weather events or by increasing pest outbreaks (Ouyang et al. 2014; Hautier et al. 2015; Giannini et al. 2017). Understanding whether natural habitat conservation can contribute to more stable food production can thus help in finding synergies between food production and biodiversity conservation (Fischer et al. 2017; Díaz et al. 2019).

Increasing crop productivity often relies on external inputs (such as fertilizers, pesticides, and irrigation), which have negative environmental impacts, further threatening biodiversity in working landscapes (Tilman et al. 2011; Knapp and van der Heijden 2018). Alternatively, integrative agronomic practices (e.g., ecological intensification, regenerative and conservative agriculture) aim to reduce the use of external inputs and rely on enhanced biodiversity contribution to crop productivity through ecosystem services provision (Cui et al. 2018; Knapp and van der Heijden 2018; Basso et al. 2019). More recently, the relevance of landscape management has been brought to light, as crop field location can determine the spatial variability in crop yields, either through topographic effects on water availability or by limiting the spillover of pollinators and pest enemies (Dainese et al. 2019; Basso et al. 2019; Medeiros et al. 2021; Leite-Filho et al. 2021). More importantly, the amount of native vegetation in the landscape determines the presence of the biodiversity that benefits crop production, but less explored is whether these landscape features also contribute to the temporal stability of crop productivity (e.g., the yield variability across years; McWilliams et al., 2019).

Habitat loss, landscape composition and configuration simplification affect the robustness of multitrophic communities' networks (Moreira et al. 2015, 2018; Aizen et al. 2019; McWilliams et al. 2019), hampering even further the ability of human-dominated landscapes to benefit from regulating services like pollination (Potts et al. 2010, 2016; Dicks et al. 2021). As the demand for pollinated crops continues to be on the rise (Aizen and Harder 2009), crop productivity across years tends to get even more unstable (Garibaldi et al. 2011b; Potts et al. 2016). There is, hence, a pressing need to identify landscape features that help stabilize crop yields over time and reduce temporal variability in crop production across years. The identification of such features can help guide the development of forest restoration programs and facilitate engagement among farmers.

Here, we tested if forest features contributed to the temporal stability of yield along climatic and soil nutrient availability gradient. We focused on landscape features related to forest cover and configuration (e.g. fragmentation). We also tested whether the effects were more pronounced for highly pollinator-dependent crops than for non-pollinator dependent corps. To this end, we used a 31-year data set for the 68 crops produced in the Atlantic Forest, a biome that, despite having been strongly transformed, still retains high levels of endemism (Joly et al. 2014) and represents a restoration *hopespots* worldwide (Rezende et al. 2018). Since forest cover contributes to yield increases, via its positive effects on density and diversity of ecosystem service providers (e.g., pollinators, González-Chaves et al, 2022), we expect that forest cover will contribute more to the temporal stability of the productivity of pollinator-dependent crops. Since the total natural habitat cover within landscape influences the variability that the landscape configuration can have (Villard and Metzger, 2014) we expect that a minimum forest habitat is needed for landscape configuration to contribute with crop yield stability, and landscape feature that favor biodiversity spillover should also be associated to higher temporal stability. Additionally, we expect that landscape simplification, which negatively affects biodiversity will also negatively affect yield stability (Fahrig et al., 2015; Garibaldi et al., 2016).

Methods

Study region

The Atlantic Forest biome is one of the largest tropical forests in the world, today reduced to a fourth of its original extension, most in small and degraded fragments within private properties (Ribeiro et al. 2009). According to international commitments, Brazil will need to restore 150 Mha of its tropical forest, and predictions have shown that 8 Mha can be restored within farms in the Atlantic Forest, mostly through natural (and assisted) forest regrowth in compliance to the Forest Code Law (Gastauer et al. 2021). Furthermore, the Atlantic Forest is home to 7 of the main cities of Brazil and where several economically traded crops such as coffee, cacao, soybean, sugar cane, oranges, and others are produced. Therefore, the Atlantic Forest is in great demand to balance between agricultural production and the environmental benefits that can be drawn from forest conservation (Metzger et al. 2019).

Annual crop yield data

We obtained the annual productivity data of each crop from the Brazilian Institute of Statistic and Geography (IBGE, https://sidra.ibge.gov.br/pesquisa/pam). We gathered information on the 68 crops produced in the region between 1985 until 2015; half of the crops benefit up to some degree from pollination service (soybean, oranges, cotton, coffee, cacao), and the other half is nondependent on pollinators (sugarcane, corn, rice, wheat). We also obtained from the IBGE database the area planted with each crop for each of the municipality within the Atlantic Forest. We only considered municipalities (2400) that were fully embedded with the Atlantic Forest biome according to the Mapbiomas initiative (Mapbiomas.org; Fig 1).

