



LETTER

Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration

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Abstract

High costs of tree planting are a barrier to meeting global forest restoration targets. Natural forest regeneration is more cost-effective than tree planting, but its potential to foster restoration at scale is poorly understood. We predict, map, and quantify natural regeneration potential within 75.5 M ha of deforested lands in the Brazilian Atlantic Forest. Of 34.1 M ha (26.4%) of current forest cover, 2.7 M ha (8.0%) regenerated naturally from 1996 to 2015. We estimate that another 2.8 M ha could naturally regenerate by 2035, and a further 18.8 M ha could be restored using assisted regeneration methods, thereby reducing implementation costs by US\$ 90.6 billion (77%)

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compared to tree planting. These restored forests could sequester 2.3 GtCO₂ of carbon, reduce the mean number of expected species at risk of extinction by 63.4, and reduce fragmentation by 44% compared to current levels. Natural regeneration planning is key for achieving cost-effective large-scale restoration.

KEY WORDS

assisted regeneration, conservation planning, restoration targets, tree planting, tropical and subtropical forests

1 | INTRODUCTION

Forest and landscape restoration has the potential to counteract some of the profound negative global impacts of human development on environmental systems. It can deliver multiple benefits such as climate change mitigation, habitat for biodiversity, and sustainable livelihoods for people (Chazdon & Guariguata, 2016; Holl, 2017). In practice, however, restoration is difficult, lengthy, expensive, and budget-limited (Chazdon & Guariguata 2016; Crouzeilles et al., 2016). Ambitious international commitments to restore 350 M ha of global degraded and deforested lands in the coming decades (Chazdon et al., 2017) could be supported by an estimated US\$ 18 billion in investment per year globally (Menz, Dixon, & Hobbs, 2013). Yet, activities involved in “active restoration” such as tree planting and soil preparation could cost up to US\$ 34,000 per ha (Catterall & Harrison, 2006), incurring a potential total implementation cost of US\$ 12 trillion to achieve such targets. Active restoration is a costly strategy for achieving forest restoration at a large scale, emphasizing the need to identify and assess alternative, cost-effective opportunities (Nunes, Soares-Filho, Rajão, & Merry, 2017).

Although natural regeneration (the spontaneous or assisted recovery of native tree species that colonize and establish in abandoned fields or natural disturbances) has been shown to provide more cost-effective outcomes compared to active restoration (e.g., Crouzeilles et al., 2017; Lamb, 2014; Nunes et al., 2017; Poorter et al., 2016), policy-makers and restoration practitioners often prefer active restoration methods (Chazdon, 2014; Chazdon & Guariguata, 2016). Factors potentially limiting greater uptake of natural regeneration are the uncertainty associated with where it occurs, how long it takes to recover forest structure and diversity, and how much area could be regenerated (Arroyo-Rodríguez et al., 2017). Several environmental and socioeconomic drivers operate across a range of scales to influence the effectiveness and likelihood of natural regeneration (Chazdon, 2014; Crk, Uriarte, Corsi, & Flynn, 2009). Environmental drivers affect plant germination, growth, and survival (e.g., temperature, rainfall, soil conditions) and the availability of seeds and sprouts (e.g., distance to existing forests, previous land use). Socioeconomic

drivers shape where regeneration is permitted to occur and persist (e.g., opportunity costs, proximity to roads and markets) (Chazdon & Guariguata, 2016; Crk et al., 2009; Reid, Fagan, Lucas, Slaughter, & Zahawi, 2019). Although predicting the potential rate and location of natural regeneration through time is inherently difficult, such knowledge is critical to assist policy-makers and stakeholders to achieve restoration targets and to deliver socio-environmental benefits cost-effectively (Chazdon & Guariguata, 2016; Nunes et al., 2017).

Here, we predict, map, and quantify the potential for natural regeneration within 75.5 M ha of deforested land in the Brazilian Atlantic Forest, one of the world’s most threatened biodiversity hotspots and the largest tropical forest restoration hotspot (Brancalion et al., 2019). Widespread deforestation across the 129 M ha of Atlantic Forest over the last centuries has spared only 34.1 M ha (26.4%) of original forest, including many highly fragmented remnants (Figure 1a). Large-scale restoration in the coming decades is being facilitated by three key factors: (i) the Native Vegetation Protection Law which requires the reforestation of ca. 6 M ha of private lands within the Atlantic Forest (Soares-Filho et al., 2014); (ii) the National Policy for Native Revegetation which fosters the enabling conditions for large-scale restoration (Ministério do Meio Ambiente, 2017); and (iii) the Atlantic Forest Restoration Pact which is a bottom-up initiative aiming to implement 15 M ha of restoration on the ground by 2050 (Holl, 2017). These proposed restoration targets of between 6 and 15 M ha by 2050 (Holl, 2017; Soares-Filho et al., 2014) could cost up to US\$ 33–82 billion if only active restoration methods are used (Benini & Adeodato, 2017). Moreover, indirect “opportunity” costs associated with removal of land from agricultural and pastoral production could add at least US\$ 20 billion to total restoration cost (opportunity and implementation costs) (Crouzeilles, Beyer, Mills, Grelle, & Possingham, 2015). Restoration targets will, therefore, be achieved only if low-cost but ecologically effective restoration strategies are identified which can be applied at scale and that minimize competition with agricultural production systems.

