ENHANCING NATURAL REGENERATION TO RESTORE LANDSCAPES

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ENHANCING NATURAL REGENERATION TO RESTORE LANDSCAPES

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Editorial: Enhancing Natural Regeneration to Restore Landscapes

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Editorial on the Research Topic

Enhancing Natural Regeneration to Restore Landscapes

Entering the UN decade of restoration, the time to bring commitments to action is now (UN, 2019). Evidence supports the potential for natural regeneration as a low-cost and effective strategy to restore ecosystems and their services (Chazdon and Guariguata, 2016; Crouzeilles et al., 2017). Natural regeneration ranges from unassisted to actively managed assisted natural regeneration. Unassisted, or passive, natural regeneration implies protection from degradation to allow regeneration to unfold by the ecological process of secondary succession (Letcher and Chazdon, 2009; Zahawi et al., 2014). Assisted natural regeneration implies managing regeneration and accelerate restoration toward specified restoration targets (Hardwick et al., 1997; Shono et al., 2007). Restoration targets may vary from fully functional forest ecosystems to productive agroforest systems. While unassisted natural regeneration has been well-studied, the practices and outcomes of assisted natural regeneration are less known. A range of management practices that enhance natural regeneration are known, but understanding of their success in different contexts is currently lagging, limiting the upscaling of natural regeneration as a restoration practice.

With this Research Topic we aimed to advance our understanding of how natural regeneration can effectively contribute to achieve restoration goals by compiling evidence on (1) processes that drive natural regeneration at the regional scale, and their consequences for spatially prioritizing natural regeneration as a restoration strategy, (2) successional processes driving recovery, (3) how management can enhance natural regeneration to achieve restoration targets, and (4) how external factors shape the restoration potential of natural regeneration.

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OCCURRENCE AND PERSISTENCE OF NATURAL REGENERATION

Allowing fields to regenerate is a decision taken by land managers, and is influenced by proximate and ultimate forces that lead to patterns of occurrence and persistence. Understanding where natural regeneration happens and how long it persists is crucial for spatial planning and for predicting and optimizing the benefits of restoration. Schwartz et al. and Espírito Santo et al. use remote sensing approaches to evaluate spatial patterns of land use and land cover changes related to natural regeneration. Schwartz et al. employed a time-series analysis (2001–2014) to identify the occurrence and persistence of naturally regenerated forests across Latin America. They found that naturally regenerating forests were 10 times more likely to be cut than to persist, representing a 76% loss in the carbon sequestration potential of restoration, and highlight the need for policies that support farmers in conserving natural regeneration. In a dry-forest region in Brazil, Espírito Santo et al. analyzed forest cover changes from 2007 to 2016 and found that natural regeneration mainly happened in pastures and was more likely in flat regions and in arid climates. Their results suggest a higher potential of natural regeneration in less productive areas, and highlight the importance of developing policies that promote sustainable cattle farming in dry-forest regions.

HISTORICAL LAND USE AND SUCCESSIONAL PROCESSES

Natural regeneration, or secondary succession, is the gradual build-up of vegetation through biomass accumulation and species turnover over time (Chazdon, 2014). The potential for natural regeneration and the speed of succession depends on the landscape context, previous land-use history and management practices (Jakovac et al., 2021). Having a basic understanding of successional processes helps to identify possible barriers to restoration and how to alleviate those. Siminski et al. highlight the potential of natural regeneration after low-intensity swidden agriculture in the Brazilian Atlantic forest, where species richness increases rapidly during succession. This potential, however may be hampered by degradation, as found by Sanchez-Tapia et al.. They show that increased frequency of fire in pasturelands slows down natural regeneration in the Brazilian Atlantic forest and induces dominance of fire-resistant species causing long-term impoverishment of diversity. Preventing fire is therefore recommended to enhance natural regeneration. Natural regeneration may also be impeded by soil disturbance, as was the case on degraded gold mines in Peru (Chambi-Legoas et al.). They found that 19 years after mine abandonment, the regenerating forest still had very different species composition and lower species richness than the undisturbed forest, although the stem density and biomass had recovered more quickly. Structural characteristics usually recover faster than biodiversity because ecological filters limit the ability of certain species to colonize, grow and survive in degraded conditions. Ishaq et al. show how a specific N_2-fixing species (*Parasponia rigida*) is essential for kick-starting natural regeneration after volcanic eruptions in Indonesia. Identifying such species and their traits will help define management practices for favoring or planting target species to enhance natural regeneration. Müller et al. show species composition and functional traits of canopy trees exert a strong influence on what regenerates in the understory of secondary forests. This emphasizes the importance of early successional communities in enhancing or inhibiting natural regeneration and suggests management of early communities could help accelerate restoration. Together, these findings illustrate that enhancing natural regeneration requires time, eliminating inhibiting factors, and favoring conditions and species that accelerate natural regeneration.

LOCAL PRACTICES AND MANAGEMENT TO ENHANCE NATURAL REGENERATION

Enrichment planting is one way to modify successional processes to achieve restoration targets. Palma et al. undertook transplant and sowing experiments of several species in the understorey of secondary forests of different ages in tropical Australia. They found that planted seedlings performed better than exposed or buried seeds, and that all buried seeds germinated. This indicates that in this system, recovery is more limited by seed availability than by seedling establishment conditions, and that enrichment planting is a suitable strategy to enhance natural regeneration. Selecting species and defining adequate management practices can be supported by traditional knowledge of local communities. Schmidt et al. found that enrichment planting was used to enhance restoration in shifting cultivation systems by indigenous communities in the Brazilian Amazon. In Africa, traditional knowledge is also applied in the practice of Farmer Managed Natural Regeneration (FMNR), which is widely promoted as a restoration success. FMNR entails that farmers select and promote naturally regenerated seedlings on active agricultural fields. Chomba et al. carried out a review to compile evidence on FMNR contributing to land restoration and identified a number of knowledge gaps. The authors recommend combining functional ecology and socio-economic assessments to promote a mechanistic understanding of the drivers of the species composition of FMNR and its consequences for ecosystem functions and livelihood benefits. In Tanzania, where FMNR is promoted as a restoration strategy, Moore et al. found that species selection and management practices are driven by farmers' autonomous decisions. This suggests a strong context-dependent effect of FMNR on restoration targets, making it hard to predict and evaluate restoration success across regions but potentially ensuring farmer empowerment.

