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Ephemeral forest regeneration limits carbon sequestration potential in the Brazilian Atlantic Forest

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Abstract

Although deforestation remains widespread in the tropics, many places are now experiencing significant forest recovery (i.e., forest transition), offering an optimistic outlook for natural ecosystem recovery and carbon sequestration. Naturally regenerated forests, however, may not persist, so a more nuanced understanding of the drivers of forest change in the tropics is critical to ensure the success of reforestation efforts and carbon sequestration targets. Here we use 35 years of detailed land cover data to investigate forest trajectories in 3014 municipalities in the Brazilian Atlantic Forest (AF), a biodiversity and conservation hotspot. Although deforestation was evident in some regions, deforestation reversals, the typical forest transition trajectory, were the prevalent trend in the AF, accounting for 38% of municipalities. However, simultaneous reforestation reversals in the region (13% of municipalities) suggest that these short-term increases in native forest cover do not necessarily translate into persistent trends. In the absence of reversals in reforestation, forests in the region could have sequestered 1.75 Pg C, over three times the actual estimated carbon sequestration (0.52 Pg C). We also showed that failure to distinguish native and planted forests would have masked native forest cover loss in the region and overestimated reforestation by 3.2 Mha and carbon sequestration from natural forest regeneration by 0.37 Pg C. Deforestation reversals were prevalent in urbanized municipalities with limited forest cover and high agricultural productivity, highlighting the importance of favorable socioeconomic conditions in promoting reforestation. Successful forest restoration efforts will require development and enforcement of environmental policies that promote forest regeneration and ensure the permanence of regrowing forests. This is crucial not only for the fate and conservation of the AF, but also for other tropical nations to achieve their restoration and carbon sequestration commitments.

KEYWORDS

forest cover change, forest persistence, land use change, reforestation, second-growth forests, tropical forests

1 | INTRODUCTION

The extent, rate, and magnitude of human-driven land modification has reached unprecedented levels in human history (Foley et al.,

2007; Lambin & Meyfroidt, 2011). The majority of natural ecosystems across the globe have been transformed to varying degrees with less of 20% currently considered as wildlands or without clear intervention of human impact, including tropical forests (Ellis et al.,

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2021). Forest loss has major ecological consequences, directly affecting biodiversity, carbon budgets and watershed conservation (Redo, Grau, et al., 2012). Tropical regions are the last agricultural frontier (DeFries & Rosenzweig, 2010), and tropical forests around the globe are threatened by high rates of habitat conversion from the expansion of agricultural and urban frontiers (Lewis et al., 2015). A better understanding of the multiple drivers of forest change in the tropics is critical for slowing down tropical deforestation and identifying potential hotspots for forest regeneration (Curtis et al., 2018; DeFries & Rosenzweig, 2010).

Although deforestation is still widespread in the tropics (Asner et al., 2009; DeFries et al., 2010; Hansen et al., 2008, 2010), many places are now experiencing significant forest recovery, suggesting that forest transitions are occurring over short timescales (Aide et al., 2013; Hansen et al., 2013; Nanni et al., 2019; Schwartz et al., 2020; Sloan et al., 2019; Song et al., 2018). The term forest transition denotes a shift from net deforestation to net reforestation, usually, but not always, associated with economic development (Barbier et al., 2010; Lambin & Meyfroidt, 2010; Mather, 1992; Rudel et al., 2005, 2010). This process can be attributed to a variety of factors, including among others, agricultural intensification, scarcity of rural labor or forest products, lack of rural economic opportunities, and urbanization (Barbier et al., 2010; Rudel et al., 2005, 2020). Forest transitions can occur at various scales, from local and regional reforestation processes to country-wide shifts in forest dynamics, usually following a period of significant decline in forested land (Rudel et al., 2005).

Shifts from net deforestation to net reforestation, which have been predominant in developed regions in the past (Nanni et al., 2019), are now occurring in developing tropical countries, particularly in Latin America, where recent agricultural intensification has resulted in forest regrowth in less productive marginal areas with steeper slopes, which are less suitable for large-scale mechanized agriculture (Aide et al., 2000, 2013; Asner et al., 2009; Costa et al., 2017; Crk et al., 2009; Grau & Aide, 2008; Nanni & Grau, 2014; Parés-Ramos et al., 2008; Redo, Grau, et al., 2012; Yackulic et al., 2011). Although reports on forest recovery in tropical regions give cause for optimism, since second-growth forests have a vast potential for carbon sequestration, biodiversity conservation and climate regulation (Barlow et al., 2007; Chazdon, Broadbent, et al., 2016; Chazdon et al., 2009; Pan et al., 2011; Poorter et al., 2016; Schwartz et al., 2017; Silver et al., 2000; Strassburg et al., 2016), the drivers of forest regrowth are highly variable and still poorly understood (Asner et al., 2009; Chazdon, Brancalion, et al., 2016; Nanni et al., 2019). Recent studies have shown that regrowing or restored forests have a high probability of being cleared within a few years of establishment (Nunes et al., 2020; Reid et al., 2017, 2018; Schwartz et al., 2017) and reversals of reforestation trends in the tropics may be common (Schwartz et al., 2020). Understanding the trajectories and drivers of forest transitions in the tropics is thus critical to ensure the success of tropical reforestation and the persistence of its contribution to climate change mitigation and biodiversity conservation.

With ambitious international restoration and tree planting commitments to combat climate change and prevent species extinctions such as the Bonn Challenge, the World Economic Forum, and the upcoming United Nations' Decade on Ecosystem Restoration (Fagan et al., 2020; Rosa et al., 2021), accurately mapping native forest regeneration is critical, as many nations are also relying on tree planting to meet their current restoration goals (Holl & Brancalion, 2020). Native forest regeneration is not only one of the most costeffective ecological restoration management strategies but also a cornerstone for achieving forest restoration goals and biodiversity conservation (Crouzeilles, Beyer, et al., 2020). In contrast, many large-scale tree plantation programs rely on one or a few nonnative tree species (Holl & Brancalion, 2020). Native second-growth forests and monoculture tree plantations have distinct consequences for landscape management and ecosystem services provision (Baral et al., 2016; Brockerhoff et al., 2013; Chazdon, 2008; Sloan et al., 2019). Although forest plantations can restore ecosystem services in degraded lands, they experience high rates of failure (Brancalion & Holl, 2020; Cao et al., 2011), rapid clearing, and, more importantly, their expansion often occur at the expense of native forest cover (Heilmayr et al., 2020). Moreover, monoculture tree plantations have a lower capacity to sustain biodiversity (lezzi et al., 2018) and can negatively impact water resources (Feng et al., 2016). Therefore, accurately distinguishing second-growth from planted forests is a crucial undertaking to guide future ecosystem restoration initiatives.

Here, we rely on a long-term, annual time series (1985 to 2019) of Landsat-derived land cover maps to investigate native forest change trajectories across the Brazilian Atlantic Forest (AF), a hotspot for Neotropical reforestation (Nanni et al., 2019). We then estimate carbon seguestration potential in the region under a scenario where regenerated forests persist versus the actual observed sequestration. We also investigate the consequences of failing to distinguish forest plantations from native forests for the study of native forest cover trajectories and carbon sequestration potential of restored forests. Finally, we evaluate the biophysical and socioeconomic factors associated with observed native forest transitions. Until recently, continental-scale studies in Latin America only covered relatively short periods (e.g., 10-15 years), and did not distinguish plantations from native forest regrowth with high accuracy due to methodological issues (Aide et al., 2013; Clark et al., 2012; Hansen et al., 2013; Nanni et al., 2019; Schwartz et al., 2020; Song et al., 2018). However, recent studies based on a new long-term time series of detailed land cover data for all Brazilian ecosystems (MapBiomas initiative), in which native and exotic tree covers are successfully differentiated, showed that the AF is experiencing substantial increases in forest cover in recent years, mostly associated with second-growth regeneration (Crouzeilles, Beyer, et al., 2020; Rosa et al., 2021). This, associated with numerous reports of forest regrowth occurring at local or regional scales (Baptista, 2008; Baptista & Rudel, 2006; Bicudo da Silva et al., 2017; Calaboni et al., 2018; Costa et al., 2017; de Rezende et al., 2015; Farinaci & Batistella, 2012; Ferreira et al., 2014; Molin et al., 2017; Silva et al., 2016), calls for a biome-wide

analysis to determine if forest transitions are regionally restricted or are occurring more broadly across the entire AF.

2 | METHODS

2.1 | Study area

The Brazilian AF is one of the world's most ecologically diverse and threatened ecosystems (Ribeiro et al., 2009). Originally occupying an area greater than 150 Mha (Figure 1), the region is home to more than 125 million people and highly developed, contributing to 70% of the Brazilian GDP and about two thirds of the country's industrial production (Rezende et al., 2018). The AF has a long history of land use change and widespread deforestation. Forest cover has been drastically reduced to 28% (32 Mha) of its original extent (Rezende et al., 2018), resulting in highly fragmented landscapes and currently over 80% of remnant forest is composed of patches <50 ha (Rezende et al., 2018; Ribeiro et al., 2009), posing extra challenges for the biome's conservation.