We use time-series remote sensing data to identify where natural regeneration occurred spontaneously between 1996 and 2015 and to identify the environmental and

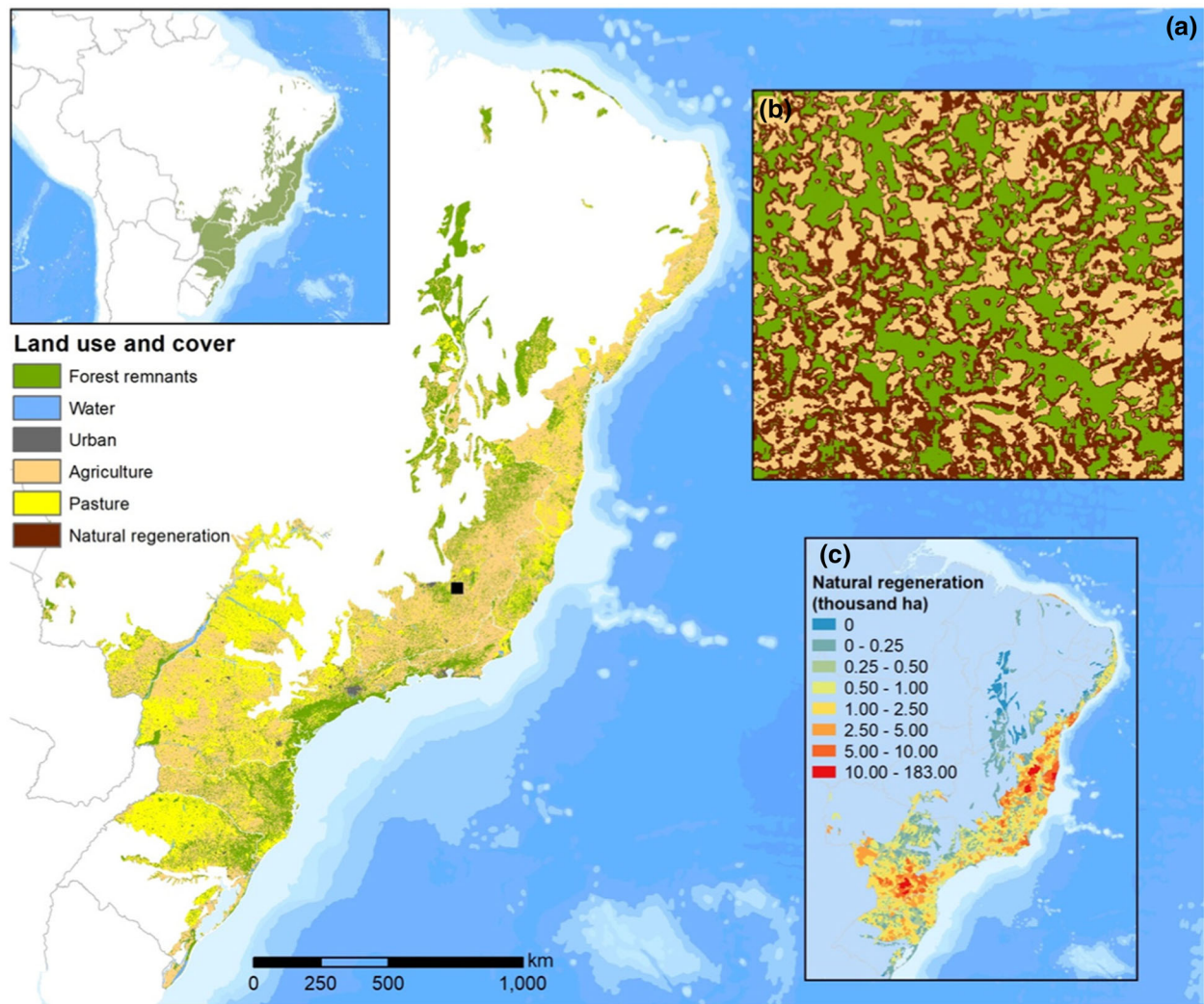


FIGURE 1 (a) Land use and cover in the Brazilian Atlantic Forest. (b) Expanded view of an area to illustrate the pattern of natural regeneration that occurred between 1996 and 2015. (c) Area that regenerated (1996–2015) expressed as a proportion of the area potentially available for regeneration within each of the 3350 counties analyzed

socioeconomic factors associated with this natural regeneration. Using validated, predictive models, we then estimate and map where and how much area could be regenerated over the next 20 years under different restoration scenarios that account for natural regeneration potential and opportunity cost. We then quantify restoration costs and benefits for each scenario. This work demonstrates how quantitative, high resolution (but large scale), spatially explicit assessments of past natural regeneration and future regeneration potential can be developed and applied to inform forest restoration planning and implementation.

