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Evidence of time-lag in the provision of ecosystem services by tropical regenerating forests to coffee yields

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Adrian David González-Chaves^{1,2,*} , Luísa Gigante Carvalheiro^{3,4} , Pedro Ribero Piffer⁵ , Francisco d'Albertas^{1,6} , Tereza Cristina Giannini⁷ , Blandina Felipe Viana⁸  and Jean Paul Metzger¹ 

¹ Departamento de Ecologia, Instituto de Biociência, Universidade de São Paulo, São Paulo, Brazil

² Department of Life Sciences, Centre for Functional Ecology, University of Coimbra, Coimbra, Portugal

³ Departamento de Ecologia, Universidade Federal de Goiás (UFG), Goiânia, Brazil

⁴ Faculdade de Ciências, Centre for Ecology, Evolution and Environmental Changes (CE3C), Universidade de Lisboa, Lisboa, Portugal

⁵ Columbia University, Ecology, Evolution and Environmental Biology, New York, United States of America

⁶ International Institute for Sustainability, Jardim Botânico, Rio de Janeiro, Brazil

⁷ Instituto Tecnológico Vale Desenvolvimento Sustentável, Belém, Pará, Brazil

⁸ Universidade Federal da Bahia, Salvador, Brazil

* Author to whom any correspondence should be addressed.

E-mail: adgonzalez86@gmail.com

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Supplementary material for this article is available [online](#)

Abstract

Restoration of native tropical forests is crucial for protecting biodiversity and ecosystem functions, such as carbon stock capacity. However, little is known about the contribution of early stages of forest regeneration to crop productivity through the enhancement of ecosystem services, such as crop pollination and pest control. Using data from 610 municipalities along the Brazilian Atlantic Forest (30 m spatial resolution), we evaluated if young regenerating forests (YRFs) (less than 20 years old) are positively associated with coffee yield and whether such a relationship depends on the amount of preserved forest in the surroundings of the coffee fields. We found that regenerating forest alone was not associated with variations in coffee yields. However, the presence of YRF (within a 500 m buffer) was positively related to higher coffee yields when the amount of preserved forest in a 2 km buffer is above a 20% threshold cover. These results further reinforce that regional coffee yields are influenced by changes in biodiversity-mediated ecosystem services, which are explained by the amount of mature forest in the surrounding of coffee fields. We argue that while regenerating fragments may contribute to increased connectivity between remnants of forest fragments and crop fields in landscapes with a minimum amount of forest (20%), older preserved forests (more than 20 years) are essential for sustaining pollinator and pest enemy's populations. These results highlight the potential time lag of at least 20 years of regenerating forests' in contributing to the provision of ecosystem services that affect coffee yields (e.g. pollination and pest control). We emphasize the need to implement public policies that promote ecosystem restoration and ensure the permanence of these new forests over time.

1. Introduction

Most landscapes across the globe have been transformed to varying degrees, with less than 20% considered *wildlands* or without clear human impact (Ellis *et al* 2021). In tropical regions, a large part of the remaining native vegetation is located within private lands (Ribeiro *et al* 2009, Watson and Venter 2017). As agricultural expansion is the main driver

of tropical native vegetation clearance (Gibbs *et al* 2010), identifying strategies to increase agricultural production through biodiversity conservation in working landscapes is crucial to aligning food system transformation with an effective biodiversity conservation strategy (Dos Santos *et al* 2020, Leclère *et al* 2020, Dicks *et al* 2021).

A combined approach to forest and landscape restoration is gaining momentum, aiming to achieve

agricultural production and conservation goals (Brancalion *et al* 2019, Arroyo-Rodríguez *et al* 2020). Many agricultural landscapes have been severely simplified, dedicated to one specific land use or crop type, with little habitat remaining, thus severely limiting their capacity to retain biodiversity, provide ecosystem services and contribute to increasing crop productivity (Benayas *et al* 2009, Garibaldi *et al* 2016, Dainese *et al* 2019, Arroyo-Rodríguez *et al* 2020). In such case, native vegetation regeneration is among the most cost-effective restoration management action and is considered the cornerstone for achieving forest restoration goals (Crouzeilles *et al* 2020). Despite the growing evidence that regenerating forests partially recover their biodiversity and the capacity to stock carbon (Barlow *et al* 2007, Poorter *et al* 2016, 2021, Rozendaal *et al* 2019), the evidence regarding their capacity to contribute to higher agricultural yields through the enhancement of ecosystem services is still scarce.