The AF is an ideal region to explore forest transition processes. Reforestation in the region occurred after original forest cover was drastically reduced (Rezende et al., 2018). The region has also experienced recent urbanization, industrialization and agricultural intensification, all potential drivers of forest transitions (Rudel et al., 2005). These changes, however, have not occurred equally in the

region, with significant differences in economic activity, degree of development, climate and seasonality across the AF. The south and southeast portions of the biome are highly industrialized and densely populated, with heavily mechanized agriculture and forestry sectors (Barretto et al., 2013; Lapola et al., 2014; Martinelli et al., 2011). Approximately 83% of the remaining forest cover in the AF is located in the southern and southeastern portions of the biome (Figure 1) while about 15% still remains in the northeast portion of the biome, where agriculture is dominated by family-owned farming and the industrial sector is still under development (IPEA, 2020).

2.2 | Forest cover data

Native forest cover and forest plantation data was obtained from the MapBiomas project, which used Landsat imagery and the Random Forest algorithm (Breiman, 2001) to derive annual land use cover maps from 1985 to 2019 for all Brazilian biomes (see Souza et al., 2020 for details). Global accuracy for the AF land use and land cover maps is 90.7% (Legend Level 1; Rosa et al., 2021). The MapBiomas product is an unprecedented tool for understanding forest dynamics in the AF (Rosa et al., 2021). Unlike recent continental-scale studies (Aide et al., 2013; Clark et al., 2012; Hansen et al., 2013; Nanni et al., 2019; Schwartz et al., 2020; Song et al., 2018), it accurately distinguishes native forest cover from forest plantations, allowing for more consistent and accurate estimations of native forest cover changes

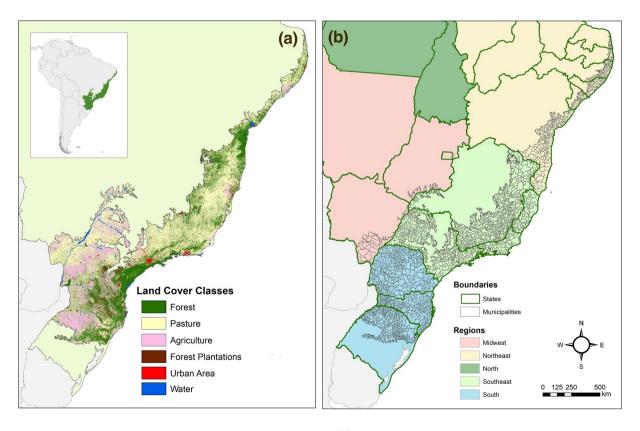


FIGURE 1 Land use cover map of the Atlantic Forest for the year 2019 (a), and Brazilian administrative regions, states, and the 3014 municipalities analyzed in the present study (b)

in the region, such as seen in the studies by Crouzeilles, Beyer, et al. (2020) and Rosa et al. (2021). The ability to distinguish native forest cover from monoculture tree plantations in MapBiomas is consistent throughout the entire time series, with a global accuracy mean value of 96% for all years (Rosa et al., 2021).

To quantify changes in vegetation cover in the AF from 1985 to 2019, we calculated yearly native forest cover and forest plantations for all 3014 municipalities within the biome using the Collection 5 from MapBiomas (Figure 1). All analyses were conducted at the municipality scale. Native forest area for each municipality was obtained by summing all the native forest pixels (pixel ID = 3) within a municipality boundary and transforming the final pixel count into an area measurement. The same was done to calculate forest plantation area for each municipality (pixel ID = 9). We only included the portions of each municipality that were within the AF limits (IBGE, 2019). Calculations were conducted using the Google Earth Engine platform.

2.3 | Socioeconomic and landscape data

Socioeconomic data at the municipality scale were obtained from the periodical national census surveys conducted by the Brazilian Institute of Geography and Statistics (IBGE). We collected data from the National Agrarian Census Surveys for the years 1985, 1996, 2006, and 2016 and from the Demographic Census Surveys for the years 1980, 1990, 2000, and 2010. All data are freely available for download at the SIDRA IBGE database (https://sidra.ibge.gov.br). We collected data at the municipality scale (Table 1) related to agricultural activity, population demographics and economic development to investigate the potential drivers of forest transitions in the AF, including: (1) population density; (2) rural-urban population ratio; (3) per capita GDP; and (4) agricultural yield. We calculated agricultural yield by dividing the total

agricultural production in tons for each municipality (annual and perennial crops combined) by the total harvested area. Since deforestation and reforestation are also associated with biophysical characteristics of the landscape (Aide et al., 2013), we also calculated average elevation and slope, and percent initial forest cover. Average slope and elevation for each municipality was calculated using the ALOS Global Digital Surface Model with 30 m of spatial resolution.

2.4 | Statistical analyses

2.4.1 | Forest cover trends

To study trends in forest cover in the AF, we used a shape selection algorithm designed for fitting trajectories to time-series data (Moisen et al., 2016), following a similar approach to Schwartz et al. (2020). The algorithm uses nonparametric statistical methods to fit a set of discrete possible shapes or trajectories to a time series of data; it picks the optimal shape based on goodness of fit and a penalty for model complexity (Moisen et al., 2016). We considered five possible trajectories for our 35-year time series of forest cover data (Appendix Figure S1): (1) flat; (2) decreasing; (3) increasing; (4) deforestation reversal (vee); and (5) reforestation reversal (inverse vee). The best fit for each municipality was determined using Bayesian information criterion (BIC). We first ran the algorithm with the complete time series of native forest cover data (1985-2019) for each of the 3014 municipalities in the AF. Since the algorithm assigns a shape to a time series regardless the magnitude of the change or consideration of outliers, we applied a bootstrapping procedure to avoid identification of spurious trajectories. For each municipality, we randomly removed 5 years from the time series and reran the algorithm, repeating this procedure 300 times. We then compared

Explanatory variables	Reasoning for inclusion in the analysis
Socioeconomic	
Population density	Concentration of population in in urban areas decreases the pressure on agricultural lands (Rudel et al., 2005)
Rural-urban population ratio	Lower rural population density decreases pressure on agricultural lands leading to abandonment of marginal and less productive lands (Rudel et al., 2005)
Per capita GDP	Economic development leads to rural—urban migration and agricultural mechanization, reducing the pressure on land (Rudel et al., 2005)
Agricultural yield	Increase in productivity due to mechanization leads to abandonment of marginal lands (Calaboni et al., 2018)
Biophysical	
Average slope	Forests are more likely to regenerate on steeper slopes (Teixeira et al., 2009)
Average elevation	Forests are more likely to regenerate on higher elevation areas (Aide et al., 2013; Asner et al., 2009)
% Initial forest cover	Proximity to existing fragments facilitates native forest regrowth (Schwartz et al., 2017)

TABLE 1 Socioeconomic and landscape variables used in the analysis, hypothesized relationship between forest cover change and each of the drivers, and rationale for inclusion

the results from the 300 iterations with the best fit shape using the complete time series (1985–2019). Municipalities in which less than 90% of the iterations matched the best fit shape using the complete time series were classified as "low confidence." We also used the algorithm to extract the year of inflection for every municipality classified as either deforestation reversal (vee) or reforestation reversal (inverse vee). Finally, we repeated this analysis using combined cover for native forest and forest plantations. We used these results to examine the consequences of failing to distinguish between these two land cover types for understanding forest cover dynamics and estimating the area and carbon sequestration potential of natural forest regeneration in the AF.