EXTERNAL INFLUENCES ON THE SUCCESS OF NATURAL REGENERATION FOR RESTORATION

Several authors pointed to the importance of the institutional context for the success of restoration strategies. Chomba et al. highlighted the importance of land and tree tenure policies, landscape governance, and the involvement of external agencies for the promotion of FMNR. Bosshard et al. reviewed market incentives that promote Forest Landscape Restoration and identified that these mostly focus on tree planting and only a few recognized natural regeneration as a restoration intervention. This is probably because the implementation and benefits of tree planting are easier to assess and communicate than those from natural regeneration. These studies highlight the role of institutions and the need for markets and policies to support natural regeneration as a restoration strategy.

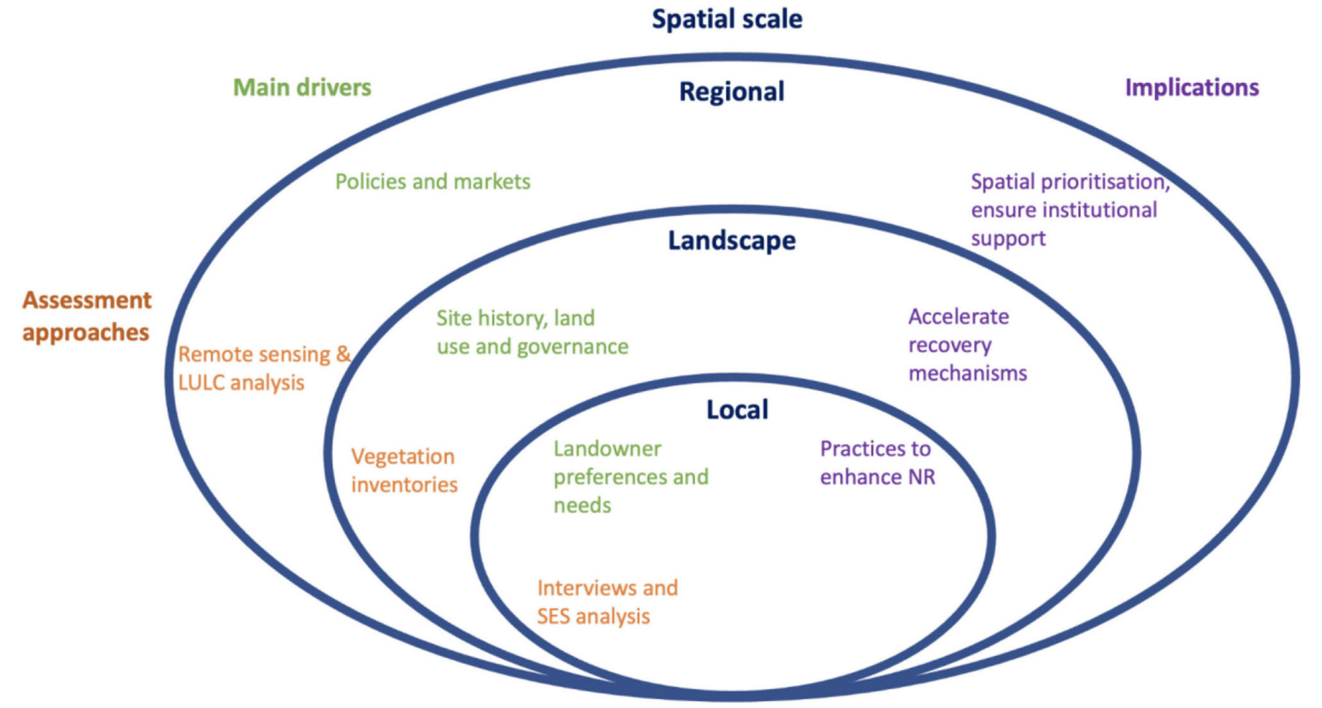

FIGURE 1 | Different spatial scales at which the role of natural regeneration for restoration was assessed, the associated assessment approaches, the main drivers that influenced its success and the implications for restoration. LULC, Land Use and Land Cover; SES, Social-Ecological Systems; NR, natural regeneration.

CONCLUSIONS AND RECOMMENDATIONS

In this Research Topic we compiled studies from across the pantropics and found diverse evidence of natural regeneration contributing to restoration targets like climate mitigation, biodiversity conservation, soil fertility, agricultural production and livelihood benefits (Chomba et al., Schwartz et al., Siminski et al.). The potential of natural regeneration is large because it builds on ecological memory and traditional practices (Chomba et al., Schmidt et al.) and has the ability to empower land-owners (Moore et al.). The realized potential of natural regeneration, however, depends on a number of factors that cut across different spatial scales (**Figure 1**). At a regional scale, geopolitical and institutional contexts shape where natural regeneration occurs, how long it persists, and who can derive what benefits from it (Chomba et al., Espírito-Santo et al., Schwartz et al., Bosshard et al.). We recommend that market-based incentives for restoration incorporate natural regeneration in their programmes (Bosshard et al.) and that governments ensure landowners have access to benefits derived from restoration efforts (Chomba et al.) in order to guarantee the persistence of natural regeneration in the long-term (Schwartz et al., Espírito-Santo et al.).

At the landscape scale, successional processes govern the speed of restoration vary amongst forest types (Siminski et al.) and are influenced by previous land-use, disturbance history (Ishaq et al., Sánchez-Tapia et al., Chambi-Legoas et al.) and functional characteristics of species and their interactions (Müller et al.). We recommend that an assessment of the landscape's regeneration potential is conducted in order to define adequate management practices to enhance the success of achieving restoration goals (cf. Lohbeck et al., 2020).