To maximize potential benefits, most restoration initiatives should occur within agricultural landscapes (Erbaugh *et al* 2020), especially in tropical regions (Pashkevich *et al* 2022). For instance, the Brazilian Atlantic Forest is a restoration ‘hotspot’ (Rezende *et al* 2018), which was historically reduced to a small fraction of its original extension (Boddey *et al* 2003, Joly *et al* 2014). Currently, the legislation requires farmers to restore or adopt some compensation mechanism when their farms have less than 20% of forest cover (de Mello *et al* 2021a, 2021b). However, trade-offs between agricultural production and conservation might be unavoidable when farmers’ interests are not aligned with ecosystem conservation goals (Metzger *et al* 2019). Therefore, assessing whether regenerating forests will result in agricultural 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 stimulate restoration and attenuate ‘production/conservation’ trade-offs, it is also crucial to understand the ecological time-lags associated with habitat restoration (Lira *et al* 2019, le Provost *et al* 2020). Biodiversity takes time to respond to changes in habitat amount; hence ecosystem functioning (and associated service provision) is likely to have a delayed response to land-use changes (Lira *et al* 2019, Poorter *et al* 2021). For instance, previous studies have shown that secondary forests take almost 20 years to partially recover their biodiversity levels and their ability to stock carbon and improve soil properties (Gageler *et al* 2014, Poorter *et al* 2016, 2021, d’Albertas *et al* 2018). 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, Mota *et al* 2022). Whether young regenerating forests (YRFs) can help explain crop productivity through the provision of ecosystem

services, such as crop pollination and pest control, remains to be tested.

For pollinator-dependent crop such as coffee (Klein *et al* 2003b, 2007), increasing the diversity of pollinators have the potential to increase crop productivity (Klein *et al* 2003a, Saturni *et al* 2016, González-Chaves *et al* 2020). The main coffee pollinators are native bees’ species that depend on tree trunks for nesting resources (Silva *et al* 2013, González-Chaves *et al* 2020, Montagnana *et al* 2021). For this reason, we expect older forests to be directly associated with higher yields as the mature forests can harbor more diverse bee communities (Sobreiro *et al* 2021), and pollination has been shown to be more relevant at predicting yields than other abiotic (precipitation or altitude) and management and socio-economic variables (González-Chaves *et al* 2022). Furthermore, considering that species’ ability to colonize regenerating environments and spillover to agricultural fields is mediated by the habitat amount (Crouzeilles *et al* 2020, Metzger *et al* 2021, Boesing *et al* 2022, González-Chaves *et al* 2022), we also expect that regenerating forests capacity to contribute with ecosystem services provision will depend on the amount of more mature forest in the landscape (i.e. >20 years).

2. Methods

2.1. Study area and focal crop species

We focused our analysis on coffee production areas within the Brazilian Atlantic Forest, where most Brazilian coffee is produced representing 20% of all the worlds’ coffee. The Atlantic Forest region produces the two most traded coffee species (*Coffea arabica* and *C. canephora*) that differ in their dependence on pollinators and influences the benefits that coffee yields draw from forests (González-Chaves *et al* 2022). Sun coffee production system benefits from pollination and pest control services, which are both associated to local and regional forest cover (Saturni *et al* 2016, Chain-Guadarrama *et al* 2019, Medeiros *et al* 2019, González-Chaves *et al* 2020, González-Chaves *et al* 2022). Moreover, the Atlantic Forest region has steadily increased in forest cover, mostly associated with second-growth regeneration (Rosa *et al* 2021, figure S2). Therefore, given that regional forest cover has been shown to be more relevant in predicting coffee yields than local management practices, abiotic characteristic, and socio-economic variables (González-Chaves *et al* 2022), here we focused our analysis on testing whether forest age is relevant in predicting regional coffee yields.

2.2. Coffee production and spatial distribution

We collected data on crop productivity from the Brazilian Institute of Geography and Statistics (IBGE, www.ibge.gov.br/), corresponding to 1.3 Mha