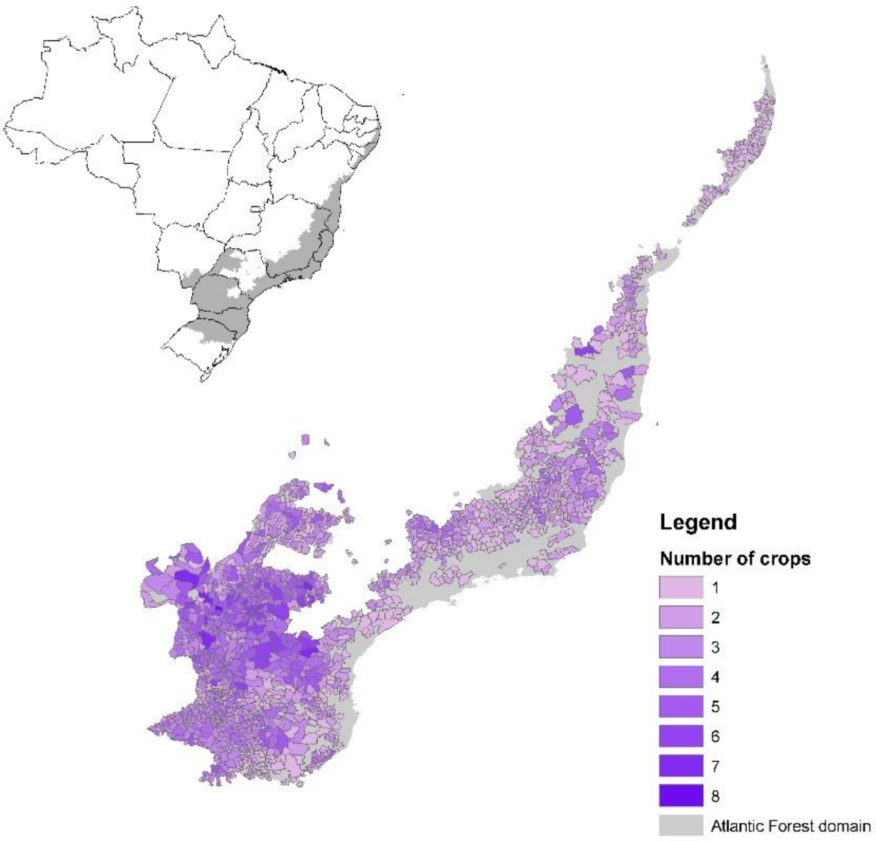


Figure 1: The Atlantic Forest biome and the municipalities for which the data was gathered. In shades of purples the number of crops in each of the municipalities considered.

With the annual productivity data, we calculated the coefficient of variation (CV) for each crop by dividing the standard deviation values by the mean yield (kg/ha) for each crop at each municipality across time (Hautier et al. 2015; García-Palacios et al. 2018). This measure of crop stability allows to compare the relative variability irrespectively of the mean production, which varies between municipalities of each crop, and varies significantly among crops (Knapp et al. 2018). The CV represents the inverse of how stable the productivity is across time in each municipality. For instance, the productivity is more stable for crop that have CV values closer to 0.

We only considered crops with more than 1000 hectares planted per municipality for at least five consecutive years and that occurred in at least 30 municipalities. The filtering process resulted in 1721 municipalities and 16 crops, with half of them depending to some degree on pollinators (Table 1). The number of crops per municipality varied, with some crops present in most municipalities (e.g., corn) and some restricted to a small region (e.g., cacao, cotton, or coconut) (see Table 1 & Fig 1).

Table 1: Crop species considered for the spatial analysis, along their scientific name, the number of municipalities in which they have more than 1000 ha planted and their pollinator dependency. The pollination dependency classification was drawn from (Giannini et al. 2015; Wolowski et al. 2019), *except for the *Phaseolus vulgaris* which was recently described to modestly benefit from pollination (Ramos et al. 2018).

Crop	Scientific name	Number of municipalities	Pollinator dependency
Cacao	*Theobroma cacao*	59	Essential
Coffee	*Coffea canephora*	47	Essential
Coconut	*Cocos nucifera*	13	Modest
Coffee	*Coffea arabica*	274	Modest
Cotton	*Gossypium hirsutum*	84	Modest
Orange	*Citrus sinensis*	59	Modest
Soybean	*Glycine max*	625	Modest
Bean	*Phaseolus vulgaris*	369	Modest*
Sugarcane	*Saccharum*	432	None
Banana	*Musa*	61	None
Cassava	*Manihot esculenta*	110	None
Corn	*Zea mays*	1196	None
Rice	*Oryza sativa*	107	None
Tobacco	*Nicotiana tabacum*	83	None
Wheat	*Triticum spp.*	380	None
Oats	*Avena sativa*	37	None

Landscape composition and configuration

We divided the area destined for each crop per municipality by the municipality's area to calculate the percentage of land use of each crop, using the data from the IBGE. The crop cover is associated to the area demanding ecosystem services (Metzger et al. 2021). Although only half of the crops benefit from pollination, all crops benefit from pest control or climate regulation. For the supply areas, we calculated the percentage of Atlantic Forest of the municipality using the mapbiomas.org initiative (collection 4.1), which provides annual data of forest cover. We calculate the average crop area and forest cover annually, from 1985 until 2015, covering a period of 31 years. Additionally, we calculated two forest configuration metrics using the *SpatialEco* package in R for each year of the time series (forest patch density and edge density per municipality). For both metrics, we used the municipality's delimitation from the IBGE dataset. We also considered the diversity of agricultural crops, by calculating the Shannon diversity index considering the area and richness of crops in each municipality (computing all 68 crops produced in the regions). Higher values would be associated to higher crop diversity or more heterogeneous agricultural landscapes.

Pollination service demand

For each crop, we attributed a pollinator dependency index based upon national review for crop dependency, which varied between 0 (for nondependent crop) to 1 for crops with production fully dependent on pollinators (Giannini et al. 2015; Wolowski et al. 2019). For the municipalities producing coffee, we considered the area destined of each coffee species produced to calculate the pollinator dependency index, as each coffee species has a different pollinator demand (González-Chaves et al. 2022) and some municipalities (35) produce both crops.

Climatic ad soil variables

Temperature, humidity, and soil condition are known to affect crop yields (DaMatta 2004; Rockström et al. 2009). Therefore, to assess the relative impact of forest cover on crop yields stability, we gathered 19 bioclimatic variables annually from the CHELSA 30 seconds resolution database (Karger et al. 2017). We extracted the mean values exclusively for the agricultural fields categories of the *Mapbiomas* initiative maps, which aggregates all type of agricultural land uses without differentiating between crop types. Given the high correlation among the climatic variables we further calculated the annual precipitation variability, which is commonly used to predict future changes in crop production (Porter and Semenov 2005). Regarding soil properties, we obtained soil quality data from FAO (https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/), which classifies soil accordingly to their nutrient availability in 7 categories from highly available (1) up to water bodies (7). We considered a continuous variables and then extracted mean values for the agricultural fields at the municipality level, as was done for climatic variables.