At the local scale, the potential of natural regeneration can be enhanced by land and tree-management practices, which include enrichment planting and favoring of selected naturally regenerating tree species (Chomba et al., Moore et al., Palma et al., Schmidt et al.). Building a portfolio of management practices in different contexts and for different restoration outcomes will facilitate its upscaling. Although knowledge gaps remain on how to enhance natural regeneration for restoration in a given context, we feel that natural regeneration provides an opportunity to learn and adapt practices based on science-based indicators that match pre-defined restoration goals. Natural regeneration includes a range of restoration techniques, should be embraced in its diversity and adapted to local contexts.

AUTHOR CONTRIBUTIONS

All authors wrote, edited, and reviewed the submission.

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Reversals of Reforestation Across Latin America Limit Climate Mitigation Potential of Tropical Forests

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Carbon sequestration through tropical reforestation and natural regeneration could make an important contribution to climate change mitigation, given that forest cover in many tropical regions increased during the early part of the 21st century. The size of this carbon sink will depend on the degree to which second-growth forests are permanent and protected from re-clearing. Yet few studies have assessed permanence of reforestation, especially not at a large spatial scale. Here, we analyzed a 14-year time series (2001–2014) of remotely sensed land-cover data, covering all tropical Latin America and the Caribbean, to quantify the extent of second-growth forest permanence. Our results show that in many cases, reforestation in Latin America and the Caribbean during the early 21st century reversed by 2014, limiting carbon sequestration. In fact, reversals of reforestation, in which some or all gains in forest cover in the early 2000s were subsequently lost, were ten times more common than sustained increases in forest cover. Had reversals of reforestation been avoided, forests could have sequestered 0.58 Pg C, over four times more carbon than we estimate was sequestered after accounting for impermanence (0.14 Pg), representing a loss of 75% of carbon sequestration potential. Differences in the prevalence of reforestation reversals across countries suggest an important role for socio-economic, political, and ecological context, with political transitions and instability increasing the likelihood of reversals. These findings suggest that national commitments to reforestation may fall short of their carbon sequestration goals without provisions to ensure long-term permanence of new forests.

Keywords: deforestation, reforestation, second growth forests, forest persistence, carbon sequestration and storage, tropical forest, land-use change

INTRODUCTION

Limiting climate warming to two degrees Celsius or less will almost certainly require negative emissions – the removal of CO_2 from the atmosphere through deliberate actions by humans (van Vuuren et al., 2013; Fuss et al., 2014). Reforestation through natural regeneration is an attractive option for achieving negative emissions, as it is relatively inexpensive, bears low environmental risks, and can have additional benefits, such as biodiversity conservation (Kindermann et al., 2008; van Vuuren et al., 2013; Lewis et al., 2019; Strassburg et al., 2019) and livelihood opportunities (Locatelli et al., 2015). The potential for natural forest regeneration to contribute to climate change mitigation is especially high in tropical regions, where second-growth forests gain 90% of the biomass of old-growth forest after an average of 66 years of regrowth (Chazdon et al., 2016; Poorter et al., 2016). Forest restoration and natural regeneration accordingly play a large role in global climate change mitigation and sustainable development commitments.

While deforestation continues in some tropical regions, forest cover has increased in others (Rudel et al., 2005; Sloan, 2008; Asner et al., 2009; Redo et al., 2012; Aide et al., 2013). Globally, tree cover has increased by over 2.24 million km^2 since 1984 (Song et al., 2018). Although many tropical regions are still experiencing net deforestation, between 2000 and 2010, woody vegetation cover increased on over 360,000 km^2 in Latin America and the Caribbean (Aide et al., 2013). These changes give cause for optimism about the contribution of tropical second-growth forests to climate change mitigation.

Though these reforestation trends are encouraging, the extent to which short-term (5–10 year) increases in forest cover persist over longer time scales, a prerequisite for carbon sequestration, remains uncertain. Increases in forest cover occur when socioeconomic and biophysical conditions are favorable (Chazdon et al., 2020). For example, industrialization, rural-to-urban migration, and agricultural intensification can lead to cessation of cultivation and forest regeneration on marginal agricultural lands (Rudel et al., 2000; DeFries and Pandey, 2010; Aide et al., 2013). Factors such as globalization, policy changes, and armed conflict also play important roles in driving forest cover change (Rudel et al., 2000; Hecht et al., 2006; Grau and Aide, 2008; Meyfroidt and Lambin, 2011; Sánchez-Cuervo and Aide, 2013). However, changing socioeconomic or biophysical conditions can inhibit or even reverse increases in forest cover (Suding et al., 2004; Aide et al., 2019).

Recent research has suggested that regenerating and restored forests have a high probability of being cleared. If second-growth forests lack permanence, their contributions to negative emissions will be limited (Schwartz et al., 2017b). For example, a study in the Peruvian Amazon found that re-growing forests had a high probability of being cleared within 5 years (Schwartz et al., 2017b), while in the Brazilian Amazon, 50% of all secondary forests were recleared within 8 years (Nunes et al., 2020). In Costa Rica, 50% of second growth forests were cleared within 20 years of regrowth (Algeet-Abarquero et al., 2015; Reid et al., 2018). However, the degree to which these findings extend to broader geographic scales has not been tested.

Impermanence of reforestation trends might have been overlooked in earlier studies of forest cover change because of the analytical methods used. These analyses typically detect trends by comparing snapshots of forest cover at two dates or by fitting linear models to time-series data, allowing for only three possibilities – deforestation, reforestation, or no change (Asner et al., 2009; Redo et al., 2012; Aide et al., 2013; Nanni et al., 2019). Restricting possible trajectories of land cover change to this narrow set of options may mask non-linear dynamics occurring at time scales shorter than study durations.

Here, we consider a broader set of possible trajectories of forest cover change to assess permanence of reforestation in Latin American and the Caribbean (LAC) between 2001 and 2014. To do so, we use a land cover time series to identify reforestation reversals – areas where forest cover initially increased but later decreased during the study period. We compare the prevalence of reforestation reversals relative to areas where reforestation was sustained or where other trends predominated. We also use these time series to estimate carbon sequestration due to reforestation from 2001 to 2014 and compare the magnitude of observed sequestration with a scenario in which no reforestation reversal occurred.