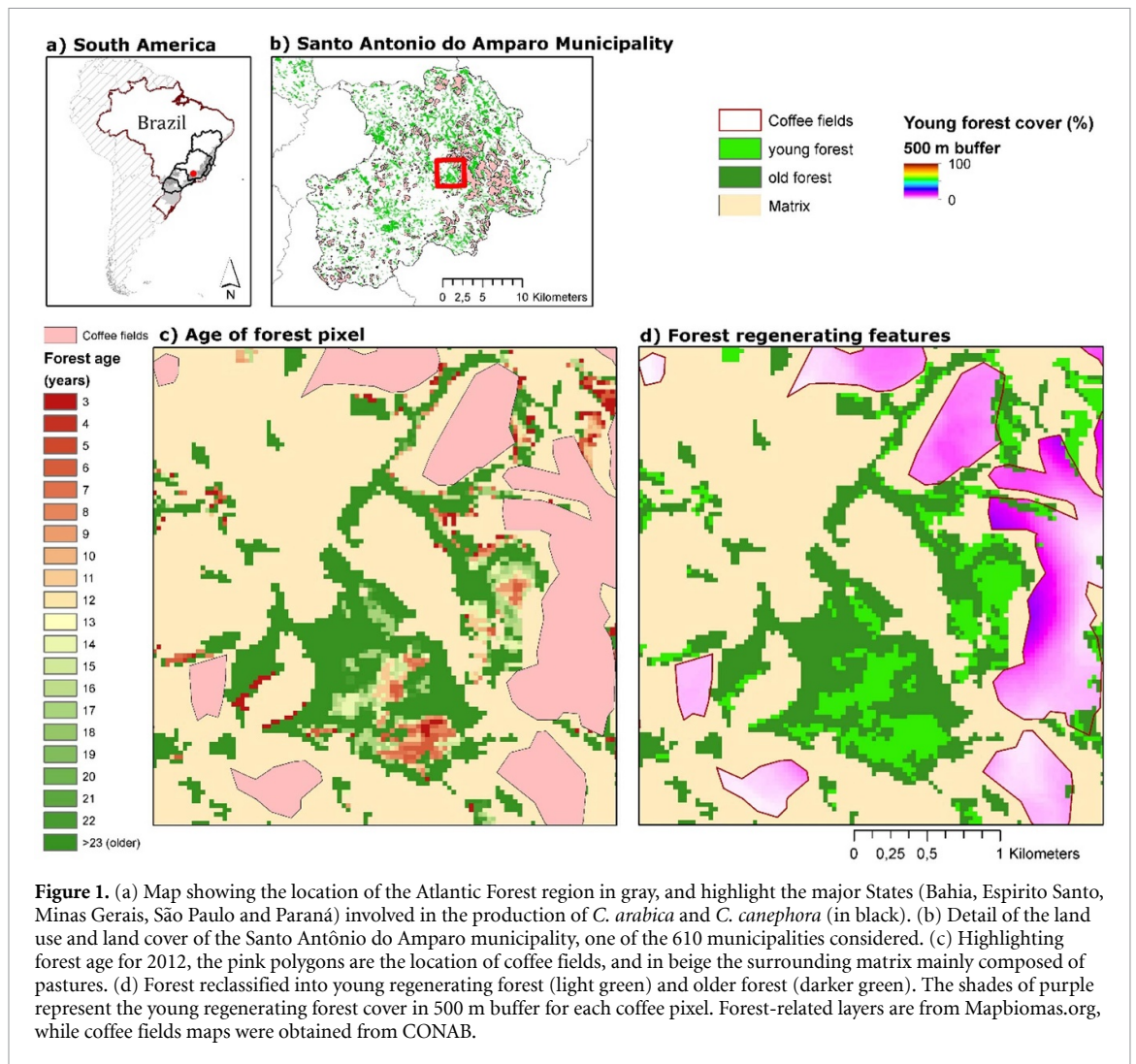


Figure 1. (a) Map showing the location of the Atlantic Forest region in gray, and highlight the major States (Bahia, Espírito Santo, Minas Gerais, São Paulo and Paraná) involved in the production of *C. arabica* and *C. canephora* (in black). (b) Detail of the land use and land cover of the Santo Antônio do Amparo municipality, one of the 610 municipalities considered. (c) Highlighting forest age for 2012, the pink polygons are the location of coffee fields, and in beige the surrounding matrix mainly composed of pastures. (d) Forest reclassified 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 layers are from Mapbiomas.org, while coffee fields maps were obtained from CONAB.

destined for 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 area planted with each coffee species planted in the municipalities using a pollinator demand index (PD), which considers the benefits drawn from animal pollination (either 30% or 100%) weighted by the area destined to each species (Klein *et al* 2003a, González-Chaves *et al* 2022). The index varies between 0.3 and 1, whether the municipalities produce exclusively *C. arabica* or *C. canephora* respectively. Intermediate values will be obtained when a combination of both species is found in the same municipality. We calculated the mean coffee yields (60 kg bags per hectare) from three consecutive years for each municipality, according 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, www.conab.gov.br/) who shared the data.