2 | METHODS

We identified where natural regeneration occurred in the Atlantic Forest during the last 20 years (from 1996 to 2015) using 30-m resolution remote-sensing products (“Map-

biomas” Collection 3; <http://mapbiomas.org>) and geospatial mapping to exclude any areas of regrowth that resulted from either active restoration initiatives or commercial forestry operations (see Supporting Information for details). We define natural regeneration conservatively as areas of at least 5 contiguous pixels (0.45 ha) that were previously classified as agriculture or pasture for at least 5 consecutive years and that persisted for at least 3 consecutive years (and were standing in 2017) to minimize the potential for pixel-scale classification error to influence the assessment (following Crouzeilles et al., 2019; Supporting Information).

We modeled the observed proportion of natural regeneration within each “município” (henceforth “county”; $n = 3350$) as a function of a suite of environmental and socioeconomic factors that we postulated are potential drivers of natural regeneration using Random Forest regression models (see Supporting Information for details). The proportion of natural regeneration was defined as the area of land

that regenerated divided by the area of potentially restorable land, excluding areas that were already forested or that were unavailable for regeneration, such as urban and water areas. We used the predictive model to estimate the proportion of remaining potentially restorable land within each county that could regenerate naturally over the next 20 years within each county, under the assumption that the environmental, climatic, and socioeconomic conditions related to natural regeneration over the past two decades persisted for another two decades.

We also modeled the local (pixel-based) spatial probability of occurrence of natural regeneration as a function of a suite of environmental and socioeconomic factors using Random Forest classification models (see Supporting Information for details). The dependent variable was a balanced sample of 10,000 pixels that naturally regenerated (1) or could have naturally regenerated but did not (0), randomly sampled within each class. We then applied this model to all pixels that were potentially restorable to generate a spatially explicit prediction of the potential for natural regeneration at a 30-m resolution. For both the county and pixel-scale models, we used k -fold cross validation to validate the predictive power of the models. We provide details of modeling procedures and variables in the Supporting Information.

We used both the predicted area of natural regeneration within each county over the next 20 years and occurrence of natural regeneration to predict where natural regeneration may occur under four scenarios. In a “maximum potential” scenario, we assumed that land management practices that currently inhibit natural regeneration, such as cultivation and grazing, cease in the areas with potential for natural regeneration (>50%). The other three scenarios limited natural regeneration to areas in which the probability of natural regeneration is at least 50% and the opportunity cost is ranked as “low” (<US\$ 1,289 ha⁻¹ year⁻¹), “medium” (<US\$ 2,577 ha⁻¹ year⁻¹) or “high” (<US\$ 5,155 ha⁻¹ year⁻¹). Focusing regeneration in areas of low opportunity cost reduces potential conflicts with agricultural production. For each scenario, we used the spatially explicit map of regenerated areas to estimate the: (i) implementation cost savings relative to tree planting, (ii) annual opportunity cost, (iii) change in sequestered carbon (Strassburg et al., 2019), (iv) biodiversity community integrity index (the proportion of 200 ha areas in the landscape that contain at least 30% forest; Banks-Leite et al., 2014), (v) change in the extinction risk of 794 endemic species (Strassburg et al., 2019), and (vi) three measures of forest fragmentation (the number of patches, the mean patch size, and the largest patch size), relative to current conditions (see Supporting Information for details). We assumed a 2018 exchange rate of US\$ 1 to R\$ 3.88 throughout.

3 | RESULTS

We found that 2.72 M ha of forest regenerated naturally between 1996 and 2015 (Figure 1b), representing an area equivalent to 8.0% of the existing remnant forest area. The area that regenerated, expressed as a proportion of the area potentially available for regeneration (cleared, agricultural and active pasture lands) within each of the 3350 counties analyzed, averaged 5.5% (range 0.0–85.7%; 6.80% SD) (Figure 1c). A predictive model based on 10 variables related to landscape conditions, soil properties, climate, topographic relief, and past disturbance intensity related to pasture and sugarcane production explained 80.2% of the variation among counties in the proportion of area that naturally regenerated (Figure S1A). The proportion of area regenerated was particularly strongly associated with the proportion of the county that was forested (Figure S2). The predictive model accuracy, assessed using Pearson's r correlation between predicted and observed areas, was, on average, 0.91 (range 0.83–0.95 accessed using k -fold cross validation, where $k = 10$; Figure S3). Based on this model, and assuming that the conditions that facilitated natural regeneration over the last 20 years persist for the next 20 years, we predicted that another 2.80 M ha could naturally regenerate between 2015 and 2035 (Figure 2a).