MATERIALS AND METHODS

Remote Sensing of Forest Cover

We used annual land cover maps for Latin America and the Caribbean (LAC) for the period 2001–2014 (detailed descriptions of the dataset can be found in Clark et al., 2012; Aide et al., 2013; Graesser et al., 2015; Nanni et al., 2019). The annual maps were created by classifying 250 m Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data using Random Forest land-cover classification models defined for each biome. The models included the following land cover categories: woody vegetation (including natural tree and shrub cover), tree plantations, cropland, pastureland, and other (i.e., bare soil, ice, snow, rock, sand dunes, built-up structures, and water).

Training data for each classifier were collected by overlaying a grid of MODIS pixels (250 × 250 m) onto multi-temporal high-resolution imagery in Google Earth and registering the land cover class and date. More than 60,000 MODIS pixels from labeled polygons were used to create the classification models in this study. For training data, woody vegetation pixels were defined as pixels with $>80\%$ cover of trees or shrubs, based on visual interpretation of high-resolution Google Earth imagery. Plantations were distinguished from woody vegetation by obvious rows and homogenous color and height. Crop and pasture were frequently confused and these two classes were combined. Because of the relatively large size of MODIS pixels, many pixels are mixed. In training data, the use of mixed pixels was limited: only pixels with $> 80\%$ cover were included as training data. In the classification, the class that received the most votes in the Random Forest was assigned. Validation pixels were assigned a class based on the majority land cover class present in that pixel from visual inspection. More details on in the collection and interpretation of the training and validation data can be found in Clark and Aide (2011).

These data were associated with the pixel statistics to create a Random Forest classification model for each mapping zone, defined by ecoregions and biomes (Olson et al., 2001). To train a zone-specific Random Forest model, land cover samples within the mapping zone of interest and the samples' Google Earth high-resolution image acquisition date were paired with MODIS time series variables. Then, all samples within the biome (for all years) were aggregated and used to fit a model for the biome. The zone-specific Random Forest models were then applied annually to produce 14 land cover maps for each mapping region.

Previous assessments of this dataset have indicated that at the pixel level, overall accuracy of the classification is 80% (Clark et al., 2012) and that the classification distinguishes woody vegetation from other land cover types with 87% accuracy (Nanni et al., 2019), with accuracy as high as 93% in the tropical humid forest biome (Aide et al., 2013). A comparison of woody vegetation change in our dataset and annual land cover maps from the Brazilian government's PRODES program[1] yielded an R^2 of 0.88 (Clark et al., 2012). For this study, to further assess the agreement between our dataset estimate of pixel-level changes and that of other global forest cover datasets, we compared pixel-level changes in our dataset to the Hansen et al. Global Forest Cover dataset (Hansen et al., 2013). We found that pixel-level changes in our dataset showed 79% overall agreement with the Global Forest Cover dataset (**Supplementary Table S1**, see **Supplementary Material** for more details).

For further analysis, we summed land cover classes within 40 km wide hexagonal grid cells ($\sim$1200 km^2). This hexagon size is approximately equal to the average municipality in LAC (Graesser et al., 2015). By summing land cover within these hexagons, we capture dynamics on relatively fine scales, while limiting per pixel geo-registration and misclassification errors. For all analyses, we considered only hexagons that overlapped at least 80% with tropical forest biomes (Tropical and Subtropical Moist Broadleaf Forest, Tropical and Subtropical Dry Broadleaf Forest, and Tropical and Subtropical Coniferous Forest biomes) according to (Olson et al., 2001).

Identification of Trends in Forest Cover

To describe trends in forest cover in individual hexagons, we used a shape selection algorithm designed for time series of Landsat data (Moisen et al., 2016). The algorithm uses non-parametric statistical methods to fit several candidate shapes to a time series of data. These candidate shapes include flat, increasing (hereafter reforestation), decreasing (hereafter deforestation), vee (hereafter deforestation reversal), and inverse vee (hereafter reforestation reversal, **Figure 1**). For each time series the algorithm fits all five candidate shapes to the data. It then uses the Bayesian information criterion (BIC) to select the shape with the best fit for each cell's time series.

We applied this algorithm to the 14-year time series of woody vegetation cover (tree and shrub cover, not including plantations) for each hexagon. To reduce the influence of outliers and inter-annual noise in the time series, we developed a bootstrapping procedure to determine the best-fit shape for each cell. For each time series, we removed three observations at random and used the shape selection algorithm to determine the best-fit shape for the subset of the time series. We repeated this procedure 300 times and identified the shape that was identified as the best fit in the largest number of iterations. We restricted subsequent analyses to hexagons whose shapes were selected with high confidence, which we defined as being selected in $\geq$90% of iterations. Hexagons in which the majority shape was selected in less than 90% of iterations were designated as "low confidence" and excluded from subsequent analyses (30.3% of hexagons). Furthermore, because the shape selection algorithm will assign a shape to a time-series regardless of the magnitude of change, we classified trajectories where the total change in forest cover was less than 1% of the grid cell ($\sim$20 km^2) as "flat" (28% of hexagons). This was done to avoid including locations with only very slight changes in our analysis so as not to inflate the frequency of change.

To understand the trajectories in more detail, for each grid cell, we calculated the total magnitude of reforestation in each grid cell as the difference between the initial and maximum forest cover. We calculated the net change during the study period as forest cover in 2014 minus forest cover in 2001. To investigate the geographic patterns of reforestation reversals, we compared the relative frequency of trajectory shapes across the seven LAC countries with over 100 hexagons that fall within forest biomes (**Supplementary Table S2**).

Carbon Potential Calculation

We quantified the implications of reversals of reforestation for carbon sequestration with a bookkeeping approach in which we estimated carbon accumulation in each hexagon given the observed trajectory and a region-specific rate of carbon uptake in young second-growth forests. We compared two quantities: (1) the carbon potential, i.e., the amount of carbon that would have been sequestered by new forests had no re-clearing occurred and (2) carbon sequestration observed in new forests when accounting for reversals of reforestation. We considered only reforestation relative to forest cover in 2001 and clearing of these new forests. We ignored deforestation relative to 2001, as our goal was not to quantify emissions due to deforestation, but rather, foregone carbon sequestration potential due to reversals of reforestation.