2.3. 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 available of coffee field maps (figure 1, table S1). First, we mapped native forest cover since 1985 (older forest), which is the first year of the Mapbiomas time series. We then identified regenerating forests as forest pixels classified either as cropland or pasture for at least 3 years and remained as forest until the correspondent year from the coffee field reference map, considering a minimum of 3 years as forest (Rosa *et al* 2021). Forest regenerating age was the number of years between the regeneration event (the year a pixel was classified as regenerating forest) and the year of the coffee reference map for each state (Piffer *et al* 2022b).

Regenerated forests are still a small fraction of the forest cover in the regions, but they are present in all municipalities. Most forests in the region have >30 years (80.6%; Rosa *et al* 2021), and the mean age of the forest regenerating after 1989 is around

14 years (Piffer *et al* 2022b). Thus, we subdivided the Atlantic Forest fragments from our study region into two age groups: those with less than 20 years of age YRF and those with 20 or more years, named as older forest (see figure 1(d)). The 20 years age threshold was established due to limitations in our data, as the Mapbiomas time series started in 1985 and the oldest coffee map available for Espírito 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 forests 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). Our final maps contained three forest features: (a) young regenerating forest (YRF) under 20 years of age, (b) forest with more than 20 years of age, and (c) overall forest cover disregarding forest age.

We calculated the percentage of YRF and older forest surrounding coffee fields by using a moving window analysis for each coffee pixel at 2 km and 500 m buffer radius, with the raster package (Hijmans 2018) using R 4.1 (R Development Core Team 2020). The spatial scales were considered based on studies showing that above and below-ground biodiversity responds to those scales in human-modified landscapes (le Provost *et al* 2021), as well as pollination and pest control services benefitting coffee production (Saturni *et al* 2016, Librán-Embíd *et al* 2017, Aristizábal and Metzger 2019, González-Chaves *et al* 2020). Moreover, regeneration is also known to respond to the landscape at similar scales (Crouzeilles and Curran 2016, Piffer *et al* 2022c).

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 forest features at the three different scales (500 m, 2 km, and municipality level).

2.4. Statistical analysis

To evaluate and compare the effect of forests with different ages on coffee yield, we considered all variables identified in a previous study (González-Chaves *et al* 2022) as relevant predictors of coffee yields: local management practices, climatic features, soil characteristics, and topography. However, we created alternative models using the three different forest features: (a) old (>20 years old) forest cover, (b) just young regenerating forest cover (YRF, <20 years old), in

addition (c) to the former model with the total forest cover. We also considered the three different spatial scales (500 m, 2 km, and municipality level), leading to a total of 9 alternative models (table 1). Additionally, we tested if the amount of YRF modulates the effect of overall forest cover or older forest cover; thus, we included three more models (one for each spatial scale) with an interaction term between YRFs and older forests (table 2). Moreover, to test if the amount of YRF modulated the effects on any of the known previous fixed effect variables described to predict coffee yields, we created a full model with all possible two-way interactions between YRF and the rest of the variables (pollinator dependency index, coffee cover, and forest cover) (figure S1).

We then used a multi-model inference approach based on information theory using Akaike Information Criterion (AIC) (Burnham and Anderson 2002). We used linear mixed-effects 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 a spatial correlation had been previously detected (using 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 Δ AIC lower than two were considered equally plausible. Finally, we checked the Gaussian and homoscedasticity assumptions for the standardized residuals.

Complementarily, we also tested if coffee yield could be related to deforestation, as the high opportunity costs in areas with higher yields are expected to boost deforestation. More specifically, we tested whether coffee yield and other socioeconomic variables (i.e. Gross Domestic Product, irrigation system, pesticide use, farm size) were good predictors of accumulated forest deforestation during the study period. Using the same Mapbiomas database, we calculated forest deforestation at the municipality level, and created similar models as for coffee yields, but now using deforestation as the response variable.