2.4.2 | Carbon sequestration potential

To quantify the carbon sequestration implications of the reclearance of newly regenerated forests, we used the bookkeeping approach developed by Schwartz et al. (2020), which compares two scenarios: (1) the amount of carbon that would have been sequestered by new forests without re-clearing (i.e., total carbon potential of forest regeneration) and (2) observed carbon sequestration by new forests when accounting for re-clearing. We only considered

carbon sequestration from reforestation that occurred after 1986 and ignored emissions due to deforestation, as our goal was to quantify the carbon sequestration potential lost due to the re-clearing of new forests. This approach analyzes the time series of yearly forest cover for each municipality in a process analogous to a stage-structured population model (Schwartz et al., 2020). In the first

$$r_{\mathsf{t}} = f_{\mathsf{t}} - f_{\mathsf{t}-1} \, \mathsf{if} \, f_{\mathsf{t}} \ge f_{\mathsf{0}},$$

scenario (observed carbon sequestration), change in forest cover (r)

was calculated as:

$$r_{t} = 0 \text{ if } f_{t} < f_{0},$$

where f is the forest cover (in hectares) and f_0 is the initial forest cover in 1985. This only considers reforestation and re-clearing of forests that were emerged after 1985. When $r_{\rm t}$ is positive, the number of hectares of new forests are added to the previous stage class and a negative $r_{\rm t}$ is subtracted from the existing "population." After the final time step, we calculated the total observed carbon stored in second-growth forest for each municipality. We first estimated the rate of carbon sequestration for each municipality (zonal average) using values for total aboveground biomass after 20 years of forest regrowth from the study by Poorter et al. (2016). Since

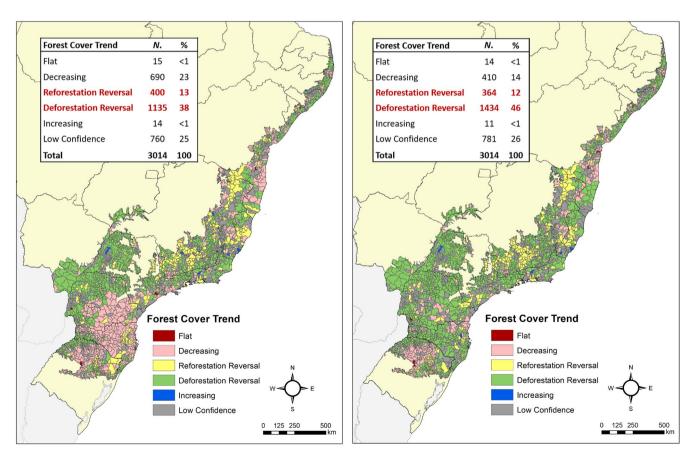


FIGURE 2 Trajectories of forest cover changes in the Atlantic Forest for the two scenarios: (1) native forest cover (left); and (2) native forest and forest plantations combined (right). Both show a prevalence of deforestation reversals between 1985 and 2019, which is exacerbated when forest plantations are not properly distinguished from native forest

regrowth in the first 20 years is approximately linear (Poorter et al., 2016), we approximated annual rates of biomass accumulation as 1/20th of this quantity. We then multiplied the accumulated area of secondary forests in hectares by the calculated aboveground biomass values and divided the result by 2 to estimate stored carbon, under the assumption that carbon makes up 50% of biomass (Schwartz et al., 2020).

For the second scenario (carbon sequestration potential), $r_{\rm t}$ was calculated as follows:

$$r_{t} = f_{t} - f_{t-1} \operatorname{if} f_{t} > f_{t-1} \operatorname{and} f_{t} \ge f_{0},$$

$$r_{t} = 0 \operatorname{if} f_{t} \le f_{t-1} \operatorname{or} f_{t} < f_{1}.$$

No deforestation occurs under this scenario and all new forests are added to the "population" until the end of the study period. We then repeated the carbon sequestration analysis using the combined dataset of native forest cover and forest plantations.

2.4.3 | Drivers of forest trends

We used one-way ANOVA and post hoc Tukey's test to investigate the relationships between socioeconomic and landscape variables and the different trajectories of native forest cover change identified by the shape selection algorithm. Because we were interested in the factors that influence natural forest regeneration, we only conducted this analysis with the trajectories of native forest cover, but not for the combined dataset of forest cover and plantations (Scenario 1). We excluded from this analysis the municipalities that were classified as "low confidence" after the bootstrapping procedure and restricted the analysis to the three trends that accounted for over 99% of the remaining municipalities (decreasing, deforestation reversal, and reforestation reversal). Socioeconomic variables from different years were highly correlated (Pearson's r > .85), so used values from the earliest available and reliable data for all 3014 municipalities (1990 Demographic Census and 1996 National Agrarian Census) in order to reflect the conditions of each municipality at the beginning of our study period (Table 1).

3 | RESULTS

3.1 | Patterns of change in forest cover

Native forest cover in the AF is unevenly distributed and concentrated in the south and southeast regions (~83%; Figure 1; Appendix Figure S2). We observed a steady decrease in forest cover between 1985 and 2019 (~3.28 Mha), with a slight, temporary increase between 2004 and 2015 (~435 Kha), which was followed by a second period of forest loss through 2019 (~526 Kha) Appendix Figure S3). Forest loss in the AF decreased after 2000 (Appendix Figure S4). We found that 73.16% of the 3014 municipalities had net losses in

forest cover between 1985 and 2000 (~3.5 Mha) and 26.54% experienced net gains (~500 Kha; Appendix Figure S5). Between 2000 and 2019, however, 58.4% of municipalities had net gains in forest cover (~1.2 Mha) while 41.4% experienced net losses (~1.45 Mha). Most of the states in the AF experienced net gains in forest cover between 2000 and 2019 compared to the earlier period (Appendix Figure S6).

Deforestation reversals, the typical forest transition curve, were the predominant trajectory of forest cover change between 1985 and 2019, occurring across the entire AF and accounting for 38% of the 3014 municipalities (Figure 2). Decreasing or continuous forest loss trends were observed in 23% of the municipalities, with a higher prevalence in the southern portions of the biome and in the northeastern state of Bahia (Figure 2; Appendix Figure S8). Reversals in reforestation occurred in 13% of the municipalities in a clustered pattern across the biome, and were more common in the southeast. mainly in the state of Minas Gerais (Appendix Figure S8). Less than 1% of the municipalities experienced either a sustained increase (n = 14) or no change in forest cover (n = 15). The remaining 25% of the municipalities were classified as "low confidence." Reversals in deforestation occurred mostly between 1990 and 1995, while reversals in reforestation trends were more common between 2010 and 2015 (Appendix Figure S9).

In municipalities where deforestation reversals occurred, 47.5% of 1135 municipalities had net losses in forest cover relative to 1985, while 52.5% had net gains. As a consequence, native forest cover decreased by 1,703,060 ha before the trend reversed, with a subsequent gain of 1,175,209 ha, resulting on a net loss of 527,851 ha of native forest cover by 2019 relative to 1985. In municipalities where reforestation reversals occurred, 62% of 400 municipalities had net gains in forest cover relative to 1985, while 38% had net losses. In these municipalities, native forest cover increased by 760,010 ha before the trend reversed, with a subsequent loss of 575,247 ha, resulting on a net gain of 184,763 ha of native forest cover relative to 1985.

Running the shape selection algorithm with the combined dataset of native forest cover and forest plantations increased the number of municipalities with deforestation reversal trends by 26% and reduced the number of decreasing trajectories by 41% (Figure 2). We also observed a small decrease in the number of reforestation reversal trends (Figure 2). The municipalities that changed trend and were classified as deforestation reversals when not distinguishing native forests from forest plantations replaced 173 municipalities with decreasing trends, 27 with reforestation reversals, and 134 municipalities with low confidence trends (Figure 2).

The analysis of net gains and losses in forest cover with the combined dataset of native and planted forests led to an underestimation of native forest loss in municipalities with reforestation reversals of 512 Kha, where native forest loss was largely compensated by the expansion of forest plantations (Table 2). In municipalities with deforestation reversals, the loss of initial forests increased by 770 Kha. This was expected considering that most of the new deforestation trends occurred in municipalities with decreasing trends, accentuating this initial loss. The net losses in forest cover

TABLE 2 Comparison of the net gains and losses in forest cover in municipalities with deforestation and reforestation reversal trends for the two explored scenarios of native forest and native and planted forests combined

	Deforestation reversal (vee)		Reforestation reversal (Invee)	
Changes in forest cover	Native forest	Native + planted forests	Native forest	Native + planted forests
Initial gain/loss	-1.7 Mha	-2.47 Mha	+760 Kha	+681 Kha
Subsequent gain/ loss	+1.17 Mha	+2.39 Mha	-575 Kha	-63 Kha
Net change	-527 Kha	-77/7 Kha	+185 Kha	+628 Kha
Number of municipalities with net gains	539 (of 1135)	801 (of 1343)	246 (of 400)	282 (of 384)
Number of municipalities with net losses	597 (of 1135)	633 (of 1343)	152 (of 400)	80 (of 364)

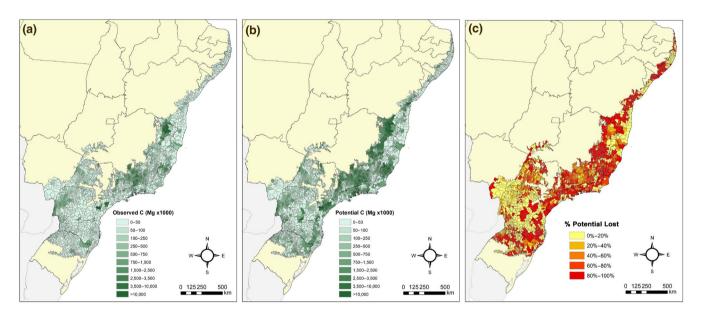


FIGURE 3 Observed carbon sequestration by new forests when re-clearing is present (a), potential carbon sequestration had no re-clearing of reforestation occurred (b), and percent potential lost due to re-clearing of reforestation (c)

in municipalities with deforestation reversals in this second scenario was just 77.7 Kha from the original 527 Kha from the analysis that only used native forest cover, emphasizing that failing to distinguish between these two land cover types would significantly mask native forest loss in the AF (Table 2).