To quantify carbon potential and observed carbon sequestration, we analyzed the time series of yearly observations of woody vegetation cover for each grid cell (w_0, w_1, w_2, ..., w_{13}), in a process analogous to a stage structured population model. For each year (t), starting in 2002, change in forest cover (r) is calculated as:

$$r_t = w_t - w_{t-1} \;\; if \;\; w_t > w_0$$

$$r_t = 0 \;\; if \;\; w_t < w_0$$

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[1] www.obt.inpe.br/prodes

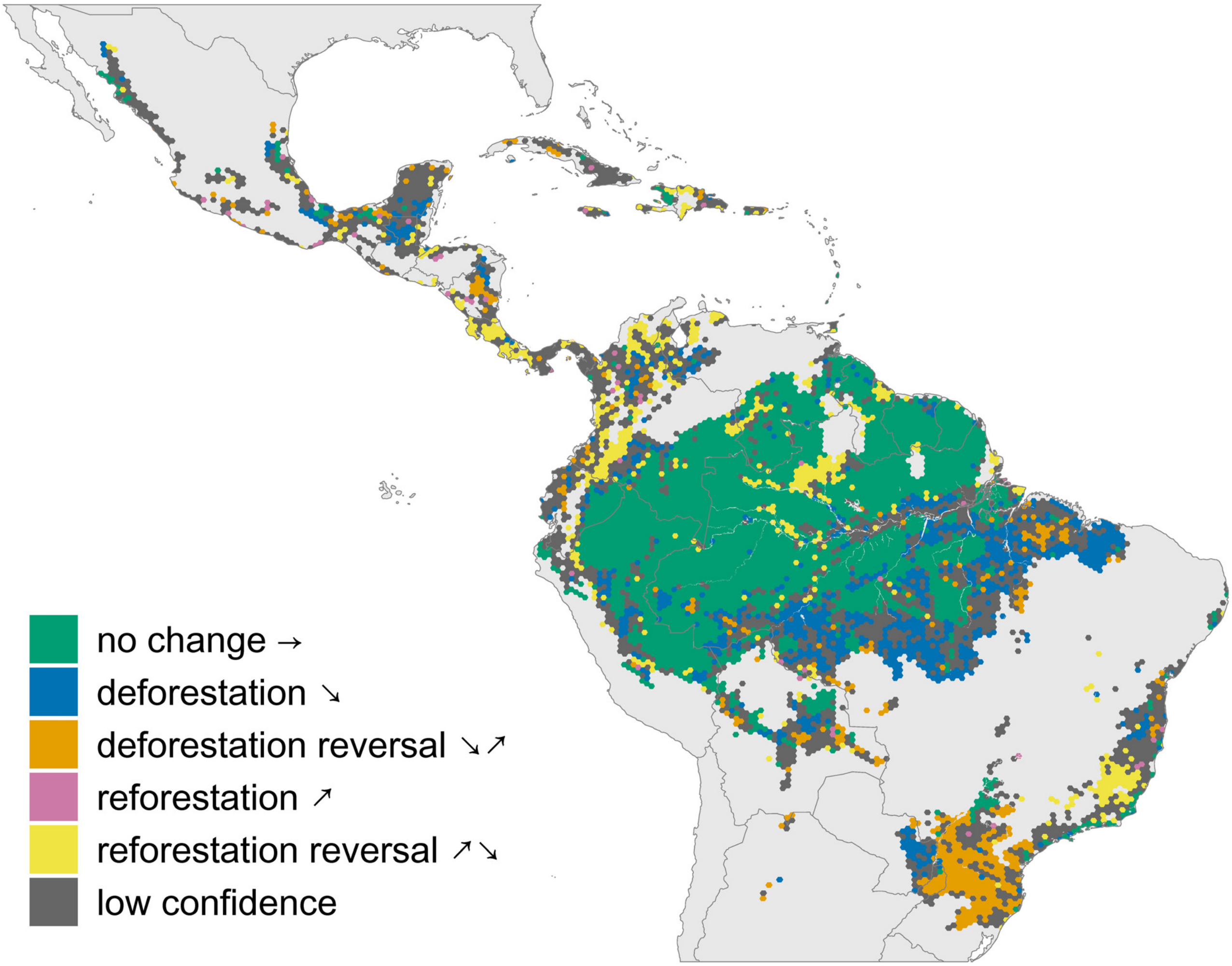

FIGURE 1 | Trajectories of forest change in tropical Latin America and the Caribbean. Light gray areas indicate biomes other than tropical forest. Dark gray areas indicate forested regions where noisy trajectories prevented classification. Arrows in the legend illustrate the shape of the forest cover trajectory change over time.

where w is woody vegetation cover (in hectares) and w_0 is initial forest cover in 2001, such that we are only considering reforestation and reversal of reforestation, and do not account for deforestation of forests established prior to 2001. When r_t is positive, the corresponding number of hectares are added to the youngest stage class. In subsequent time steps, those forests will advance to the next stage class, i.e., age 1 year. Negative r_t is analogous to death, and is subtracted from the existing "population," i.e., previous years' reforestation, removing the youngest forests first until the corresponding number of hectares have been removed from the total or there are no remaining forests. At the end of each time step, forests in the "population" advance to the next stage, i.e., age 1 year.

After the final time step, we calculated carbon stored in second-growth forest. To do so, we first calculate a regional rate of carbon sequestration in each hexagon as the zonal average of total aboveground biomass and its uncertainty after 20 years of secondary forest growth, using the geographic data from Poorter et al. (2016). We approximated annual rates of biomass accumulation as 1/20th of this quantity, which assumes linear accumulation of carbon during the first 20 years of succession. We used this value to calculate total AGB stored in second-growth forests in each hexagon, given the age class structure in 2014 derived from the yearly woody vegetation cover observations as described above. To estimate stored carbon, AGB values were divided by two, under the assumption that carbon makes up 50% of biomass (Chave et al., 2009).