3. Results

Coffee yield varied considerably across the municipalities, between 4.7 and 47.3 coffee bags per hectare (282–2838 kg ha⁻¹), with a mean and median value of

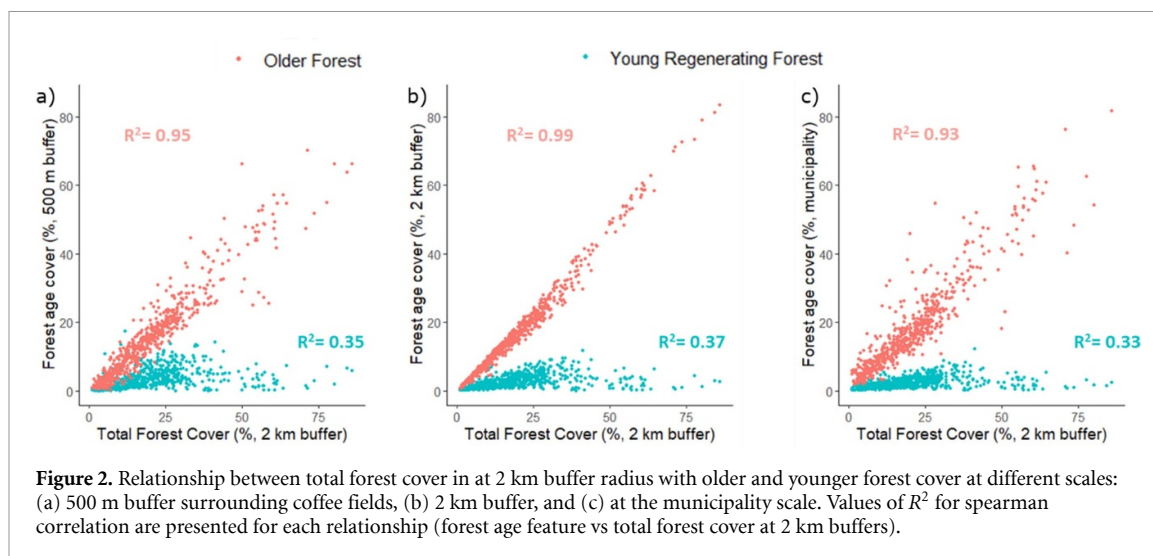


Figure 2. Relationship between total forest cover in at 2 km buffer radius with older and younger forest cover at different scales: (a) 500 m buffer surrounding coffee fields, (b) 2 km buffer, and (c) at the municipality scale. Values of R^2 for spearman correlation are presented for each relationship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

Table 1. Model performance predicting coffee yields at different scales (500 m, 2 km, and municipality) as a function of each of the following forest age features: (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	$R^2 m/R^2 c$	Model rank
(a) Total forest cover (FC) at different scales						
	FC*(PD + Cc)		122.0	1.77	0.08/0.55	2
		FC*(PD + Cc)	125.7	5.40	0.06/0.50	3
	FC*(PD + Cc)		129.1	8.81	0.06/0.53	6
(b) Older forest (OF) cover at different scales						
	OF*(PD + Cc)		120.3	0.00	0.09/0.56	1
		OF*(PD + Cc)	126.9	6.58	0.06/0.51	4
	OF*(PD + Cc)		129.3	9.05	0.06/0.53	7
(c) Young regenerating forest (YRF) cover at different scales						
		YRF*(PD + Cc)	127.2	6.92	0.07/0.55	5
	YRF*(PD + Cc)		132.1	11.79	0.07/0.53	8
	YRF*(PD + Cc)		134.6	14.32	0.06/0.53	9
	Null model		138.4	18.14	0.00/0.34	10

20 bags ha^{-1} (1200 kg ha^{-1}). Total forest cover varied at the 2 km scale, between 0.4% and 91% (figure 2), with less than half (45%) of the municipalities having more than 20% of forest cover within a 2 km radius (table 1). Most of the forest cover ($\sim 90.5\%$) was composed of forests older than 20 years, the reason why we found that old forest cover was highly correlated with overall forest cover (figure 2). Almost a quarter (23.6%) of the municipalities had less than 1% of YRF cover. Nonetheless, for 14% of the municipalities, YRFs represented more than half of the forest cover surrounding the coffee fields at a 500 m radius (figure 2(a)), which was the scale at which YRF most relates to coffee yield (tables 1 and 2).