3.2 | Carbon sequestration potential

Forests that were established between 1985 and 2019 had sequestered 0.52 Pg of carbon (Figure 3a) by the end of the study period. Without re-clearing, new forests would have sequestered 1.75 Pg of carbon (Figure 3b), which represents a loss of almost 70% of the carbon potential of reforestation in the AF over the past 35 years (Figure 3c). If forest plantations were not distinguished from native forest cover, however, our estimates of carbon sequestration would

have been higher, 0.89 Pg of carbon between 1985 and 2019 versus the original 0.52 Pg (Figure 4). In this second scenario, the potential carbon sequestration without re-clearing would have been 3.29 Pg of carbon, still with a similar proportional loss in carbon potential of reforestation (73%; Appendix Figure S10). The almost twofold difference in observed and potential carbon sequestration between both scenarios shows that failure to distinguish between these land cover types leads to significant overestimations of the magnitude of carbon sequestration from forest regeneration.

3.3 | Drivers of forest cover change

Deforestation reversals were more prevalent in municipalities with lower elevations, flatter slopes and low forest cover (Table 3; Appendix Figure S11). Deforestation reversals were also more

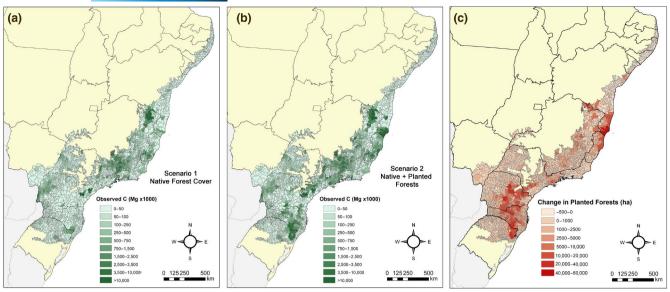


FIGURE 4 Comparison of observed carbon sequestration for native forest cover (a) and native forest and forest plantations combined (b) and net change in planted forests between 1985 and 2019 (c). Note that municipalities with an increase in observed carbon sequestration in scenario (b) coincide with areas of expansion of planted forests (c), leading to an overestimation of carbon sequestration of forest regeneration when these two types of forest formation are not properly distinguished

Predictor variable	Decreasing	Deforestation reversal	Reforestation reversal
Mean elevation (m)	542.80 (±12.28) ^a	473.99 (±7.53) ^b	625.53 (±15.39)°
Mean slope (degrees)	10.28 (±0.16) ^a	8.75 (±0.15) ^b	11.52 (±0.25) ^c
Percent initial forest cover	39.88 (±0.81) ^a	20.74 (±0.47) ^b	30.34 (±1.09)°
Rural-urban population ratio	1.63 (±0.11) ^a	0.92 (±0.04) ^b	1.19 (±0.07) ^c
Agricultural yield (tons/ha)	10.65 (±0.65) ^a	18.41 (±0.67) ^b	12.58 (±1.06)°
Per capita GDP	5076.5 (±157.83)	5146.4 (±154.75)	5033.7 (±318.54)
Population density	186.73 (±35.77)	116.61 (±15.71)	106.82 (±20.75)

TABLE 3 Mean and standard error showing the differences between the three major trajectories (decreasing, deforestation reversal, and reforestation reversal) for socioeconomic and landscape variables

Note: Letters indicate significant differences between means from the ANOVA at p < .001. We did not find significant differences for per capita GDP and population density.

common in municipalities with low rural-urban population ratios (Table 3; Appendix Figure S12). Agricultural intensification was another important driver of forest transition, as deforestation reversals occurred at higher yields (Table 3; Appendix Figure S12). We did not find discernible patterns or significant differences between the three predominant forest trends (decreasing, deforestation reversal and reforestation reversal) in per capita GDP and population density.

4 | DISCUSSION

Our analysis of forest cover change in the AF over the past 35 years revealed that reversals of forest cover trajectories, either deforestation or reforestation, prevailed across the biome, with a prevalence of deforestation reversals. The region was on the verge of a forest transition by early 2000s, as reforestation between 2004 and

2015 led to the recovery of almost 430 Kha in native forest cover. Nearly 58% of the municipalities in the AF had net gains in forest cover after the early 2000s, casting a positive outlook for the biome's conservation. However, re-clearance of regenerated forests in the region reduced carbon sequestration in regrowing forests to roughly one third of their potential. Deforestation reversals in the region were predominant in municipalities with low forest cover, low elevation, and flatter slopes. Municipalities with low rural-urban population ratios and high agricultural yield were also more likely to undergo forest transitions.

Natural tropical regeneration has been increasingly recognized as an emergent phenomenon in Latin America (Nanni et al., 2019) and our study revealed that the AF is a hotspot for forest transitions. Deforestation reversals, the typical forest transition trajectory, was the predominant trend in the biome, accounting for 1135 of the 3014 municipalities, particularly in the southern and southeastern portions of the biome, where local forest transition processes have

been recently observed (Bicudo da Silva et al., 2017; Calaboni et al., 2018; de Rezende et al., 2015; Farinaci & Batistella, 2012; Ferreira et al., 2014; Molin et al., 2017; Silva et al., 2016). Deforestation reversals played a crucial role in the recent forest recovery in the AF, as gains following the transition amounted to over 1Mha of forest cover in these municipalities, largely compensating for losses since 1985.

Although this scenario gives hope for the conservation of the AF, our results also demonstrate that gains from reforestation might be ephemeral. Even though we observed a net gain of almost 430 Kha of forest cover at the biome scale between 2004 and 2015, forest loss after 2015 nearly canceled the recovery. Reforestation reversals occurred in 13% of the municipalities in the AF, mainly focused in the southern and southeastern states, suggesting a strong influence of regional and local context on land cover dynamics, as suggested by Schwartz et al. (2020) for Latin America. Reversals in reforestation have been observed in other tropical countries such as Panama, where forest regrowth in uncultivated lands were later re-cleared for agriculture or forest plantations (Sloan, 2016), and in Costa Rica, where pressures from agricultural development on land increased deforestation after a period of forest recovery (Fagan et al., 2013). The presence of forest plantations in municipalities with reforestation reversals suggests that planted forest could also be replacing native forests in these areas, as highlighted by Rosa et al. (2021). Although these reversals occurred in only a relatively small percentage of the municipalities in the AF, they could become pervasive if effective policies are not put in place to protect these new emerging forests (Crouzeilles et al., 2019).

In the tropics, both rapid deforestation and forest regrowth can occur simultaneously (Nanni & Grau. 2014: Redo. Grau. et al., 2012). resulting in a shifting land use dynamics where new emerging forests replace older forests that were cleared for agriculture (Asner et al., 2009; Rosa et al., 2021; Rudel et al., 2016). Concomitant deforestation and reforestation have been reported for several regions in Latin America (Aide et al., 2013; Clark et al., 2012), including parts of Central America (Redo, Grau, et al., 2012), northern Argentina (Nanni & Grau, 2014), and tropical and subtropical Andes (Aide et al., 2019). Our results showed that, despite the widespread occurrence of reforestation in the region, continuous deforestation remains pervasive in certain parts of the AF, especially in the South Region in Brazil, where forest loss reached almost 2Mha between 1985 and 2019, mostly driven by the expansion of plantation forestry and agriculture in the region (Rosa et al., 2021), similar to the dynamics reported in the Argentinian portion of the AF by Izquierdo et al. (2008).

Re-clearance of native secondary forests greatly limited carbon sequestration in the AF. Our estimates of carbon sequestration in secondary forests for the AF (0.52 Pg C) are similar to recent estimates for the Brazilian Amazon (~0.33 Pg C; Nunes et al., 2020; Smith et al., 2020). Without re-clearance, second-growth forests in the region could have sequestered over three times more carbon between 1985 and 2019 than the actual estimated carbon sequestration. The loss of almost 70% of this potential (1.23 Pg C) is comparable to the estimates of Schwartz et al. (2020) for Latin America and

raises questions on the long-term effectiveness of large-scale natural regeneration as a solution for climate change mitigation (Chazdon & Brancalion, 2019). Although estimates of carbon sequestration from reforestation in the Amazon can vary (Bullock & Woodcock, 2021), recent studies demonstrate that re-clearing of secondary forests in the Amazon significantly reduced the carbon sequestration potential of these new forests in the region (Heinrich et al., 2021; Smith et al., 2020; Wang et al., 2020). Without permanence, secondary forests remain relatively small carbon sinks (Nunes et al., 2020), and the contribution of reforestation to climate mitigation will be severely reduced (Schwartz et al., 2020; Wang et al., 2020). Re-clearance in the AF, and in the tropics in general, also has drastic consequences for habitat loss, landscape connectivity, and biodiversity conservation (Crouzeilles, Beyer, et al., 2020). Furthermore, it also compromises the conservation potential and quality of regenerated forests, as these are occurring in areas of low forest cover with reduced species diversity (Banks-Leite et al., 2014; Crouzeilles, Maurenza, et al., 2020). Ensuring that regenerated forests persist over time is crucial for a sustained ecosystem services provision from landscape forest restoration.