The pixel-based occurrence of natural regeneration, i.e. presence or absence of natural regeneration rather than the amount of area as reported above, could be predicted, on average, with 76.9% accuracy (range 74.4–79.7%, assessed using k -fold cross validation) based on a model with 15 variables related to landscape conditions, soil properties, climate, topographic relief, and agricultural production (Figure S4). Spatially explicit predictions based on this model indicated that the potential for natural regeneration is widespread across the Atlantic Forest, but is lower in the southwestern areas and higher in the “Floresta de Interior” biogeographic subregion (Figure 2b). The most important predictor of the occurrence of natural regeneration was the proximity to forest, with 90% of regeneration sites occurring within 192 m of other forested areas. Indeed, this variable alone could discriminate between presence and absence of regeneration sites with an accuracy of 72.3% (range 70.4–75.1%) (Figure S4).

We estimated that 0.89, 7.97, 15.7, or 21.6 M ha of the degraded land could be suitable for natural regeneration under the low, medium, high, and maximum scenarios respectively (Figure 3). The regeneration resulting from these four scenarios would result in cost savings (assisted natural regeneration relative to tree planting) of US\$ 3.74, 33.6, 65.6, and 90.6 billion, above-ground carbon sequestration of 0.08, 0.85, 1.69, and 2.30 GtCO₂, an increase in the biodiversity community integrity index of 0.9%, 8.4%, 16.9%, and 20.6%, and a