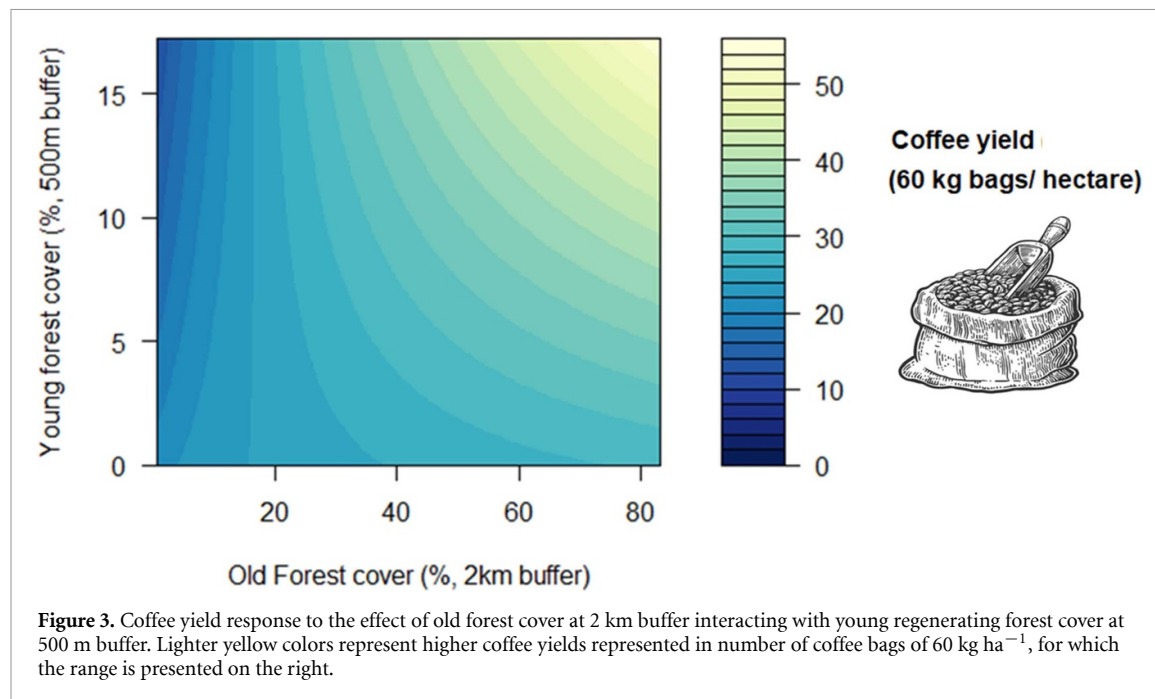
Older forests and overall forest cover were equally associated with coffee yield variations, which was expected given the high correlation between both variables (tables 1 and 2, figure 2). Therefore,

hereafter, we will refer to older forest cover's effect on spatial variability of coffee yields. YRFs alone did not relate to the variations in coffee productivity (table 1). However, the interaction between YRFs with older forest cover was essential to explain variations in coffee yield (table 2). This effect occurred on a particular combination of scales (table 2), with young regenerating contributing at a smaller scale, 500 m, while total or older forest cover contributed at a 2 km buffer (tables 1 and 2).

More specifically, the relationship between YRF cover (at 500 m) and coffee yields was modulated by the amount of older forest cover in the larger 2 km landscape (figure 3). When older forest cover is above 20%, higher amounts of YRF were positively associated with coffee yield, contrary to what happened in landscapes with less than 20% of older forest cover (figure 3). Landscapes with low forest cover

Table 2. Model performance predicting coffee yield which also considers the interaction between young forest fragment (YRF) and older forest cover (OF). The different scales were tested for young regenerating forest while we maintained constant the 2 km buffer scale for the old forest cover. All the models considered the interaction between the old forest features and the pollinator dependence (PD) and the additive effect with the coffee cover (Cc). R^2m and R^2c are the marginal and conditional R squared values, presenting the values associated to the fixed effects of the models (marginal) and joint R squared of both the fixed and random effects of the models (conditional).

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



dominated by YRF were thus associated with low coffee yields. Finally, neither the effects of pollinator dependency index nor coffee cover were influenced by the YRF (table 2, figure S1), but they were still relevant for explaining coffee yield (tables 1 and 2).

Additionally, deforestation among municipalities was not predicted by coffee yields (figure S3). However, deforestation did respond to spatial features of coffee production systems, coffee cover and farm size (table S2). Municipalities in which coffee cover dominates the landscape and that presented larger farms were also the ones with the highest deforestation accumulated (figure S3).