Recent studies highlighted the value of the MapBiomas to map and quantify forest regeneration in Brazil, particularly with regard to the ability to distinguish between native secondary forests and exotic commercial forest plantations (Crouzeilles, Beyer, et al., 2020; Nunes et al., 2020; Rosa et al., 2021; Silva Junior et al., 2020; Smith et al., 2020). A comparison of our results with previous studies using lower resolution imagery (MODIS 250m) shows that most of the reforestation previously reported in the South Region is probably an artifact of the presence of new forest plantations that were not properly distinguished from native forests (Nanni et al., 2019). Forest plantations also account for deforestation reversals observed in the region by Schwartz et al. (2020), as we observed a prevalence of decreasing trends instead. These studies corroborate the results with the combined dataset of native and planted forests, where we saw that most of the decreasing trends in the southern portions of the biome were replaced by deforestation reversals. The area of forest plantations (mostly Eucalyptus) almost quadrupled in the AF between 1985 and 2019 (Appendix Figure S13), mostly in the south and southeast, often at the expense of native forest cover (Rosa et al., 2021; Souza et al., 2020). Most importantly, our results demonstrate that failing to distinguish forest plantations from second-growth forests would have led to an overestimation of total reforested area by more than 3 Mha and substantially masked native forest cover loss in some areas in the AF that were dominated by decreasing trends, highlighting the importance of using land use cover data that can successfully differentiate native from planted forests for accurately assessing the area and carbon sequestration potential of forest regeneration in tropical regions. This issue is also critical for biodiversity conservation since monoculture tree plantations do not typically sustain the same levels of biodiversity as native forests (Brockerhoff et al., 2013; lezzi et al., 2018).

Forest transitions occurred in municipalities with low elevation and flatter slopes, which is contrary to previous findings of forest regeneration occurring predominantly at higher elevation and steeper slopes throughout Latin America (Aide et al., 2013, 2019; Borda-Niño et al., 2020; Crk et al., 2009; Nanni & Grau, 2014; Redo, Aide, et al., 2012, 2013), including in the AF (Calaboni et al., 2018; Molin et al., 2017; Teixeira et al., 2009). However, our results suggest that, in a region with a long and pervasive history of land cover changes, forest transitions are occurring in areas that have been heavily altered by past agricultural activity, which are predominant at lower elevations and flatter slopes. Over the last decades, large areas of pasturelands were replaced by intensive agriculture in the AF, resulting in abandonment of less productive and marginal agricultural lands, where native forest regeneration has taken place (Rosa et al., 2021). Native forest regeneration in riparian buffers, protected as areas of permanent vegetation by federal legislation, was also an important factor in flatter areas, accounting for almost 300 Kha of regenerated young forests between 1985 and 2019 (Rosa et al., 2021). Deforestation reversals also occurred in municipalities with lower percentage of forest cover (i.e., scarcity pathway), as predicted by the forest transition theory (Rudel et al., 2005, 2016, 2020). To some degree, our results also reflect the particular geography of the AF, particularly in the south and southeast, where the steepest topography is located in areas along the coast that have not been deforested in the past and are largely protected by a network of protected areas (Bicudo da Silva et al., 2020). Deforestation reversals occurred in municipalities with lower rural-urban population ratios, showing that urbanization can lead to forest regeneration, as observed elsewhere in Latin America (Aide et al., 2019; Redo, Grau, et al., 2012). It also occurred in municipalities with higher agricultural yield. According to the forest transition theory, high yields, usually associated with mechanization, encourage agricultural abandonment of less productive and marginal lands, where natural regeneration occurs, a pattern extensively identified by Rudel et al. (2016).

We still lack a comprehensive understanding of where and under what circumstances native forest regeneration is occurring in tropical regions (Chazdon et al., 2020) and when it is likely to persist. Identifying conditions that foster forest regeneration to occur and persist is a crucial undertaking. As for other tropical regions (Aide et al., 2013; Nanni et al., 2019; Redo, Grau, et al., 2012; Sloan, 2008; Yackulic et al., 2011), we found that recent forest transitions are occurring broadly in the AF. However, we also found that pressure on land is still a major driver of deforestation in certain regions. Although our results give hope for the fate of this highly threatened tropical biome, ongoing conservation efforts are needed to mitigate the pervasive effects of centuries of continuous deforestation in the AF. Reforestation reversals in the region underscore the ephemeral nature of tropical secondary forest regrowth (Nunes et al., 2020; Smith et al., 2020) and the need for stronger conservation guidelines and policy enforcement if we are to prevent clearing of regrowing forests in tropical regions (Fagan et al., 2013; Reid et al., 2017, 2018; Schwartz et al., 2017; Sloan, 2008).

Strong environmental policies and law enforcement are particularly needed, given ongoing political turmoil in Brazil, where

environmental conservation is not a priority and deforestation rates are increasing nationally (Rosa et al., 2021; Souza et al., 2020). Moreover, forest losses and gains in the region are extremely sensitive to political context and election cycles (Ruggiero et al., 2021). The decline in deforestation rates and increases in reforestation rates in Brazil occurred in a period of relative political and economic stability (2004-2015), and were sustained by a strong commitment to reduce deforestation, coupled with the expansion of protected areas and aggressive law enforcement (Nepstad et al., 2009; Tacconi et al., 2019). The AF still has a vast supply of suitable land for forest regeneration (Brancalion et al., 2019; Crouzeilles, Beyer, et al., 2020) and forest recovery we observed in the region between 2004 and 2015 highlights the importance of environmental policies, such as the Atlantic Forest Law created in 2006, for the biome's conservation (Calmon et al., 2011; Rezende et al., 2018). Future policies should aim to not only promote forest regeneration, but also ensure the conservation and permanence of existing forest, both old and new. This approach is also paramount for Brazil to reach its national and international restoration commitments, including its pledge to the Bonn challenge, the Atlantic Forest Restoration Pact (15 Mha by 2050), and the national Native Vegetation Recovery Plan (12 Mha by 2030; Crouzeilles et al., 2019).

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

P.R.P. and M.U. conceptualized the paper. P.R.P., M.R.R., N.B.S., and M.U. developed the methods for analyses. P.R.P. conducted the formal analysis. P.R.P and M.U. wrote the original draft and all authors contributed to the final draft.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in a Dryad repository at https://doi.org/10.5061/dryad.x3ffbg7kw. These data were derived from the following resources available in the public domain: http://mapbiomas.org and https://sidra.ibge.gov.br.

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REFERENCES

Aide, T. M., Clark, M. L., Grau, H. R., López-Carr, D., Levy, M. A., Redo, D., Bonilla-Moheno, M., Riner, G., Andrade-Núñez, M. J., & Muñiz, M. (2013). Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica*, 45, 262–271. https://doi.org/10.1111/j.1744-7429.2012.00908.x

Aide, T. M., Grau, H. R., Graesser, J., Andrade-Nuñez, M. J., Aráoz, E., Barros, A. P., Campos-Cerqueira, M., Chacon-Moreno, E., Cuesta,