Statistical Analysis

We used linear mixed models (LMM) with normal distribution for the temporal variability coefficient (CV) of crop yield and we ran model comparisons to select the best-fixed structure among the landscape, climatic and soil variables. First, we tested whether the spatial location of municipalities contributed significantly to crop yield stability by incorporating every municipality's centroid coordinate in the models using DHARMa packages in R. We then compared the best spatial autocorrelation structure and included a rational quadratic term associating the coordinates of the centroids of the municipalities (Pinheiro and Bates 2000). In all models we specified the crop associated to each CV values by including crop as a random variable, which allows the intercept to vary for each crop, and we also included the nested random structure between the crops and the geopolitical mesoregion of the municipality were each crop is produced. This nested structure is essential because there is an inherent variation between crops and between the socioeconomic and agronomic practices that affect crop productivity across the central producing regions within each state of Brazil (Bliska et al., 2009).

As we had several highly correlated landscape metrics (Fig S1), to define the full model we initially compared which forest landscape metric was better at predicting crop yield temporal variability, by creating three full models, each with one of the forest metrics: (i) forest cover, (ii) forest edge density and (iii) forest patch density (Table S1). The full model included two-way interactions between the chosen forest metric and the crop related landscape metrics, plus the additive effect of environmental variables (soil, precipitation, and temperature). The crop metrics for which two-way interactions were considered are: (i) crop pollinator dependency, (ii) the crop Shannon diversity index, and (iii) crop cover, as interactions with soil nutrient availability and precipitation variability would lead to multicollinearity issues. We compared all combinations using a multi-model inference approach based on information theory using Akaike Criterion Information (AIC)(Burnham et al., 2002). Moreover, we also considered a quadratic term for the forest metrics variables to consider the non-linear relationship between forest cover and biodiversity which also affects crop productivity (Banks-Leite et al. 2014; Boesing et al. 2018a; González-Chaves et al. 2022). The full model was constructed after checking for correlation among the variables to avoid multicollinearity, excluding variables with Spearman correlation coefficient higher than 0.6, or if the variable presented Variance Inflation Factor (VIF) higher than three, using the *vif* function of the *car packages* on the full model constructed.

We compared all possible combinations derived from the full model, including a model without fixed effects (null model), using a multi-model inference approach based on information theory using Akaike Criterion Information (AIC) (Burnham et al., 2002). The best models (all with ΔAIC <2) were selected from comparing all the possible combinations of the full model (Fig. 2) using the "dredge" function of the MuMIn package in R (Barton, 2018). For the best-fitting models (i.e., lowest AIC), we tested the Gaussian and homoscedasticity assumptions for the standardized residuals (Fig. S2). To calculate each variable's importance at predicting crop yield temporal variability, we summed the model weights of all models in which explanatory variable was present (Barton, 2015). Variable strength of effect we obtained from the standardized coefficient of the best selected models.

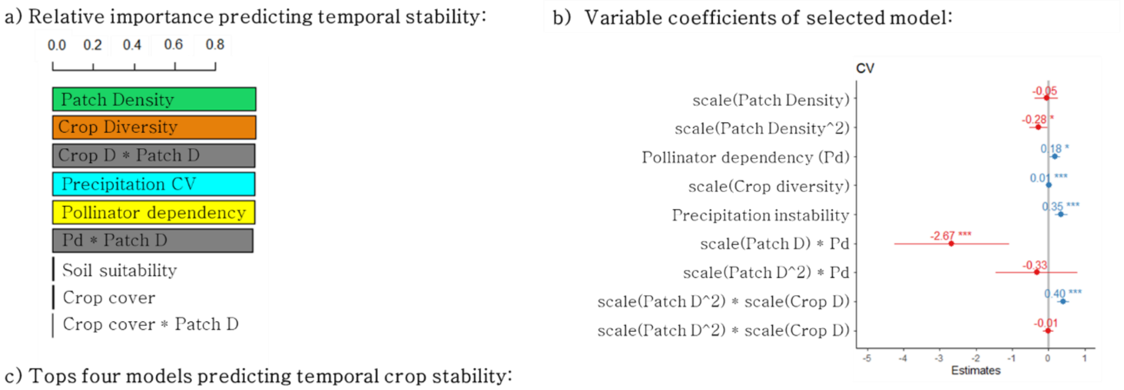
Additionally, to see the how each crop responded to changes in forest patch density (the chosen forest variable; Table S1), we created an extra model based on the variables from the best model selected and allow for patch density slope to vary for each crop species, by incorporating patch density metric in the random structure of the new model. For this additional model we eliminated the pollinator dependency index as we were interested in evaluating the individual response of each crop (Fig. 4).

Results

Our model explained 69% of the variability in crops yields temporal stability across the Atlantic Forest biome and included pollinator dependency, crop diversity, forest patch density and precipitation variability. We found that landscape variables were as relevant as precipitation variability affecting crop stability (Fig 2), and forest patch density much better at predicting yields stability than forest cover or forest edge density (Table S1).

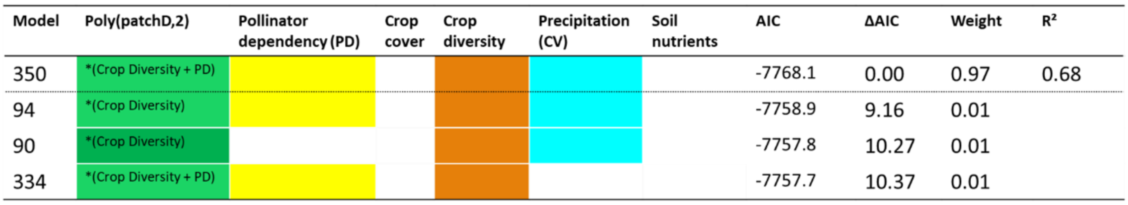
The effect of forest patch density was stronger for highly dependent crop and mildly benefitted crop nondependent on pollinators (Fig 4).