4. Discussion

Promoting synergies between agriculture production and biodiversity conservation is vital for achieving sustainable development in working landscapes (Bommarco *et al* 2013). Our results show that coffee yields benefit from multifunctional landscapes that preserve 20% or more of mature forests (older than 20 years), most likely through the enhancement of ecosystem service provision. Nevertheless,

this may take a long time to occur, as, in almost half of the coffee regions within the Atlantic Forest, the landscape has been reduced to less than 20% of forest cover and regenerating forest are highly ephemeral (González-Chaves *et al* 2022, Piffer *et al* 2022b). Moreover, we found that in landscapes dominated by coffee plantations and YRFs alone, coffee productivity was lower probably because coffee demand for ecosystem services is not being met (González-Chaves *et al* 2022). Therefore, efforts to ensure that YRFs will reach older ages are crucial, in addition to avoiding the deforestation of mature forests (Brown and Zarin 2013), given that we also found that coffee cover was associated with deforestation (figure S3 and table S2). Our results indicate important temporal and spatial dynamics that affect the potential contribution of regenerating forests to increase coffee productivity, which should be considered for implementing public policies that guarantee the succession and permanence of forest regeneration.

4.1. Temporal dynamics

Our results suggest a temporal lag effect in restoration, where full ecosystem functioning and

the associated ability of YRFs to contribute to agricultural production is only recovered several years after the forest is restored. Such delay may be due to early forest succession stages lacking adequate nesting and feeding resources for the establishment of invertebrate populations capable of meeting ecosystem services demand (Cockle *et al* 2010, Styring *et al* 2011, Sobreiro *et al* 2021). For instance, many 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, Montagnana *et al* 2021). Forests' ability to harbor more diverse bee communities might be limited to the more mature forest with higher carbon stocks. Precisely, forest regeneration was associated with highly productive municipalities only when the habitat amount was above 20% of older forest, threshold above which biodiversity extinctions are less likely to occur (Keitt 2009, Banks-Leite *et al* 2014, Boesing *et al* 2018, Pillay *et al* 2022).

Municipalities with lower productivity were characterized by low forest cover and a high predominance of YRFs. In highly altered landscapes composed of regenerating or degraded forests, a higher abundance of flower resources is expected but with lower plant species diversity (le Provost *et al* 2022), because of the longer flowering periods given the increments in light availability (Liow *et al* 2001, Kang and Bawa 2003). The lower plant diversity will host less diverse pollinators, composed of super generalist species (Giannini *et al* 2015, Jaffé *et al* 2015, Moreira *et al* 2015), whose interaction might result in lower pollination service (González-Chaves *et al* 2020). Moreover, the impoverished biological communities may not sustain large populations of pest enemies able to suppress pest populations, which are strengthened given the landscape simplification (Blitzer *et al* 2012). These landscapes are unlikely benefiting from the same favorable micro-climatic conditions provided by a broader coverage of mature forest fragments (Mendes and Prevedello 2020).

In landscapes with more than 20% of forest cover, the expected increment in flower resources from forest regrowth should further enhance the more diverse arthropods community present and thus favor ecosystem service provision (Moreira *et al* 2015, Martin *et al* 2016, Dainese *et al* 2019, le Provost *et al* 2022). Among the enhanced insect communities, the bees of the Meliponini tribe, the main coffee flower visitors, should play a significant role along the successional gradient of a tropical forest as they become more functionally diverse (Ramalho 2004, Ramos-Fabiel *et al* 2019). Species turnover is expected to be especially relevant at predicting pollination service stability across larger regions (Winfree *et al* 2018, Senapathi *et al* 2021).

4.2. Spatial dynamics

Landscapes with intermediate forest cover amounts (20%–40%) have spatial arrangements that favor the

spillover of pollinator and pest enemies from natural areas to crop fields, as well as the arrival of seeds needed for natural regrowth (Villard and Metzger 2014, Mitchell *et al* 2015, Moreira *et al* 2018). Regenerating fragments combined with older fragments contribute to achieving such intermediate levels of forest cover, hence mediating the landscape regenerating capacity to recover its biodiversity (Crouzeilles *et al* 2020).

In landscapes that favor biodiversity integrity, YRFs are likely to occur in the proximity of older fragments. Further reducing the distance between forest and coffee fields, facilitating forest connectivity and making the landscape more permeable to pollinators and pest enemies (Medeiros *et al* 2021, González-Chaves *et al* 2022). Hence, we would expect that these spatial dynamics will contribute to biodiversity recovery. For instance, as regenerating forest fragments mature, 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 surrounding older forest fragments (M'gonigle *et al* 2015, Woodward and Jha 2017, Iles *et al* 2018).