We repeated this procedure twice. First, we conducted the calculations exactly as described above. This calculation yielded estimates of "observed carbon." Second, we conducted the same procedure, but calculated r_t as follows:

$$r_t = w_t - w_{t-1} \quad if \ w_t > w_{t-1}$$

$$r_t = 0 \quad if \ w_{t-1} \leq w_t$$

Under this set of rules, no deforestation occurs, and all new forests added to the "population" continue to age until the end of the study period. The amount of carbon stored in second-growth forests in this scenario is the "carbon potential." This procedure was done for all cells that experienced a net increase in forest cover relative to 2001 at some point during the study period, including all trajectory shapes.

RESULTS

Trajectories of Forest Cover Change

Most classified hexagons (59.7%) experienced no change in forest cover during the study period. Where forest cover changed, deforestation was the most common trajectory, observed in 18.8% of classified hexagons. Deforestation reversals occurred in 8.7% of hexagons. Reversals of reforestation were nearly ten times as common as sustained increases in forest cover, occurring in 11.7% of classified hexagons (**Figures 1**, **2**). Only 1.1% of hexagons experienced sustained reforestation.

In regions where reforestation reversals occurred, forest cover increased by a total of 5,983,781 hectares (across hexagons mean = 9.0%, *SD* = 9.2%) before it began to decline. By 2014, only 31% (1,832,394 hectares) of these new forests remained. Although most of the reforestation reversal regions still experienced a net increase in forest cover between 2001 and 2014 (mean = 1.8%, sd = 5.8%; **Supplementary Figure S2**), these gains were significantly smaller than in regions where reforestation was sustained (mean = 9.7%, *SD* = 9.5%, **Supplementary Figure S2**, $t = 6.9$, $p < 0.0001$). Where deforestation reversals occurred, 61.8% of hexagons underwent net reforestation relative to 2001. Across deforestation reversal hexagons, forest cover increased by a net total of 1,945,119 hectares relative to forest cover in 2001 (across hexagons mean = 2.2%, *SD* = 7.6%).

We found significant differences in the distribution of forest cover change trajectories across countries (**Figure 2A**, $\chi^2 = 673.99$, $p < 0.0001$). Reforestation reversals were relatively rare in Bolivia (7.5% of hexagons) and Brazil (7.3%), where deforestation and deforestation reversals were more common, and in Peru (5.5%), where forest cover is still high in remote regions. Colombia and Venezuela had the highest rates of reforestation reversals, at 29.4 and 17.6% of hexagons, respectively.

Effects of Reforestation Reversals on Carbon Sequestration

Without reclearing, forests that established between 2001 and 2014 would have sequestered 0.58 Pg C (95% c.i.: [0.09, 1.15]; **Figure 3A**). Only 0.14 Pg C (95% ci: [0.02, 0.28]) was captured in new forests by the end of the study period (**Figure 3B**). This gap represents a loss of 76% of the carbon potential of reforestation in Latin America and the Caribbean between 2001 and 2014 (**Figure 3C**). The magnitude of lost carbon potential differed across countries, ranging from 27% (Guyana) to 87% (Venezuela; **Figure 2B**).

DISCUSSION

Our results show that reforestation trends in Latin America and the Caribbean in the early 2000s reversed in many regions, undoing some or all the previous forest cover gains. These reversals severely limit carbon sequestration: we estimate that in their absence, tropical second-growth forests could have sequestered over four times more carbon between 2001 and 2014. This result further calls into question the recent claims that "global tree restoration [is] our most effective climate solution to date" (Bastin et al., 2019). Reversals of reforestation also limit second-growth forests' contribution to biodiversity conservation, as tropical second-growth forests require a median time of 50 years to recover species richness similar to that of old growth forests (Rozendaal et al., 2019). Without permanence, the contribution of reforestation to climate mitigation and biodiversity conservation will be severely curtailed, though clearing of second-growth forests may ultimately serve to buffer primary forest loss (Wang et al., 2020).

Detection of reforestation reversals in this study was possible only because our methods allowed for flexible trajectories and because we analyzed a multi-date time series of land cover data. Because most reforestation reversals still resulted in net gains in forest cover from 2001 to 2014, a methodological approach to identify binary deforestation/reforestation trends in forest cover would have led to most of these trajectories being classified as reforestation (e.g., Nanni et al., 2019). While this is strictly correct, our method reveals a more complex and dynamic reality, where short-term increases in forest cover do not necessarily indicate persistent trends. Reforestation and deforestation, which occurred in 19.9% of hexagons, were no more common than the more dynamic categories of reforestation reversals or deforestation reversals (20.4%). Together with recent findings of cyclical "reforestation treadmills"' in planted areas in tropical regions (Sloan et al., 2019), our results contribute to a growing body of evidence that suggests that fitting linear trends or calculating net changes across two dates can mask important dynamics at shorter time scales. Detailed land cover time series and non-linear methods are essential for better understanding land cover dynamics. Furthermore, our conceptual models must move beyond classical conceptions of forest transition theory where forest cover increases are assumed to be sustained (Mather, 1992).

Several methodological limitations add uncertainty to our results. First, we used land cover data derived from MODIS imagery (6.25 hectare pixels). This relatively large pixel size may result in omission of some second-growth forests from our dataset, as many second-growth forest patches are quite small (less than one hectare; Schwartz et al., 2017a). These small patches comprising mixed pixels with other land cover types might not be detected by the classification, especially during early stages of growth when canopies are open and short. Overlooking these young forests and small patches might bias our estimates of carbon storage of second growth forest. However, our estimates of carbon potential lost are likely conservative since smaller and younger patches are more prone to reclearing (Schwartz et al., 2017b; Reid et al., 2018).