Yield temporal stability of crops highly dependent on pollinator nearly doubles with increasing forest patch density from 1 to 3 forest patches per hectare (Fig. 4). For forest patch density to be high, landscapes most have between 10 – 40 % of forest cover within the municipalities, with highest peaks around 20% (Fig S1). Nonetheless, all crops benefitted to some degree on forest occurrence, although it was very variable among crops. The greatest effect was present for crop that benefit from crop pollination (Fig 3a), like cacao, coffee arabica and oranges (Fig 4).


a) Relative importance predicting temporal stability:

b) Variable coefficients of selected model:

c) Tops four models predicting temporal crop stability:



Model	Poly(patchD,2)	Pollinator dependency (PD)	Crop cover	Crop diversity	Precipitation (CV)	Soil nutrients	AIC	ΔAIC	Weight	R²
350	🟩 *(Crop Diversity + PD)	🟨		🟧	🟦		-7768.1	0.00	0.97	0.68
94	🟩 *(Crop Diversity)	🟨		🟧	🟦		-7758.9	9.16	0.01	
90	🟩 *(Crop Diversity)			🟧	🟦		-7757.8	10.27	0.01	
334	🟩 *(Crop Diversity + PD)	🟨		🟧			-7757.7	10.37	0.01	

Figure 2: a) Relative importance of each variable or the interaction terms (in grey), according to the weight of the model that each variable; b) the effect size of the variables at predicting coffee yield. c) The first four best models after applying the dredge function to the full model which includes all terms presented in (a). Forest Patch density "2" represent the second-degree polynomic form. The colors in (a) and (c) represent the factors that each variable is associated to and are present when the variable is included in the model. Green for metrics related to forest. Brown represents landscape variables associated to crop management and yellow the crop demand for pollination service. Blue is related to soil and climatic variables. Grey represents the relative importance of the interaction terms. The Crop Diversity refers to the Shannon Index considering the area of each crop per municipality; Patch D, refers to forest patch density and Pd refers to pollinator dependency. Full model: lme(CV ~ poly(patchD.s,2)*(P_dependency+div_crop_area.s+log(crop_cover))+soil.s+prepCV, random=list(~1|crop, ~1|mesoregion), correlation=corRatio(form~x+y), data)

Increasing forest patch density favored annual crop stability, but this effect was stronger in municipalities with lower diversity of crops planted (Fig 3b), as municipalities with higher crop diversity had lower temporal stability. Moreover, precipitation instability across the years was associated to higher instability of the crop yields and was the only climatic variable affecting temporal yield stability, as soil suitability had no influence on crop yield stability (Fig 2). Crop cover also did not influence crop yield temporal stability.

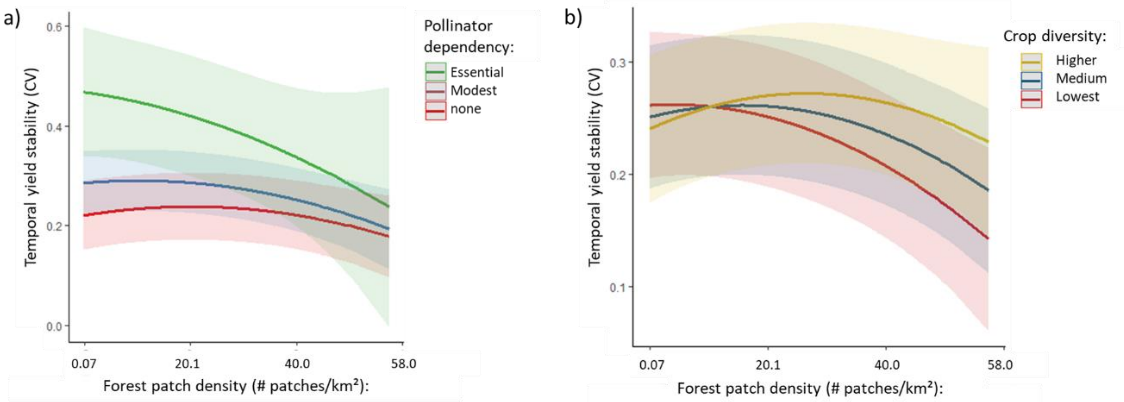


Figure 3: Forest patch density effect on crop yield stability, depending on a) crop pollinator dependency, b) crop diversity (Shannon diversity index), categorized according to the mean value and the 1st and third quartile.