- F., Espinoza, R., Peralvo, M., Polk, M. H., Rueda, X., Sanchez, A., Young, K. R., Zarbá, L., & Zimmerer, K. S. (2019). Woody vegetation dynamics in the tropical and subtropical Andes from 2001 to 2014: Satellite image interpretation and expert validation. *Land Use Policy*, 3, 2112–2126. https://doi.org/10.1111/gcb.14618
- Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., & Marcano-Vega, H. (2000). Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. *Restoration Ecology*, 8, 328–338. https://doi.org/10.1046/j.1526-100X.2000.80048.x
- Asner, G. P., Rudel, T. K., Aide, T. M., Defries, R., & Emerson, R. (2009). A contemporary assessment of change in humid tropical forests. *Conservation Biology*, 23, 1386–1395. https://doi.org/10.1111/j.1523-1739.2009.01333.x
- Banks-Leite, C., Pardini, R., Tambosi, L. R., Pearse, W. D., Bueno, A. A., Bruscagin, R. T., Condez, T. H., Dixo, M., Igari, A. T., Martensen, A. C., & Metzger, J. P. (2014). Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science, 345(6200), 1041–1045. https://doi.org/10.1126/science.1255768
- Baptista, S. R. (2008). Metropolization and forest recovery in southern Brazil: A multiscale analysis of the Florianópolis City-Region, Santa Catarina State, 1970 to 2005. *Ecology and Society*, 13, 5.
- Baptista, S. R., & Rudel, T. K. (2006). A re-emerging Atlantic forest? Urbanization, industrialization and the forest transition in Santa Catarina, southern Brazil. Environmental Conservation, 33, 195–202. https://doi.org/10.1017/S0376892906003134
- Baral, H., Guariguata, M. R., & Keenan, R. J. (2016). A proposed framework for assessing ecosystem goods and services from planted forests. *Ecosystem Services*, 22, 260–268. https://doi.org/10.1016/j.ecoser.2016.10.002
- Barbier, E. B., Burgess, J. C., & Grainger, A. (2010). The forest transition: Towards a more comprehensive theoretical framework. *Land Use Policy*, 27, 98–107. https://doi.org/10.1016/j.landusepol.2009.02.001
- Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Nunes-Gutjahr, A. L., Overal, W. L., ... Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America, 104, 18555–18560. https://doi.org/10.1073/pnas.0703333104
- Barretto, A. G. O. P., Berndes, G., Sparovek, G., & Wirsenius, S. (2013). Agricultural intensification in Brazil and its effects on land-use patterns: An analysis of the 1975–2006 period. *Global Change Biology*, 19, 1804–1815. https://doi.org/10.1111/gcb.12174
- Bicudo da Silva, R. F., Batistella, M., Moran, E. F., & Lu, D. (2017). Land changes fostering Atlantic forest transition in Brazil: Evidence from the Paraíba Valley. *The Professional Geographer*, *69*, 80–93. https://doi.org/10.1080/00330124.2016.1178151
- Bicudo da Silva, R. F., Millington, J. D. A., Moran, E. F., Batistella, M., & Liu, J. (2020). Three decades of land-use and land-cover change in mountain regions of the Brazilian Atlantic Forest. *Landscape and Urban Planning*, 204, 103948. https://doi.org/10.1016/j.landurbplan.2020.103948
- Borda-Niño, M., Meli, P., & Brancalion, P. H. S. (2020). Drivers of tropical forest cover increase: A systematic review. *Land Degradation & Development*, 31, 1366–1379. https://doi.org/10.1002/ldr.3534
- Brancalion, P. H. S., & Holl, K. D. (2020). Guidance for successful tree planting initiatives. *Journal of Applied Ecology*, *57*, 2349–2361. https://doi.org/10.1111/1365-2664.13725
- Brancalion, P. H. S., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F. S. M., Almeyda Zambrano, A. M., Baccini, A., Aronson, J., Goetz,

- S., Reid, J. L., Strassburg, B. B. N., Wilson, S., & Chazdon, R. L. (2019). Global restoration opportunities in tropical rainforest landscapes. *Science Advances*, 5, 1–12. https://doi.org/10.1126/sciadv.aav3223
- Breiman, L. (2001). Random forests. Machine Learning, 45, 5-32.
- Brockerhoff, E. G., Jactel, H., Parrotta, J. A., & Ferraz, S. F. B. (2013). Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. *Forest Ecology and Management*, 301, 43–50. https://doi.org/10.1016/j.foreco.2012.09.018
- Bullock, E. L., & Woodcock, C. E. (2021). Carbon loss and removal due to forest disturbance and regeneration in the Amazon. *Science of the Total Environment*, 764, 142839. https://doi.org/10.1016/j.scitotenv.2020.142839
- Calaboni, A., Tambosi, L. R., Igari, A. T. et al (2018). The forest transition in São Paulo, Brazil: Historical patterns and potential drivers. *Ecology and Society*, 23.
- Calmon, M., Brancalion, P. H. S., Paese, A., Aronson, J., Castro, P., da Silva, S. C., & Rodrigues, R. R. (2011). Emerging threats and opportunities for large-scale ecological restoration in the Atlantic forest of Brazil. Restoration Ecology, 19, 154–158. https://doi. org/10.1111/j.1526-100X.2011.00772.x
- Cao, S., Chen, L. I., Shankman, D., Wang, C., Wang, X., & Zhang, H. (2011). Excessive reliance on afforestation in China's arid and semi-arid regions: Lessons in ecological restoration. *Earth-Science Reviews*, 104, 240–245. https://doi.org/10.1016/j.earscirev.2010.11.002
- Chazdon, R. L. (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, 320(5882), 1458– 1460. https://doi.org/10.1126/science.1155365
- Chazdon, R., & Brancalion, P. (2019). Restoring forests as a means to many ends. *Science*, 365(6448), 24–25 https://doi.org/10.1126/science.aax9539
- Chazdon, R. L., Brancalion, P. H. S., Laestadius, L., Bennett-Curry, A., Buckingham, K., Kumar, C., Moll-Rocek, J., Vieira, I. C. G., & Wilson, S. J. (2016). When is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. *Ambio*, 45, 538–550. https://doi.org/10.1007/s13280-016-0772-y
- Chazdon, R. L., Broadbent, E. N., Rozendaal, D. M. A., Bongers, F., Zambrano, A. M. A., Aide, T. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Craven, D., Almeida-Cortez, J. S., Cabral, G. A. L., de Jong, B., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ... Poorter, L. (2016). Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances*, 2, e1501639. https://doi.org/10.1126/sciadv.1501639
- Chazdon, R. L., Lindenmayer, D., Guariguata, M. R., Crouzeilles, R., Rey Benayas, J. M., & Lazos Chavero, E. (2020). Fostering natural forest regeneration on former agricultural land through economic and policy interventions. *Environmental Research Letters*, 15. https://doi.org/10.1088/1748-9326/ab79e6
- Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., Stork, N. E., & Miller, S. E. (2009). The potential for species conservation in tropical secondary forests. *Conservation Biology*, *23*, 1406–1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x
- Clark, M. L., Aide, T. M., & Riner, G. (2012). Land change for all municipalities in Latin America and the Caribbean assessed from 250-m MODIS imagery (2001–2010). *Remote Sensing of Environment*, 126, 84–103. https://doi.org/10.1016/j.rse.2012.08.013
- Costa, R. L., Prevedello, J. A., de Souza, B. G., & Cabral, D. C. (2017). Forest transitions in tropical landscapes: A test in the Atlantic Forest biodiversity hotspot. *Applied Geography*, 82, 93–100. https://doi.org/10.1016/j.apgeog.2017.03.006
- Crk, T., Uriarte, M., Corsi, F., & Flynn, D. (2009). Forest recovery in a tropical landscape: What is the relative importance of biophysical, socioeconomic, and landscape variables? *Landscape Ecology*, 24, 629–642. https://doi.org/10.1007/s10980-009-9338-8

- Crouzeilles, R., Beyer, H. L., Monteiro, L. M., Feltran-Barbieri, R., Pessôa, A. C. M., Barros, F. S. M., Lindenmayer, D. B., Lino, E. D. S. M., Grelle, C. E. V., Chazdon, R. L., Matsumoto, M., Rosa, M., Latawiec, A. E., & Strassburg, B. B. N. (2020). Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. *Conservation Letters*, 13. https://doi.org/10.1111/conl.12709
- Crouzeilles, R., Maurenza, D., Prieto, P. V., Barros, F. S. M., Jakovac, C., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Brancalion, P. H. S., Ceccon, E., Adams, C., Lazos-Chavero, E., Monteiro, L., Junqueira, A. B., Strassburg, B. B. N., & Guariguata, M. R. (2020). Associations between socio-environmental factors and landscape-scale biodiversity recovery in naturally regenerating tropical and subtropical forests. *Conservation Letters*, 14, 1–9. https://doi.org/10.1111/conl.12768
- Crouzeilles, R., Santiami, E., Rosa, M., Pugliese, L., Brancalion, P. H. S., Rodrigues, R. R., Metzger, J. P., Calmon, M., Scaramuzza, C. A. D. M., Matsumoto, M. H., Padovezi, A., Benini, R. D. M., Chaves, R. B., Metzker, T., Fernandes, R. B., Scarano, F. R., Schmitt, J., Lui, G., Christ, P., ... Pinto, S. (2019). There is hope for achieving ambitious Atlantic Forest restoration commitments. *Perspectives in Ecology and Conservation*, *17*, 80–83. https://doi.org/10.1016/j.pecon.2019.04.003
- Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers of global forest loss. *Science*, 361(6407), 1108–1111. https://doi.org/10.1126/science.aau3445
- de Rezende, C. L., Uezu, A., Scarano, F. R., & Araujo, D. S. D. (2015). Atlantic forest spontaneous regeneration at landscape scale. *Biodiversity* and Conservation, 24, 2255–2272. https://doi.org/10.1007/s1053 1-015-0980-y
- DeFries, R., & Rosenzweig, C. (2010). Toward a whole-landscape approach for sustainable land use in the tropics. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 19627–19632. https://doi.org/10.1073/pnas.1011163107
- DeFries, R. S., Rudel, T., Uriarte, M., & Hansen, M. (2010). Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience*, *3*, 178–181. https://doi.org/10.1038/ngeo756
- Ellis, E. C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C., & Watson, J. E. M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences of the United States of America*, 118, 1–8. https://doi.org/10.1073/pnas.2023483118
- Fagan, M. E., DeFries, R. S., Sesnie, S. E., Arroyo, J. P., Walker, W., Soto, C., Chazdon, R. L., & Sanchun, A. (2013). Land cover dynamics following a deforestation ban in northern Costa Rica. *Environmental Research Letters*, 8. https://doi.org/10.1088/1748-9326/8/3/034017
- Fagan, M. E., Reid, J. L., Holland, M. B., Drew, J. G., & Zahawi, R. A. (2020). How feasible are global forest restoration commitments? Conservation Letters, 13, 1–8. https://doi.org/10.1111/conl.12700
- Farinaci, J. S., & Batistella, M. (2012). Variação na cobertura vegetal nativa em São Paulo: Um panorama do conhecimento atual. *Revista Árvore*, *36*, 695–705. https://doi.org/10.1590/S0100-6762201200 0400011
- Feng, X., Fu, B., Piao, S., Wang, S., Ciais, P., Zeng, Z., Lü, Y., Zeng, Y., Li, Y., Jiang, X., & Wu, B. (2016). Revegetation in China's Loess Plateau is approaching sustainable water resource limits. *Nature Climate Change*, 6, 1019–1022. https://doi.org/10.1038/nclimate3092
- Ferreira, M. P., Alves, D. S., & Shimabukuro, Y. E. (2014). Forest dynamics and land-use transitions in the Brazilian Atlantic Forest: The case of sugarcane expansion. *Regional Environmental Change*, 15, 365–377. https://doi.org/10.1007/s10113-014-0652-6