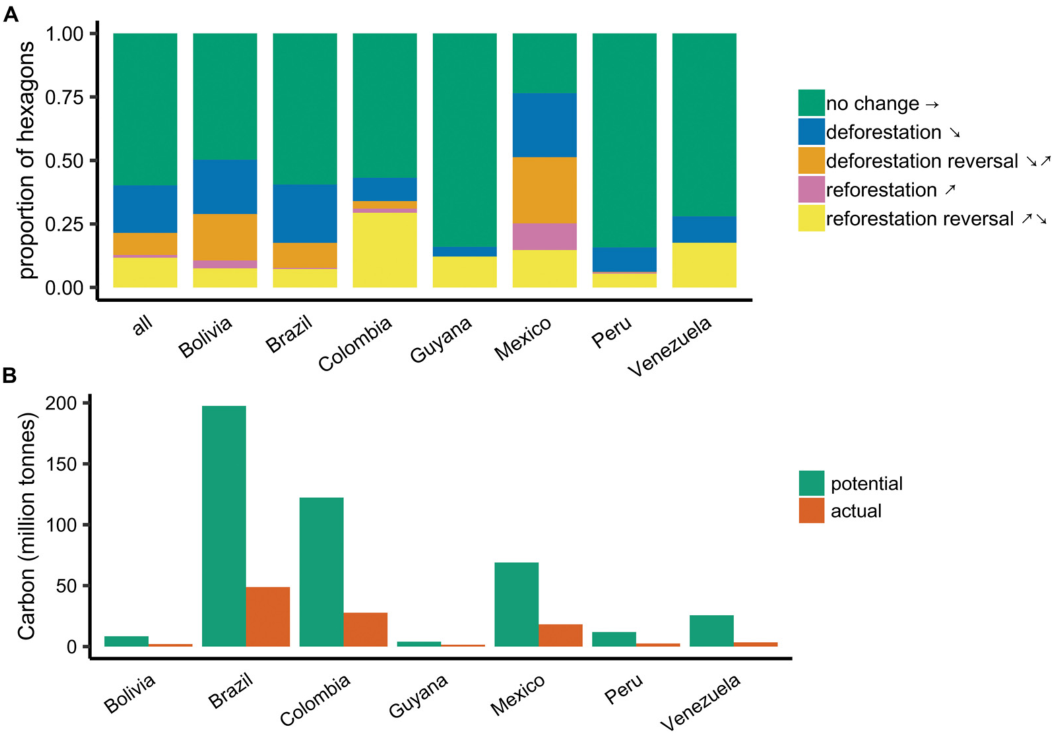

FIGURE 2 | (A) Relative proportions of hexagon forest cover change trajectories across countries and biomes. Seven countries with the largest amount of tropical forest area are shown; see **Supplementary Table S1** for data on additional countries. Hexagons that could not be assigned a trajectory with high confidence are omitted. **(B)** Comparison of carbon sequestration potential without reforestation reversal and estimated actual carbon uptake in seven LAC countries with most tropical forest area.

Second, our analysis was not able to classify all land-cover time series as one of the candidate shapes. Specifically, about 30% of hexagons were assigned the "low confidence" trajectory. This class likely reflects noisiness in the underlying classification as it was common in regions where, according to a previous study with this dataset, our random forest classifier showed lower rates of internal agreement (Clark et al., 2012). This class could also occur in places that experienced frequent, cyclical disturbances during the study period, though it is not possible to distinguish between these scenarios with this dataset. Local-scale analyses of forest permanence and future improvements to land cover data products will help resolve some of these uncertainties.

Some reforestation is ephemeral by nature. Specifically, activities such as timber harvesting and shifting cultivation involve cyclical reforestation and deforestation dynamics (Rudel et al., 2016). We expect these activities would lead to cycles on local scales – e.g., on individual fields or within forest stands. Rather than reflecting these inherently cyclical activities, our results reflect landscape- to regional-scale trends since we aggregated land cover pixels to 1200 km^2 hexagons. This aggregation may mask important local-scale dynamics such as simultaneous deforestation and reforestation, which would result in no net change in aggregated forest cover. Though beyond the scope of this study, further research into the prevalence of these dynamics and the drivers of reforestation and clearing at the pixel scale (e.g., Schwartz et al., 2017b; Nunes et al., 2020) could help better understand regional trends in forest cover and improve estimates of carbon sequestration through reforestation.

Variation in the prevalence of reforestation reversals across countries highlights the strong influence of regional and local context on land cover dynamics. For example, the high rates of reforestation reversals observed in Colombia and Venezuela likely reflect complex political, social, and economic realities. Much of the reforestation reversal in Colombia occurred in the Andes. There, during the early part of the study period, woody vegetation cover increased, associated with rural-to-urban migration and land abandonment driven by violence and conflict (Sánchez-Cuervo et al., 2012). But, as the peace process progressed (2007–2014) much of this reforestation reversed. More recently, rates of deforestation have accelerated, particularly in the lowlands. These trends suggest that the post-conflict peace process, including rural development incentives and the government's difficulties establishing a presence in remote regions, has initiated new land-use dynamics (Hettler et al., 2017; Armenteras et al., 2019; Clerici et al., 2019).

In Venezuela, deforestation has been associated with large dam projects (Sy et al., 2015), oil exploration (Richards and VanWey, 2015; de Cárdenas García, 2017) and gold mining in the Orinoco basin. Reforestation reversals in Venezuela could be linked to food shortages, though how recent political and economic challenges have influenced land-use change