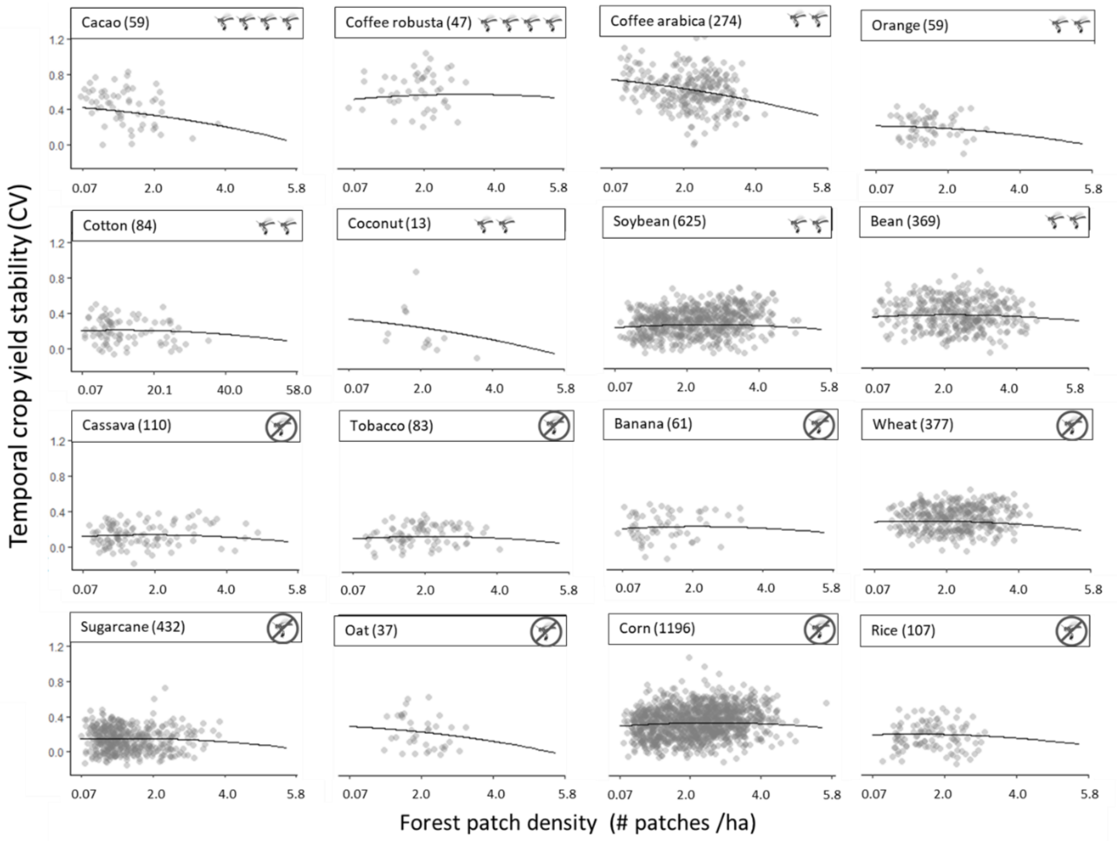


Figure 4: The effect of forest cover on each of the crop species considered. The common name of each crop species is specified above each plot along with the number of municipalities, and bees design representing the level of animal pollinator dependency, the scientific name of each crop is specified in Table 1.

Discussion

Conciliating biodiversity conservation within agricultural landscapes has much relied on reducing agronomic inputs associated with negative impact on biodiversity (such as fertilizers and pesticides) as well as reducing habitat loss and avoiding landscape simplification (Bommarco et al. 2013; Garibaldi et al. 2019). Beyond these initiatives, the paradigm shift towards incorporating pollination service and pest regulation as agronomic inputs, which can be spatially managed, allows to search for landscape configuration synergies that benefit biodiversity conservation and contribute to crop production(Kremen and Merenlender 2018; Egan et al. 2020). Here, we show that landscape composition and configuration can strongly contribute to stabilizing crops yield over the years. Moreover, we point out potential synergies between biodiversity conservation and crop stability, since landscape characteristics that benefit biodiversity are also those that contribute to crop stability.

Forest patch density is positively correlated with crop temporal stability, which is highest in landscape with intermediate levels of forest (around 20%; Figure S1). Although we cannot establish casual relationships, the most reasonable explanatory hypothesis for this relationship is that landscapes with greater forest cover are those with greater biodiversity (Fahrig 2003, 2013), and thus the greatest potential to supply mobile organisms that provide pollination and pest control services (Winfree and Kremen 2009; Winfree et al. 2018). Landscapes with less than 20% of forest cover hold biodiversity impoverished biological communities compared with landscapes above such biodiversity extinction threshold (Lima and Mariano-Neto 2014; Banks-Leite et al. 2014). Moreover, landscape with forest cover above the 20% threshold also favors biodiversity spillover that provides ecosystem services such as pest control and crop pollination (Boesing et al. 2018b; González-Chaves et al. 2022). Considering that forest cover at the municipality level is highly related to the forest cover in the surrounding coffee fields (González-Chaves et al. 2022), it is expected that forest amount and configuration at the municipality level reflects what is occurring in the surroundings of crop fields. A lack of forest fragments would result in lower species redundancy/complementary needed to buffer climatic variability and guarantee service provision (Winfree et al. 2007; Hoehn et al. 2008; Brittain et al. 2013), hence a lower supply of pest enemies and pollinators from small, fragmented forest might be leading to lower crop yields (Rusch et al. 2016; Tscharntke et al. 2016).

As landscape become dominated by cultivated lands interaction networks become simplified (Hagen and Kraemer 2010; Moreira et al. 2015), threatening the stability of ecosystem functions (Montoya et al. 2019; McWilliams et al. 2019; Hünicken et al. 2021), which should alter the temporal stability of ecosystem service provision (Boesing et al. 2020). In the landscape that sustain community integrity, the spatial arrangement of the land use types can affect biodiversity and thus ecosystem service provision (Mitchell et al. 2015; Haddad et al. 2015; Sirami et al. 2019; Dainese et al. 2019; Metzger et al. 2021). Forest fragmentation benefits the interspersion of supply and demand areas which have been shown to contribute to crop yield, by decreasing the distance between supply and demand areas (Karp et al. 2013; Mitchell et al. 2015; González-Chaves et al. 2020). Precisely, as we found, landscapes with more fragmented forest were more stable across the years than those municipalities with lower forest patch density. We would expect landscape effect on pollinators are mediating this relationship, given that this effect was higher for crops that fully depend on pollinators, a feature known to be associated to higher temporal instability (Deguines et al., 2014; Garibaldi et al., 2011). Thus, when considering crop productivity temporal stability, conserving forest fragments within the municipalities is crucial to ensure pollinator functional complementarity if we want landscapes to constantly contribute to crop yield.

In human-dominated landscapes, such as most of the Atlantic Forest biome, agriculture is the main land use, and the amount and spatial arrangement of such land use is expected to influence the way pollinators and biodiversity would be contributing to crop yield (Avelino et al. 2012; Kebede et al. 2019; Redhead et al. 2020). Although we found that municipalities specialized in one crop were more stable, for stability to be highest forest patchiness needs to be maintained in the municipality. Oversimplified landscapes, with very low forest cover (<10%), are less likely to contribute with the stability of crop yields over time, reinforcing the detrimental effect of landscape simplification on crop stability (Dainese et al. 2019), which is probably related to a less diverse community of pollinators and pest enemies.