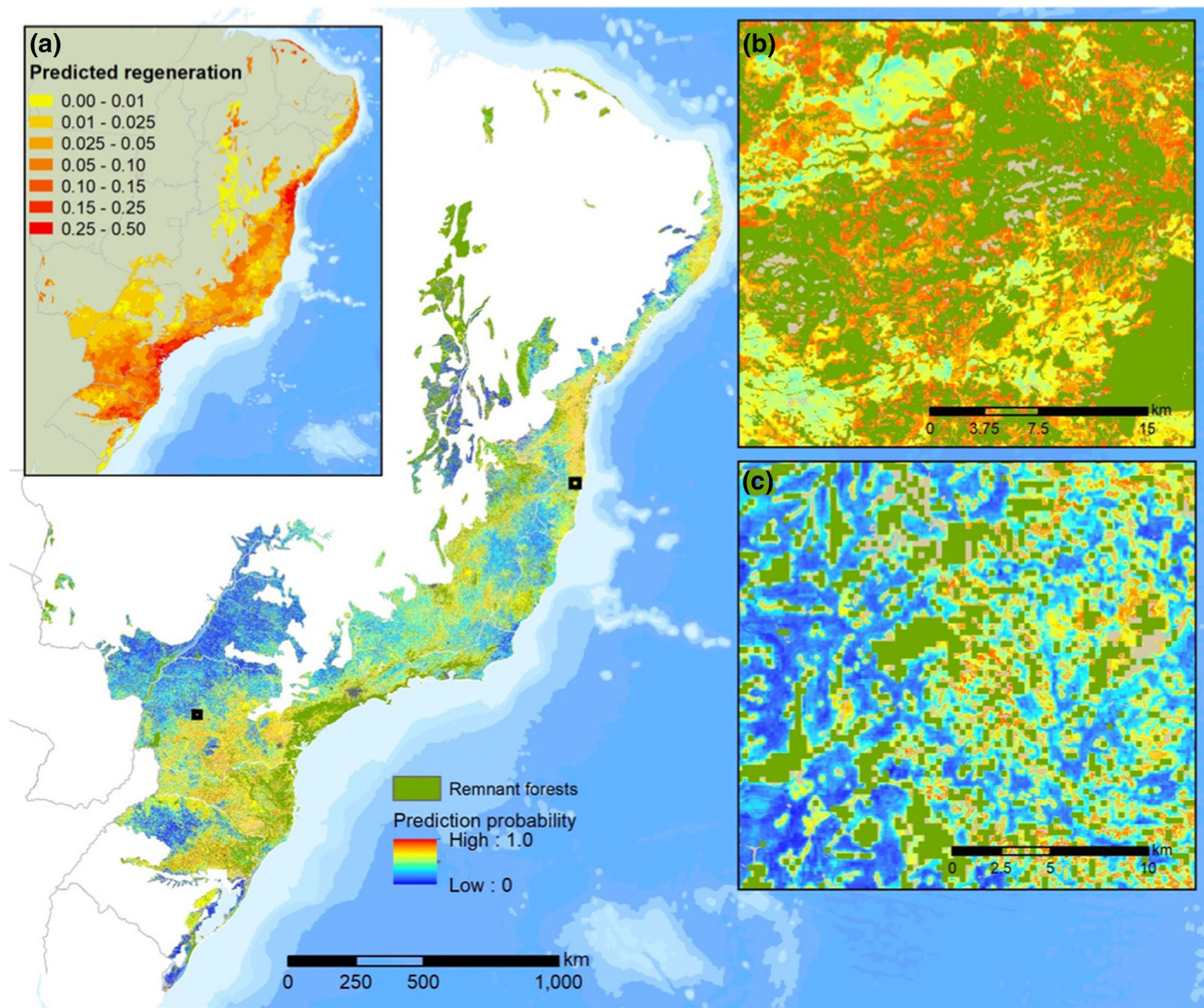


FIGURE 2 (a) Predicted area that could spontaneously regenerate (2016–2035) expressed as a proportion of the area potentially available for regeneration within each of the 3350 counties analyzed. (b) Potential for natural regeneration in the Brazilian Atlantic Forest. (c) Expanded view of an area to illustrate the pattern of the potential for natural regeneration

reduction in the mean number of expected endemic species extinctions of 4.99, 26.6, 49.1, and 63.4, respectively, relative to current conditions (Table 1). Restoration also mitigated forest fragmentation, reducing the number of fragments from 2.19 to 2.16, 1.97, 1.74, and 1.23 M, and increasing fragment size from 15.6 to 16.2, 21.4, 28.6 and 45.4 ha, respectively (Table 1).

4 | DISCUSSION

Natural forest regeneration has occurred over a substantial area (2.72 M ha) of the Atlantic Forest over the past 20 years. The process of natural regeneration appears to be associated with enabling socioeconomic and environmental conditions, as demonstrated by the high proportion of variance explained and classification accuracy in the county-

and pixel-scale models (80.2% and 76.9%, respectively). This work indicated there is strong potential for identifying areas in which natural regeneration is likely to be feasible and, conversely, areas where more intensive and costly restoration strategies are likely to be needed to foster forest restoration at scale. Models that have strong predictive accuracy are particularly useful for informing planning and implementation because higher certainty in management outcomes can reduce the need to invest in some risk assessment and mitigation measures.

In the Atlantic Forest, there is an ample supply of land that appears to be suitable for natural regeneration (21.6 M ha) relative to the area that is targeted for restoration by 2030–2050 (6–15 M ha). Hence, there are substantial opportunities to capitalize on natural regeneration as a cost-effective strategy for achieving ambitious restoration targets (Chazdon & Guariguata, 2016; Crouzeilles et al., 2017). The potential for