- Foley, J. A., Monfreda, C., Ramankutty, N., & Zaks, D. (2007). Our share of the planetary pie. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 12585–12586. https://doi.org/10.1073/pnas.0705190104
- Grau, H. R., & Aide, M. (2008). Globalization and land-use transitions in Latin America. *Ecology and Society*, 13. https://doi.org/10.5751/ES-02559-130216
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853. https://doi.org/10.1126/science.1244693
- Hansen, M. C., Stehman, S. V., & Potapov, P. V. (2010). Quantification of global gross forest cover loss. Proceedings of the National Academy of Sciences of the United States of America, 107, 8650–8655. https:// doi.org/10.1073/pnas.0912668107
- Hansen, M. C., Stehman, S. V., Potapov, P. V., Loveland, T. R., Townshend, J. R. G., DeFries, R. S., Pittman, K. W., Arunarwati, B., Stolle, F., Steininger, M. K., Carroll, M., & DiMiceli, C. (2008). Humid tropical forest clearing from 2000 to 2005 quantified by using multi-temporal and multiresolution remotely sensed data. *Proceedings of the National Academy of Sciences of the United States of America*, 105(27), 9439–9444. https://doi.org/10.1073/pnas.0804042105
- Heilmayr, R., Echeverría, C., & Lambin, E. F. (2020). Impacts of Chilean forest subsidies on forest cover, carbon and biodiversity. *Nature Sustainability*, 3, 701–709. https://doi.org/10.1038/s41893-020-0547-0
- Heinrich, V. H. A., Dalagnol, R., Cassol, H. L. G., Rosan, T. M., de Almeida, C. T., Silva Junior, C. H. L., Campanharo, W. A., House, J. I., Sitch, S., Hales, T. C., Adami, M., Anderson, L. O., & Aragão, L. E. O. C. (2021). Large carbon sink potential of secondary forests in the Brazilian Amazon to mitigate climate change. *Nature Communications*, 12, 1–11. https://doi.org/10.1038/s41467-021-22050-1
- Holl, K. D., & Brancalion, P. H. S. (2020). Tree planting is not a simple solution. Science, 368(6491), 580–581. https://doi.org/10.1126/ science.aba8232
- IBGE (Instituto Brasileiro de Geografia e Estatística). (2019). Sistema IBGE de Recuperação Automática - SIDRA. https://sidra.ibge.gov. br/acervo
- Iezzi, M. E., Cruz, P., Varela, D., De Angelo, C., & Di Bitetti, M. S. (2018). Tree monocultures in a biodiversity hotspot: Impact of pine plantations on mammal and bird assemblages in the Atlantic Forest. Forest Ecology and Management, 424, 216–227. https://doi.org/10.1016/j.foreco.2018.04.049
- IPEA (Instituto de Pesquisa Econômica Aplicada). (2020). Base de dados econômicos e financeiros. http://www.ipeadata.gov.br/
- Izquierdo, A. E., De Angelo, C. D., & Aide, T. M. (2008). Thirty years of human demography and land-use change in the Atlantic Forest of Misiones, Argentina: An evaluation of the forest transition model. *Ecology and Society*, 13. https://doi.org/10.5751/es-02377-130203
- Lambin, E. F., & Meyfroidt, P. (2010). Land use transitions: Socio-ecological feedback versus socio-economic change. Land Use Policy, 27, 108–118. https://doi.org/10.1016/j.landusepol.2009.09.003
- Lambin, E. F., & Meyfroidt, P. (2011). Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 3465–3472. https://doi.org/10.1073/pnas.1100480108
- Lapola, D. M., Martinelli, L. A., Peres, C. A., Ometto, J. P. H. B., Ferreira, M. E., Nobre, C. A., Aguiar, A. P. D., Bustamante, M. M. C., Cardoso, M. F., Costa, M. H., Joly, C. A., Leite, C. C., Moutinho, P., Sampaio, G., Strassburg, B. B. N., & Vieira, I. C. G. (2014). Pervasive transition of the Brazilian land-use system. *Nature Climate Change*, 4, 27–35. https://doi.org/10.1038/nclimate2056
- Lewis, S. L., Edwards, D. P., & Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*, 349, 827–831. https://doi. org/10.1126/science.aaa9932

- Martinelli, L. A., Garrett, R., Ferraz, S., & Naylor, R. (2011). Sugar and ethanol production as a rural development strategy in Brazil: Evidence from the state of São Paulo. *Agricultural Systems*, 104, 419–428. https://doi.org/10.1016/j.agsy.2011.01.006
- Mather, A. (1992). The forest transition. Area, 24, 367-379.
- Moisen, G. G., Meyer, M. C., Schroeder, T. A., Liao, X., Schleeweis, K. G., Freeman, E. A., & Toney, C. (2016). Shape selection in Landsat time series: A tool for monitoring forest dynamics. *Global Change Biology*, 22, 3518–3528. https://doi.org/10.1111/gcb.13358
- Molin, P. G., Gergel, S. E., Soares-Filho, B. S., & Ferraz, S. F. B. (2017). Spatial determinants of Atlantic Forest loss and recovery in Brazil. Landscape Ecology, 32, 857–870. https://doi.org/10.1007/s1098 0-017-0490-2
- Nanni, A. S., & Grau, H. R. (2014). Agricultural adjustment, population dynamics and forests redistribution in a subtropical watershed of NW Argentina. *Regional Environmental Change*, 14, 1641–1649. https://doi.org/10.1007/s10113-014-0608-x
- Nanni, A. S., Sloan, S., Aide, T. M., Graesser, J., Edwards, D., & Grau, H. R. (2019). The neotropical reforestation hotspots: A biophysical and socioeconomic typology of contemporary forest expansion. Global Environmental Change, 54, 148–159. https://doi.org/10.1016/j.gloenvcha.2018.12.001
- Nepstad, D., Soares-Filho, B. S., Merry, F., Lima, A., Moutinho, P., Carter, J., Bowman, M., Cattaneo, A., Rodrigues, H., Schwartzman, S., McGrath, D. G., Stickler, C. M., Lubowski, R., Piris-Cabezas, P., Rivero, S., Alencar, A., Almeida, O., & Stella, O. (2009). The end of deforestation in the Brazilian Amazon. *Science*, 326(5958), 1350–1351. https://doi.org/10.1126/science.1182108
- Nunes, S., Oliveira, L., Siqueira, J., Morton, D. C., & Souza, C. M. (2020). Unmasking secondary vegetation dynamics in the Brazilian Amazon. *Environmental Research Letters*, 15. https://doi. org/10.1088/1748-9326/ab76db
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988–993. https://doi.org/10.1126/science.1201609
- Parés-Ramos, I. K., Gould, W. A., & Aide, T. M. (2008). Agricultural abandonment, suburban growth, and forest expansion in Puerto Rico between 1991 and 2000. *Ecology and Society*, 13, 1. https://doi.org/10.5751/ES-02479-130201
- Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Craven, D., de Almeida-Cortez, J. S., Cabral, G. A. L., de Jong, B. H. J., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ... Rozendaal, D. M. A. (2016). Biomass resilience of Neotropical secondary forests. *Nature*, 530, 211–214. https://doi.org/10.1038/nature16512
- Redo, D. J., Aide, T. M., & Clark, M. L. (2012). The relative importance of socioeconomic and environmental variables in explaining land change in Bolivia, 2001–2010. *Annals of the Association of American Geographers*, 102, 778–807. https://doi.org/10.1080/00045608.2012.678036
- Redo, D., Aide, T. M., & Clark, M. L. (2013). Vegetation change in Brazil's dryland ecoregions and the relationship to crop production and environmental factors: Cerrado, Caatinga, and Mato Grosso, 2001–2009. Journal of Land Use Science, 8, 123–153. https://doi. org/10.1080/1747423X.2012.667448
- Redo, D. J., Grau, H. R., Aide, T. M., & Clark, M. L. (2012). Asymmetric forest transition driven by the interaction of socioeconomic development and environmental heterogeneity in Central America. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 8839–8844. https://doi.org/10.1073/pnas.1201664109
- Reid, J. L., Fagan, M. E., Lucas, J., Slaughter, J., & Zahawi, R. A. (2019). The ephemerality of secondary forests in southern Costa Rica. *Conservation Letters*, 12(2). https://doi.org/10.1111/conl.12607