As expected, yields were more stable in where precipitation was less variable between years. What is noteworthy is that they are equally relevant than landscape features predicting crop stability. This represents an opportunity for coming years, as crop production gains a central role for a more sustainable future (Rockström et al. 2021). As climate change is expected to alter both biodiversity distribution and crop suitability (Giannini et al. 2017; Imbach et al. 2017), maintaining and restoring forest that allow biodiversity migration across the regions will thus be crucial for forest to continue to contribute with crop temporal stability.

Animal management is increasingly being promoted as agricultural input, within strategies such as Integrated Pest and Pollination Managements (Egan et al. 2020; Merle et al. 2022). Nonetheless, landscape management has maintained a secondary role regarding the ways in which ecological intensification can be achieved (Stanturf et al. 2019). Forests have the potential of providing a wide variety of benefits to society, from climate change mitigation to harvestable resources, as well as helping to safeguard biodiversity (Hipólito et al. 2019; Brauman et al. 2020; Melo et al. 2021). Our work further contributes to recognize the central role of forest conservation in society well-being by identifying where and how forest is already contributing to temporal crop yield stability of one of the main agricultural regions of the world. Furthermore, we provide evidence of the importance for agricultural production of maintaining forest fragments near or adjacent to crops, in a more fragmented configuration, where interspersion with crop fields is stimulated. These landscape configurations should guide forest restoration efforts not only to achieve conservation goals, but also to combine agricultural goals with biodiversity conservation.

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Supplementary Information

Table S1: Model selection to compare the performance of forest metrics at predicting crop temporal yield stability, using linear mixed model, we incorporated in all models the nested random structure in which each crop is first compared with the municipalities of the mesoregions where it is produced. The forest metric with the lowest Akaike criterion was considered for subsequent analysis.

Yield stability	Forest Cover (FC)	Edge density (ED)	Patch density (PD)	Precipitation (CV)	Random variables	AIC	ΔAIC	Weight
CV ~			-0.4**PD**-0.3**PD**^{2}	0.37	~1|crop/region	-7744.2	0.00	0.97
CV ~		-0.3**ED**-0.1**ED**^{2}		0.38	~1|crop/region	-7736.4	7.76	0.02
CV ~	-0.2**FC**-0.1**FC**^{2}			0.37	~1|crop/region	-7734.0	10.37	0.01

Figures

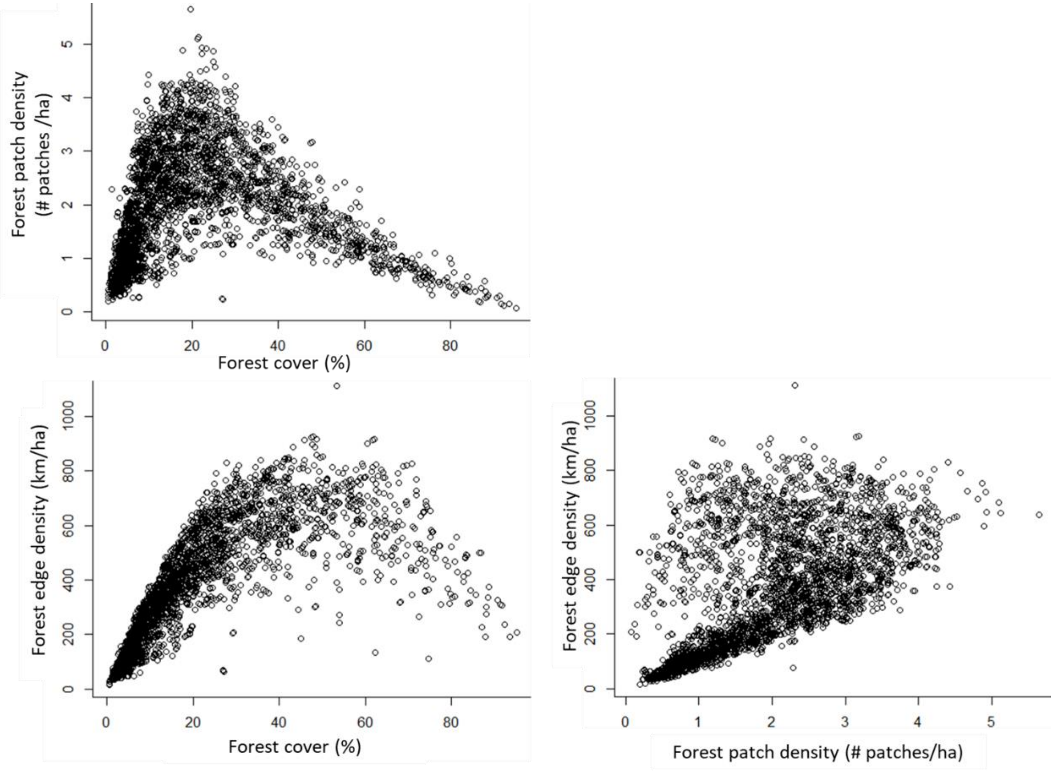

Figure S1: Relationship between the three forest landscape metrics considered.

a)
```
Selected CV model <-lme(CV~poly(patch.s,2)*(P_dependency+div_area.s)+ prepCV,
                    random=list(~1|crop,~1|meso), correlation=corRatio(form=~x+y),  data=spatial)
```