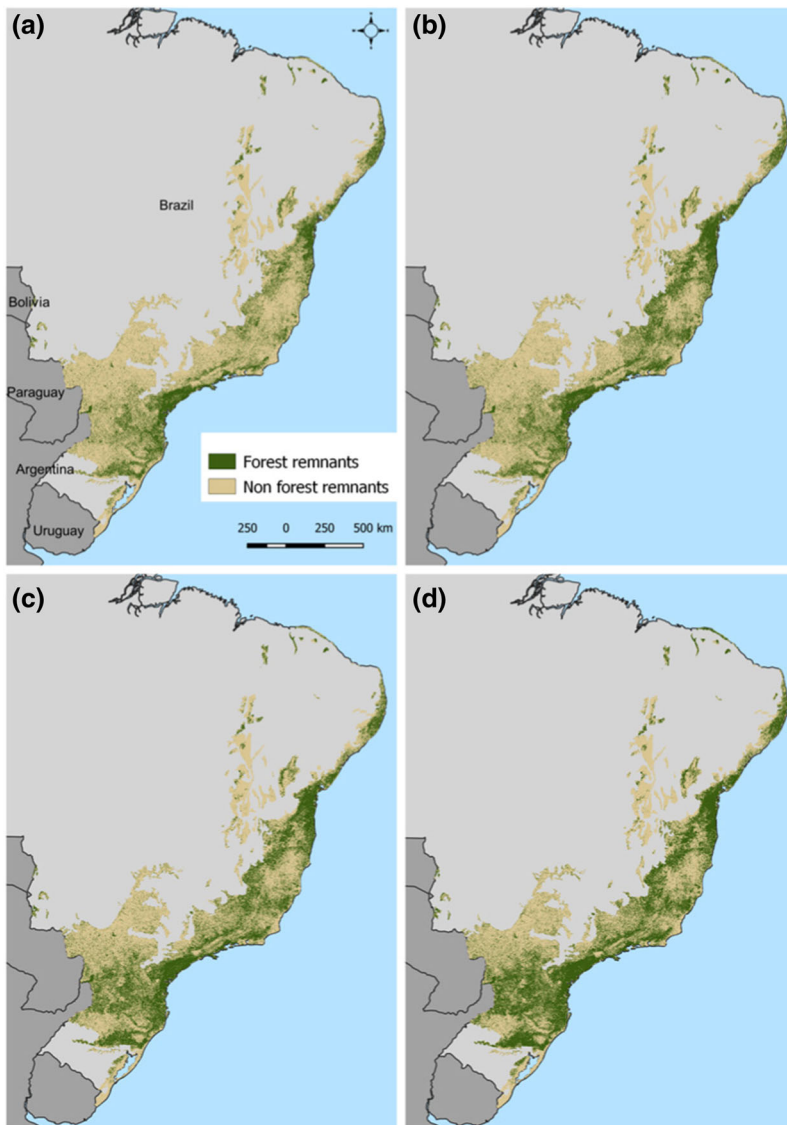


FIGURE 3 New configuration of the Atlantic Forest remnants in a restored scenario including areas with >50% potential for natural regeneration: (a) and opportunity costs ranked as “low” (<math><US\\$ 1,289 \text{ ha}^{-1} \text{ year}^{-1}</math>), (b) and opportunity costs ranked as “medium” (<math><US\\$ 2,577 \text{ ha}^{-1} \text{ year}^{-1}</math>), (c) and opportunity costs ranked as “high” (<math><US\\$ 5,155 \text{ ha}^{-1} \text{ year}^{-1}</math>), and (d) only (Maximum potential)

natural regeneration is greater in areas with intermediate levels of forest cover as these areas tend to have the most amount of cleared land near a remnant forest edge. The mechanism by which proximity to forest promotes natural regeneration is through greater diversity and rates of seed dispersal (Chazdon, 2014; Crk et al., 2009). Other factors that may be contributing to natural regeneration in the Atlantic Forest include laws that prohibit deforestation in secondary forests (Atlantic Forest Law), improved monitoring and enforcement actions (e.g., SOS Mata Atlântica & INPE), and the activities of a bottom-up restoration program—the Atlantic Forest Restoration Pact (Crouzeilles et al., 2019).

Natural forest restoration is a particularly important management strategy because it has the potential to be applied cost-effectively and at scale, which is a key obstacle for achieving globally significant levels of carbon sequestration, biodiversity benefits, and improvement to the provision of other ecosystem services (Chazdon & Guariguata,

2016; Crouzeilles et al., 2017). In the Atlantic Forest, for example, increasing total forest cover in the biome by 16.7% under the “maximum potential” scenario could increase biodiversity community integrity (the proportion of 200 ha units containing at least 30% forest) from the current value of 32.7% to 53.3%, reduce fragmentation by 43.9%, and reduce the expected mean number of endemic species extinction by 63.4 species (Table 1). Natural regeneration also can improve landscape configuration and connectivity, which will benefit species persistence in the long-term (Molin, Chazdon, Frosini de Barros Ferraz, & Brancalion, 2018; Strassburg et al., 2016). It is also a low-tech, low-energy, low-risk climate mitigation strategy relative to some labor intensive or technology focused alternatives, hence can be widely implemented by a broad range of stakeholders globally.

Assisted natural regeneration could save up to US\$ 90.6 billion compared to a restoration scenario based on tree planting (Table 1), corresponding to cost savings of 76% among the

TABLE 1 Assessment of the costs and benefits (carbon, biodiversity, fragmentation) associated with four scenarios of natural forest regeneration in the Atlantic Forest. The Low, Medium and High scenarios reflect restoration occurring in lands below three thresholds in opportunity cost (US\$ 1,289, US\$ 2,577, and US\$ 5,155 ha⁻¹ year⁻¹ respectively), while Maximum potential refers to the restoration of all lands where the potential for natural restoration is greater than 0.5. Cost savings refers to savings relative to the estimated costs of active reforestation methods based on full tree planting protocols