- Reid, J. L., Wilson, S. J., Bloomfield, G. S., Cattau, M. E., Fagan, M. E., Holl, K. D., & Zahawi, R. A. (2017). How long do restored ecosystems persist? *Annals of the Missouri Botanical Garden*, 102, 258–265. https://doi.org/10.3417/2017002
- Rezende, C. L., Scarano, F. R., Assad, E. D., Joly, C., Metzger, J., Strassburg, B., Tabarelli, M., Fonseca, G. A., & Mittermeier, R. (2018). From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation*, 16, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002
- Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021
- Rosa, M. R., Brancalion, P. H. S., Crouzeilles, R. Tambosi, L. R., Piffer, P. R., Lenti, F. E. B., Hirota, M., Santiami, E., & Metzger, J. P. (2021). Hidden destruction of older forests threatens Brazil's Atlantic Forest and challenges restoration programs. *Science Advances*, 7(eabc4547).
- Rudel, T. K., Coomes, O. T., Moran, E., Achard, F., Angelsen, A., Xu, J., & Lambin, E. (2005). Forest transitions: Towards a global understanding of land use change. *Global Environmental Change*, 15, 23–31. https://doi.org/10.1016/j.gloenvcha.2004.11.001
- Rudel, T. K., Meyfroidt, P., Chazdon, R., Bongers, F., Sloan, S., Grau, H. R., Van Holt, T., & Schneider, L. (2020). Whither the forest transition? Climate change, policy responses, and redistributed forests in the twenty-first century. Ambio, 49, 74–84. https://doi.org/10.1007/ s13280-018-01143-0
- Rudel, T. K., Schneider, L., & Uriarte, M. (2010). Forest transitions: An introduction. *Land Use Policy*, 27, 95–97. https://doi.org/10.1016/j. landusepol.2009.09.021
- Rudel, T. K., Sloan, S., Chazdon, R., & Grau, R. (2016). The drivers of tree cover expansion: Global, temperate, and tropical zone analyses. *Land Use Policy*, 58, 502–513. https://doi.org/10.1016/j.landu sepol.2016.08.024
- Ruggiero, P. G. C., Pfaff, A., Nichols, E., Rosa, M., & Metzger, J. P. (2021). Election cycles affect deforestation within Brazil's Atlantic Forest. Conservation Letters, 1–11. https://doi.org/10.1111/conl.12818
- Schwartz, N. B., Aide, T. M., Graesser, J., Grau, H. R., & Uriarte, M. (2020). Reversals of reforestation across Latin America limit climate mitigation potential of tropical forests. *Frontiers in Forests and Global Change*, 3, 1–10. https://doi.org/10.3389/ffgc.2020.00085
- Schwartz, N. B., Uriarte, M., DeFries, R., Gutierrez-Velez, V. H., & Pinedo-Vasquez, M. A. (2017). Land-use dynamics influence estimates of carbon sequestration potential in tropical second-growth forest. Environmental Research Letters, 12, 074023. https://doi. org/10.1088/1748-9326/aa708b
- Silva Junior, C. H. L., Heinrich, V. H. A., Freire, A. T. G., Broggio, I. S., Rosan, T. M., Doblas, J., Anderson, L. O., Rousseau, G. X., Shimabukuro, Y. E., Silva, C. A., House, J. I., & Aragão, L. E. O. C. (2020). Benchmark maps of 33 years of secondary forest age for Brazil. Scientific Data, 7, 1–9. https://doi.org/10.1038/s41597-020-00600-4
- Silva, R. F. B. D., Batistella, M., & Moran, E. F. (2016). Drivers of land change: Human-environment interactions and the Atlantic forest transition in the Paraíba Valley, Brazil. *Land Use Policy*, 58, 133–144. https://doi.org/10.1016/j.landusepol.2016.07.021
- Silver, W. L., Ostertag, R., & Lugo, A. E. (2000). The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration Ecology*, 8, 394–407. https://doi.org/10.1046/j.1526-100X.2000.80054.x
- Sloan, S. (2008). Reforestation amidst deforestation: Simultaneity and succession. Global Environmental Change, 18, 425–441. https://doi. org/10.1016/j.gloenvcha.2008.04.009
- Sloan, S. (2016). Tropical forest gain and interactions amongst agents of forest change. Forests, 7, 1–23. https://doi.org/10.3390/f7030055
- Sloan, S., Meyfroidt, P., Rudel, T. K., Bongers, F., & Chazdon, R. (2019). The forest transformation: Planted tree cover and regional dynamics

- of tree gains and losses. *Global Environmental Change*, *59*, 101988. https://doi.org/10.1016/j.gloenvcha.2019.101988
- Smith, C. C., Espírito-Santo, F. D. B., Healey, J. R., Young, P. J., Lennox, G. D., Ferreira, J., & Barlow, J. (2020). Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon. *Global Change Biology*, 26(12), 7006–7020. https://doi.org/10.1111/gcb.15352
- Song, X.-P., Hansen, M. C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E. F., & Townshend, J. R. (2018). Global land change from 1982 to 2016. *Nature*, 560, 639–643. https://doi.org/10.1038/ s41586-018-0411-9
- Souza, C. M., Z. Shimbo, J., Rosa, M. R., Parente, L. L., A. Alencar, A., Rudorff, B. F. T., Hasenack, H., Matsumoto, M., G. Ferreira, L., Souza-Filho, P. W. M., de Oliveira, S. W., Rocha, W. F., Fonseca, A. V., Marques, C. B., Diniz, C. G., Costa, D., Monteiro, D., Rosa, E. R., Vélez-Martin, E., ... Azevedo, T. (2020). Reconstructing three decades of land use and land cover changes in Brazilian biomes with landsat archive and earth engine. *Remote Sensing*, 12, 2735. https:// doi.org/10.3390/rs12172735
- Strassburg, B. B. N., Barros, F. S. M., Crouzeilles, R., Iribarrem, A., Santos, J. S. D., Silva, D., Sansevero, J. B. B., Alves-Pinto, H. N., Feltran-Barbieri, R., & Latawiec, A. E. (2016). The role of natural regeneration to ecosystem services provision and habitat availability: A case study in the Brazilian Atlantic Forest. *Biotropica*, 48, 890–899. https://doi.org/10.1111/btp.12393
- Tacconi, L., Rodrigues, R. J., & Maryudi, A. (2019). Law enforcement and deforestation: Lessons for Indonesia from Brazil. Forest Policy and Economics, 108, 101943. https://doi.org/10.1016/j. forpol.2019.05.029

- Teixeira, A. M. G., Soares-Filho, B. S., Freitas, S. R., & Metzger, J. P. (2009). Modeling landscape dynamics in an Atlantic Rainforest region: Implications for conservation. Forest Ecology and Management, 257, 1219–1230. https://doi.org/10.1016/j.foreco.2008.10.011
- Wang, Y., Ziv, G., Adami, M., Almeida, C. A. D., Antunes, J. F. G., Coutinho, A. C., Esquerdo, J. C. D. M., Gomes, A. R., & Galbraith, D. (2020). Upturn in secondary forest clearing buffers primary forest loss in the Brazilian Amazon. *Nature Sustainability*, 3, 290–295. https://doi.org/10.1038/s41893-019-0470-4
- Yackulic, C. B., Fagan, M., Jain, M., Jina, A., Lim, Y., Marlier, M., Muscarella, R., Adame, P., DeFries, R., & Uriarte, M. (2011). Biophysical and socioeconomic factors associated with forest transitions at multiple spatial and temporal scales. *Ecology and Society*, 16, 15. https://doi. org/10.5751/ES-04275-160315

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