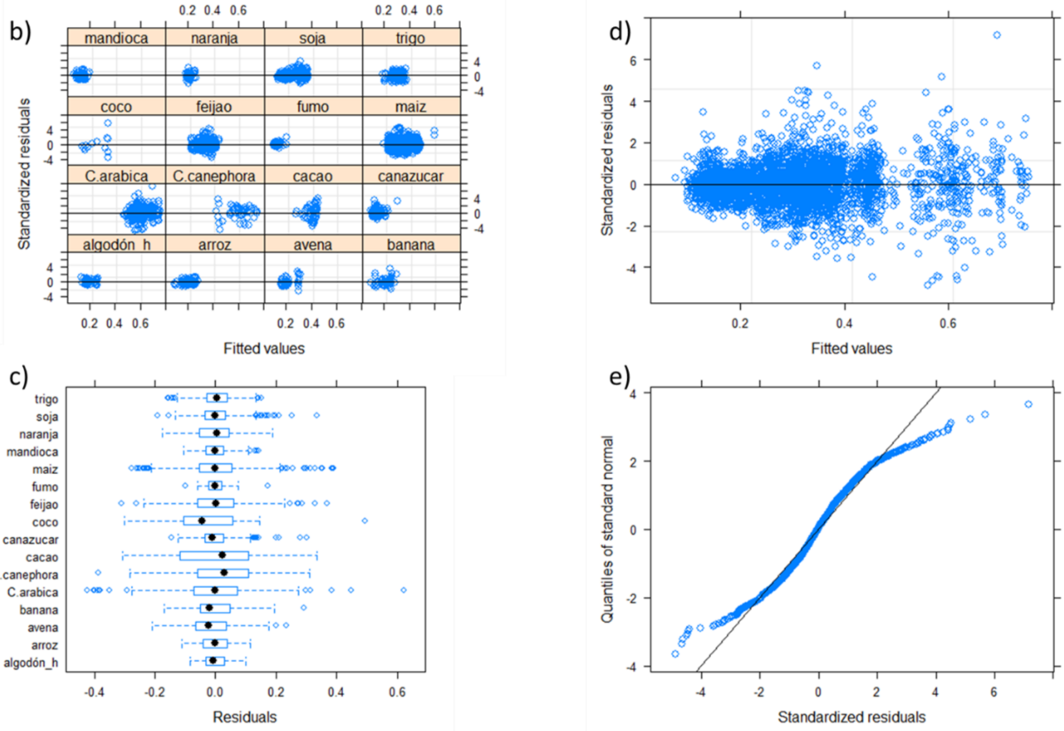

Figure S2: The Residual distribution (a & b), against fitted values, for the d) whole model and for b) each specific crop, and e) QQ plot for the selected model presented in the top (a).

Conclusion

Brazil is one of the largest crop producers in the world, and tension between the agricultural lobby and conservation continues to exist (Metzger et al., 2019). This work addressed the spatial and temporal contribution of the Atlantic Forest to agricultural production along a gradient of climatic and soil characteristics at an unprecedented scale. With this work, we intended to identify where synergies between conservation and agriculture occur and provide evidence that forest conservation has underpinned the region's economic development (Sparovek et al., 2012). We demonstrated that the municipalities with the highest coffee productivity preserve more than 20% of the forest in the coffee fields' surroundings and provided evidence that pollinators are central to such synergies (Chapter 1). Moreover, we show the importance of conserving mature forests to guarantee ecosystem service provision and indicate where forest regrowth has contributed to enhancing coffee yields (Chapter 2). Finally, we showed that the Atlantic Forest helps stabilize crop yield across the years. In municipalities with lots of interspersion between crop fields and forests, landscape configuration helps with this crop yield stability (Chapter 3).

The first chapter's results emphasize landscape management's vital role in agricultural planning. We found that forest fragments were more relevant for predicting coffee yields than management practices like pesticide use, irrigation, and organic management. Moreover, the positive effect of forest conservation on yields was consistent across the climatic and soil conditions of the 610 municipalities considered. Over the past years, efforts have been made to consider pollination service as an agronomic input that needs to be managed, which was often lacking in the agricultural literature (Garibaldi et al., 2020; Ratto et al., 2022). We have shown that forest conservation underpins ecosystem services provision at an unprecedented scale by combining regional maps and governmental databases. Although extensive literature exists on the benefits of natural habitat conservation on biodiversity and ecosystem services, our methodological approach showed that forest conservation is crucial for 20% of the world's coffee production (González-Chaves et al., 2022).

The moment this work is being completed cannot be more accurate. According to the United Nations, we are in the decade of forest restoration, and pathways to implement and achieve restoration goals are needed more than ever. Considering that much of the restoration will have to occur in private lands, providing guidance, with farmers' participation, on where restoration would contribute to agricultural production and stability is crucial (Erbaugh et al., 2020). Our second chapter provides some insights into this increasing demand. Apart from reinforcing the importance of conserving mature forest fragments (Barlow et al., 2007), we suggest there is a delay in regenerating forest fragments to provide ecosystem services. However, young regenerating forest fragments can enhance the landscape's ability to provide ecosystem services, probably by facilitating the movement of pollinators through the landscape and providing additional floral resources, which would enhance pollinator populations and increase crop productivity.

Temporal dynamics are among the less studied topics in the ecosystem services literature (Boesing et al., 2020), probably by the difficulty of getting long-term data. We have tackled this limitation by integrating temporal national databases (from the Brazilian Institute of Geography and Statistics - IBGE) with recently available annual land use maps (Mapbiomas.org). Previous works have shown that the productivity of crops highly dependent on pollinators is the most unstable from year to year (Garibaldi et al., 2011). Here we showed that forests in the landscape considerably reduce this instability, making them as stable as crops that do not depend on animal pollinators. Furthermore, we showed that the spatial arrangement of forest fragments is the most relevant for contributing to crop yield temporal stability with higher forest fragmentation in landscapes with at least 20% forest cover being a convenient design for multiple benefits. Preserving higher forest patch densities (e.g., higher forest fragmentation) and designing crop fields closer to the forest to facilitate the spillover of pollinators towards crops fields can enhance spatiotemporal stability. Considering that the demand for pollinated crops is rising (Aizen et al., 2019) and the landscape is becoming more simplified, securing forests within working landscapes is crucial to guarantee food sovereignty for years.