Scenario	Regenerated area (M ha)	Cost saving (US\$ Bi)	Opportunity costs (US\$ Bi year ⁻¹)	Delta sequestered Carbon (GtCO ₂)	Delta biodiversity community integrity (%)	Delta # reduction expected in species extinctions	Number of patches (M)	Mean patch size (ha)	Largest patch size (M ha)
Low	0.89	3.7	1.07	0.08	0.9	4.99	2.16	16.2	8.04
Medium	7.97	33.6	16.4	0.85	8.4	26.6	1.97	21.4	8.05
High	15.7	65.6	41.7	1.69	16.9	49.1	1.74	28.6	19.8
Maximum potential	21.6	90.6	49.1	2.30	20.6	63.4	1.23	45.4	23.5

four scenarios evaluated. However, although active restoration is more expensive than tree planting, it provides greater control over the mix of tree species grown and can therefore provide more certain long-term financial returns through the provision of sustainable forestry and agroforestry products (Baral, Guariguata, & Keenan, 2016). Further work is required to examine the cost and benefits to landowners of these alternative strategies to forest restoration in order to better inform landowner decisions and policy changes.

Total restoration costs include both implementation and opportunity costs, but opportunity costs can be substantially higher than implementation costs for natural regeneration (Molin et al., 2018). One limitation of our analysis is that the opportunity costs do not account for profitability that could eventually arise from sustainable forestry and forest products, nor do they include potential landowner compensation through Payments for Environmental Services schemes (Ruggiero, Metzger, Reverberi Tambosi, & Nichols, 2019), hence the opportunity costs we report are an overestimate. Transitions to forest industries could be more profitable than marginal agricultural lands in some areas, thereby more than offsetting opportunity costs over the long-term. A transition from agricultural land to sustainably managed forest could take 20 years or more. Strategies are needed to bridge this “forest restoration gap” to ensure that livelihoods can be maintained during transition periods, such as through the use of crops that can be grown in regenerating areas without impeding regeneration (Maier, Benini, Fachini, & Santana, 2018). Given that the poorest landowners are the least able to afford the costs of restoration, Payment for Ecosystem Services and other public investments are important for helping to avoid the risk that legislated restoration targets exacerbate social inequality (Ruggiero et al., 2019). However, payments need to be implemented at a substantially higher rate than the current US\$ 70 ha⁻¹ year⁻¹ even to cover implementation costs.

Forest restoration strategies must minimize competition with food production in the context of a growing human population over the coming decades (Strassburg et al., 2019). Some impact on food production may be unavoidable as the potentially restorable areas are agricultural and pasture lands. However, rates of food production from marginal agricultural lands are often low, and could be straightforward to offset through intensification of food production in more fertile areas, and a gradual shift to a more plant-based diet (Willett et al., 2019). Moreover, low productivity agricultural areas are being abandoned in the State of São Paulo, as people migrate into urban areas for employment (Calaboni et al., 2018; da Silva, Batistella, & Moran, 2018). Market trading schemes that allow landowners in areas of strong agricultural production to buy restoration offsets from landowners in other areas may be an important mechanism for reducing competition with food production and ensuring that poorer landowners are not disadvantaged.

The work we have reported here demonstrates a substantial opportunity for cost-effective, large-scale natural and assisted regeneration in Brazil's Atlantic Forest that would provide both biodiversity and ecosystem service benefits. It is, however, essential that government, funders, NGOs, landowners and local communities cooperate to facilitate natural forest regeneration and reduce the opportunity costs. Given the modest data requirements, it would be straightforward to extend the methods developed here to other biomes and regions. Prioritizing natural forest regeneration in the most suitable areas will ensure that limited funds for restoration can achieve maximum benefit (Chazdon & Guariguata, 2016). A central challenge for the coming years is to develop environmental policies and initiatives that use restoration planning to maximize return-on-investment in forest regeneration across multiple socioeconomic and ecological objectives while minimizing competition with food production, consequently helping countries worldwide to achieve the ambitious targets of global forest restoration.