Previous works strongly suggest that the associations found between forest cover and coffee yields are mediated by changes in biodiversity (Nelson and Burchfield 2021, González-Chaves *et al* 2022). An alternative explanation would be that higher yields could act as a driver of deforestation. However, the observed findings do not support this explanation. Deforestation was related to an increase in coffee cover independently from coffee yields, which further reinforces the relevance of the main pattern observed in this study: maintaining older forest cover is crucial to provide adequate landscape conditions for higher coffee productivity. Moreover, the benefit of regenerating forests might not be limited exclusively to pollination and pest control services, as soil properties and climatic benefits are also being recovered in the proximity of regenerating forest fragments (Mendes and Prevedello 2020, Poorter *et al* 2021, Huang *et al* 2022). While we may not be able to underpin the process mediating such a relationship, the large-scale pattern observed in our work may guide landscape management (Nelson and Burchfield 2021).

4.3. Searching for synergies between conservation and agriculture

Forest regrowth can recover ecosystem functions faster than previously expected (Poorter *et al* 2021), but relying on forest regeneration will only benefit agricultural production if we can guarantee that older forest remains within the landscapes. Given that the native vegetation is still scarce around most coffee fields within the Atlantic Forest region (González-Chaves *et al* 2022), the initial benefits of vegetation regeneration will not overcome restoration

costs. Assisted forest regrowth, which is a low-cost management option to recover forest cover, might be needed to avoid overloading the burdens of restoration on farmers (Gastauer *et al* 2021). Spatial planning of forest restoration is also crucial to avoid discouraging farmers' widespread uptake of restoration in regions where restoration is most needed and recover landscape's capacity to provide ecosystem services (Arroyo-Rodríguez *et al* 2020). Therefore, apart from the opportunity cost of 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 (Chazdon *et al* 2020).

Our work further reinforces the importance of implementing policies that help guarantee the permanence of regenerating natural forests for achieving restoration goals (Piffer *et al* 2022b), besides securing at least 20% of native vegetation as an active part of agricultural landscapes. Avoiding deforestation is especially relevant in tropical regions, where older forests are constantly being cut down and replaced by younger forests, a hidden factor affecting biodiversity and carbon stock capacity (Chazdon *et al* 2016, Rosa *et al* 2021, Piffer *et al* 2022a). Complementary policies such as payments for ecosystem services (Ruggiero *et al* 2019), or the adoption of certification schemes (d'Albertas *et al* 2023) might also help boost regeneration and compliance with environmental policies, in addition to the command-control governance actions, which can be hard to implement and enforce (Metzger *et al* 2020).

Ecological restoration is becoming mainstream and can greatly benefit from understanding the economic outcomes across large regions (Strassburg *et al* 2019). Here we provide evidence that Atlantic Forest conservation is already contributing to coffee yields while identifying that the permanence of YRF is crucial to leverage even more crop production and revenue. Despite the evidence showing that restoration is economically viable, the temporal delay of ecological recovery needs to be considered when implementing forest restoration and analyzing the revenue of restoring biodiversity within the farm. An economical alternative to promote forest restoration is incorporating cash crops and fruit trees, between native trees (agroforestry), at the beginning of the forest succession, providing farmers revenue until forest maturity is achieved (Wanger *et al* 2020). With such practices, the time-lag associated with forest biodiversity recovery can be compensated by the direct cash crops income associated with forest regeneration (Melo *et al* 2021).

Overall, given that the positive effects of forest restoration will take at least 20 years to be realized in highly simplified landscapes, it is essential to promote public policies stimulating and guarantying the

permanence of YRFs. Moreover, we need policies to stimulate and promote farmers to protect older forests through economic opportunities, like payment for ecosystem services or market tools that recognize the value of more sustainable development.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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Author contributions

A G C H, L C and J P M conceptualize the paper. A G C H, L C, P R P, F D A and J P M develop the analyses methods. A G C H wrote the first draft and all the authors contributed to the final draft.

Conflict of interest

We declare there are no conflicts of interest.

ORCID iDs

Adrian David González-Chaves 


<https://orcid.org/0000-0002-5233-8957>

Luísa Gigante Carvalheiro  <https://orcid.org/0000-0001-7655-979X>

Pedro Ribero Piffer  <https://orcid.org/0000-0001-9706-4745>

Francisco d'Albertas  <https://orcid.org/0000-0003-1684-0277>

Tereza Cristina Giannini  <https://orcid.org/0000-0001-9830-1204>

Blandina Felipe Viana  <https://orcid.org/0000-0002-4924-1257>

Jean Paul Metzger  <https://orcid.org/0000-0002-0087-5240>

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