The present work aims to subsidize public policies and market programs to enhance ecosystem services in agricultural landscapes. We could identify where the forest is already contributing to stabilizing crop productivity spatially and temporally and where restoration would be needed to secure future crop production. Our analyses also have direct implications for farmers as we provide landscape management guidance at small, local scales on how agricultural production can benefit from the presence of the forest. Moreover, as traceability becomes the central tool for sustainable food chain systems, our work provides the methodological basis to detect crop production benefits from pollination services (Gardner et al., 2019).

It is noteworthy that the interpretations and mechanisms from the correlations found are all based on field studies seeking to understand landscape-biodiversity-ecosystem services relationships at the landscape (*see* González-Chaves et al., 2020; see also interface project http://ecologia.ib.usp.br/projetointerface/). Thus, as we hope to incentivize big datasets to monitor restoration, agricultural, and conservation goals, we would like to remind the importance of field experiments to backup future regional assessments.

A few arthropod species are individually managed to provide services, like pollination and pest control, regardless of wild pollinators present in the landscape, raising concern about ecosystems service's ability to conserve biodiversity (Kleijn et al., 2015). We strongly recommend managing ecosystem service by enhancing ecosystem resilience through landscape planning for biodiversity conservation (Senapathi et al., 2015). We have used governmental databases and corroborated that the landscape structure of a biodiversity hotspot can be regionally planned to guarantee native vegetation conservation and agricultural goals.

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Abstract

Agriculture is the most dominant land use system across the globe, which continues to put pressure on native ecosystems. Understanding where biodiversity conservation contributes to agricultural production is crucial to engage farmers in conservation initiatives and to define areas which would benefit from ecosystem restoration. Field experiments across the globe suggest that maintaining natural habitats in the agricultural landscapes enhances crop yields through services like pollination and pest control. We aim to understand whether the spatial relationship is maintained across large regions and assessed the temporal variations of the importance of landscape features at influencing agricultural productivity. Using available data set on crop productivity from governmental organizations and non-governmental initiatives we gathered data on crop locations and the Atlantic Forest remains and demonstrated that the presence of tropical forest is positively associated agricultural yields across a climatic and soil characteristic gradient. We further showed that forest cover was more relevant at predicting coffee yields than agricultural management practices, like irrigation, pesticide use, organic manure among others. Moreover, the effects of forest cover are higher for municipalities producing coffee species which are highly dependent of animal pollination. On the second chapter we assessed the importance of forest fragments age at predicting coffee yields, and corroborate the importance of conserving mature forest fragments, as young regenerating fragments can only enhance coffee yields when municipalities are above the biodiversity extinction threshold. Finally, we explored the role of forest conservation on temporal stability of agricultural productivity by analyzing the 16 main crops produced in the whole Atlantic Forest. Not only did we find that the presence of forest fragments in the municipalities is crucial for crop productivity to be more stable across time, but also that a higher interspersion is most favorable for crop that fully dependent on pollinators. Probably such landscape features favor biodiversity spillover from forest fragments towards cropland and help guaranteeing yield enhancement. This work provides regional evidence of the role of landscape features for planning agricultural production and complement biodiversity conservation actions. We further reinforce the role of forest conservation for achieving ecological intensification of agriculture that are so much needed to halt the detrimental effects that agriculture have had on biodiversity. We have shown that synergies between conservation and agriculture exist and have been crucial for one of the largest crops producing regions of the world. We believe our work can help in the development of agricultural and environmental policies, to define economical goals through the enhancement of biodiversity.

Resumo

A agricultura é o uso da terra predominante, que continua a exercer pressão sobre os ecossistemas nativos. Compreender onde a conservação da biodiversidade contribui para a produtividade agrícola é crucial para promover o envolvimento de agricultores nas iniciativas de conservação e para definir áreas que poderiam se beneficiar da restauração. Experimentos de campo ao redeador do mundo sugerem que manter os habitats naturais nas paisagens agrícolas aumenta a produtividade agrícola através da provisão de serviços ecossistêmicos como polinização e controle de pragas. Pretendemos entender se a relação espacial entre biodiversidade e serviços ecossistêmicos é constante ao longo da Mata Atlântica, e avaliar as variações temporais na provisão de serviços ecossistêmicos. Usamos data governamental disponível sobre à produtividade agrícola e mapas de uso da terra, de Organizações não governamentais, da distribuição espacial dos remanescentes de Mata Atlântica para demonstrar o papel da conservação da biodiversidade na produção agrícola. Além disso, demonstramos que a cobertura florestal é fundamental para predizer a produtividade de café, por cima de práticas de manejo como irrigação, uso de pesticidas, manejo orgânico, entre outros. Os efeitos positivos da cobertura florestal foram maiores nos cultivos altamente dependentes de polinizadores. No segundo capítulo, avaliamos a importância de preservar florestas maduras, já que florestas regenerantes jovens só contribuem para a produtividade em municípios acima do limiar de extinção da biodiversidade (>20%). Finalmente no terceiro capítulo, viemos que a estabilidade anual da produtividade agrícola era maior na presença da Mata Atlântica. Os municípios com maior estabilidade temporal da agricultura têm maior densidade de Mata o que acontece principalmente em paisagens com 20% de florestas. Provavelmente a configuração interpresa de floretas e áreas de cultivos está favorecendo o descolamento dos polinizadores há os cultivos, já os cultivos altamente dependentes de polinizadores se-beneficiaram mais da presença das florestas. Esse trabalho provê evidências regionais do papel da estrutura da paisagem para planificar a produção agrícola junto com a conservação da biodiversidade. A conservação da vegetação nativa é central para alcançar a intensificação ecológica da agricultura que tanto precisamos para amenizar os impactos negativos dos sistemas agrícolas na biodiversidade. Temos demonstrado a existência de sinergias entre conservação e agricultura, numa das principais regiões agrícolas do mundo e hotspot da biodiversidade. Acreditamos que nosso trabalho pode ajudar no desenvolvimento de políticas ambientais e agrícolas, para definir metas econômicas baseadas na proteção da biodiversidade.