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REFERENCES

- Arroyo-Rodríguez, V., Melo, F. P. L., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., ... Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: New insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, *92*, 326–340.
- Banks-Leite, C., Pardini, R., Tambosi, L. R., Pearse, W. D., Bueno, A. A., Bruscajin, R. T., ... Metzger, J. P. (2014). Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science*, *345*, 1041–1045.
- Baral, H., Guariguata, M. R., & Keenan, R. J. (2016). A proposed framework for assessing ecosystem goods and services from planted forests. *Ecosystems Services*, *22*, 260–268.
- Benini, R., & Adeodato, S. (2017). *Forest restoration economy*. Retrieved from https://www.researchgate.net/publication/319044099_FOREST_RESTORATION_ECONOMY_RESTAURACAO_ECONOMIA_DA_FLORESTAL
- Brançalion, P. H. S., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F. S. M., Almeyda-Zambrano, A. M., ... Chazdon, R. (2019). Global restoration opportunities in tropical rainforest landscapes. *Science Advances*, *5*, EAAV3223.
- Calaboni, A., Tambosi, L. R., Igari, A. T., Farinaci, J. S., Metzger, J. P., & Uriarte, M. (2018). The forest transition in São Paulo, Brazil: Historical patterns and potential drivers. *Ecology and Society*, *23*. <https://doi.org/10.5751/ES-10270-230407>
- Catterall, C. P., & Harrison, D. A. (2006). *Rainforest restoration activities in Australia's tropics and subtropics*. Queensland, Australia: Rainforest CRC
- Chazdon, R. L. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation*. Chicago, IL: University of Chicago Press.
- Chazdon, R. L., Brancalion, P. H. S., Lamb, D., Laestadius, L., Calmon, M., & Kumar, C. (2017). A policy-driven knowledge agenda for global forest and landscape restoration. *Conservation Letters*, *10*, 125–132.
- Chazdon, R. L., & Guariguata, M. R. (2016). Natural regeneration as a tool for large-scale forest restoration in the tropics: Prospects and challenges. *Biotropica*, *48*, 716–730.
- 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.
- Crouzeilles, R., Beyer, H. L., Mills, M., Grelle, C. E. V., & Possingham, H. P. (2015). Incorporating habitat availability into systematic planning for restoration: A species-specific approach for Atlantic Forest mammals. *Diversity & Distributions*, *21*, 1027–1037.
- Crouzeilles, R., Curran, M., Ferreira, M. S., Lindenmayer, D. B., Grelle, C. E. V., & Rey Benayas, J. M. (2016). A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications*, *7*. <https://doi.org/10.1038/ncomms11666>
- Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J. B. B., Monteiro, L., ... Strassburg, B. B. N. (2017). Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, *3*, e1701345.
- Crouzeilles, R., Santiami, E., Rosa, M., Pugliesi, L., Brancalion, P. H. S., Rodrigues, R. R., ... Pinto, S. (2019). There is hope for achieving ambitious Atlantic Forest restoration commitments. *Perspectives Ecology Conservation*, *17*, 80–83.
- da Silva, R. F. B., Batistella, M., & Moran, E. F. (2018). Regional socioeconomic changes affecting rural area livelihoods and Atlantic Forest transitions. *Land*, *7*, 125.
- Holl, K. D. (2017). Restoring tropical forests from the bottom up. *Science*, *355*, 455–456.
- Lamb, D. (2014). *Large-scale forest restoration*. Abingdon, UK: Routledge.
- Maier, T. F., Benini, R. de M., Fachini, C., & Santanade, P. J. A. (2018). Financial analysis of enrichment model using timber and non-timber products of secondary remnants in the Atlantic Forest. *Revista Árvore*, *42*, e420602.
- Menz, M. H. M., Dixon, K. W., & Hobbs, R. J. (2013). Hurdles and opportunities for landscape-scale restoration. *Science*, *339*, 526–527.
- Ministério do Meio Ambiente. (2017). *Plano nacional de recuperação da vegetação nativa*. Brasília, Brazil: Ministério do Meio Ambiente.
- Molin, P. G., Chazdon, R., Frosini de Barros Ferraz, S., & Brancalion, P. H. S. (2018). A landscape approach for cost-effective large-scale forest restoration. *Journal of Applied Ecology*, *55*, 2767–2778.
- Nunes, F. S. M., Soares-Filho, B. S., Rajão, R., & Merry, F. (2017). Enabling large-scale forest restoration in Minas Gerais state, Brazil. *Environmental Research Letters*, *12*, 044022.
- Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., ... Rozendaal, D. M. A. (2016). Biomass resilience of neotropical secondary forests. *Nature*, *530*, 211–214.

- 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*, e12607.
- Ruggiero, P. G. C., Metzger, J. P., Reverberi Tambosi, L., & Nichols, E. (2019). Payment for ecosystem services programs in the Brazilian Atlantic Forest: Effective but not enough. *Land Use Policy*, *82*, 283–291.
- Soares-Filho, B., Rajao, R., Macedo, M., Carneiro, A., Costa, W., Coe, M., ... Alencar, A. (2014). Cracking Brazil's forest code. *Science*, *344*, 363–364.
- Strassburg, B. B. N., Beyer, H. L., Crouzeilles, R., Iribarrem, A., Barros, F., de Siqueira, M. F., ... Uriarte, M. (2019). Strategic approaches to restoring ecosystems can triple conservation gains and halve costs. *Nature Ecology & Evolution*, *3*, 62–70.
- Strassburg, B. B. N., Barros, F.S.M., Crouzeilles, R., Iribarrem, A., Santos, J. S., Silva, D., ... 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.
- Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., ... Murray, C. J. L. (2019). Food in the Anthropocene: The EAT–Lancet Commission on healthy diets from sustainable food systems. *Lancet*, *393*, 447–492.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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