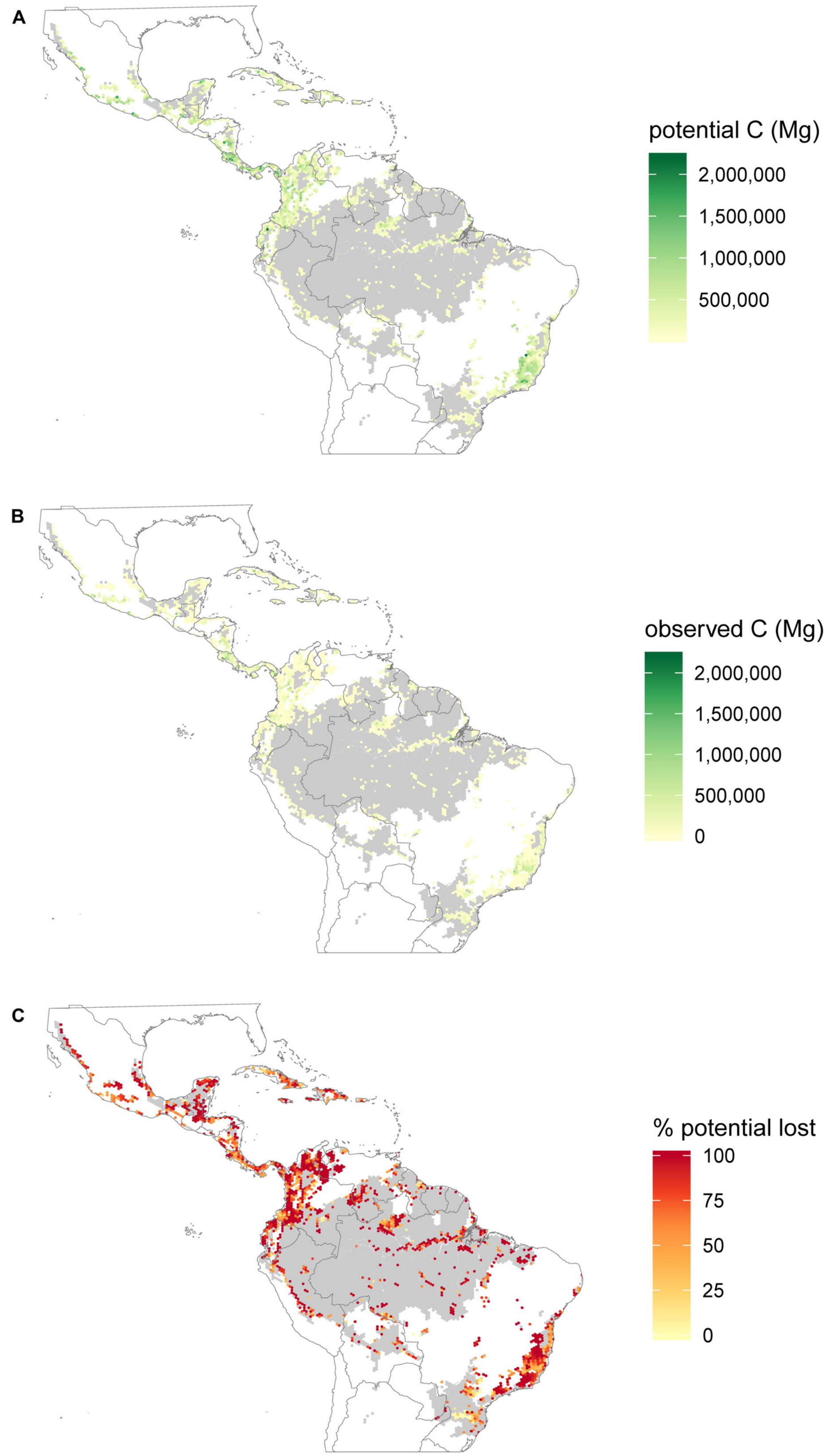

FIGURE 3 | (A) Potential carbon sequestration in new forests, had no re-clearing of reforestation occurred, **(B)** observed carbon sequestration in new forests, when accounting for re-clearing, and **(C)** percent of carbon potential foregone due to reversal of reforestation.

in Venezuela requires further research. Conventional forest transition models assume a relatively constant transition toward reforestation as countries develop (Mather, 1992; Mather and Needle, 1998) but dramatic political changes may substantially alter this pattern, in particular if considering finer temporal scales. The cases of Colombia and Venezuela illustrate that political instability (or transitions from instability toward stability) may have profound effects in land cover trajectories. More generally, the socioeconomic conditions that favor reforestation may prove to be ephemeral in the face of economic crises, political unrest, and other shifts.

Many LAC nations have committed to reforestation and forest restoration under the Bonn challenge, a global effort to restore 150 million hectares of degraded land by 2020[2]. Colombia has pledged 1 million hectares forest restoration (0.09 Pg C sequestration), while Brazil has pledged 12 million hectares (1.14 Pg). Within this context, our findings represent substantial foregone carbon sequestration, larger than Colombia's and nearly half Brazil's Bonn challenge commitments. The Bonn Challenge commitments involve establishment of new forests either through restoration or natural regeneration, but notably do not include strong provisions to ensure permanence. Our results suggest that newly established forests in LAC are often ephemeral and at risk of clearing, especially during periods of political transition and/or instability. For example, one of the first acts of the newly elected Brazilian government in 2019 was to limit enforcement of the Brazilian forest code, which would remove protection on up to 15 million hectares of forest (Freitas et al., 2018).

How to best improve permanence of tropical second-growth forests is not clear, especially given land-use tradeoffs and growing demand for agricultural land (Lambin and Meyfroidt, 2011) and the complex tradeoffs and relationships between second-growth and primary forest clearing (e.g., Wang et al., 2020). To date, limited research has focused on policies and practices to enhance permanence of second-growth forests (but see Chazdon et al., 2020). Further research into the drivers of reforestation reversals and permanence could help guide development of policies and management practices to better protect second-growth forests. Permanence can and should be incorporated into restoration planning from the earliest stages. For example, a recent study identifying restoration opportunities in tropical forest landscapes included a variable to represent the chances that restored forests persist over time (Brancalion et al., 2019). Explicit plans to promote permanence of restored or naturally regenerated forests will be necessary to achieve the Bonn Challenge goals, and for tropical second-growth forests to make a substantial contribution to climate change mitigation.

DATA AVAILABILITY STATEMENT

The data analyzed in this study are available at doi: 10.6084/m9.figshare.12502022.v1.

AUTHOR CONTRIBUTIONS

NS, TA, HG, and MU contributed to the conception and design of the study. JG analyzed the remote sensing imagery and developed the database. NS performed the statistical analysis and wrote the first draft of the manuscript. NS, TA, and HG wrote sections of the manuscript. All authors contributed to the manuscript revision, read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2020.00085/full#supplementary-material

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[2] www.bonnchallenge.org

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling Editor declared a past co-authorship with several of the authors NS and MU.

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Glass Half-Full or Half-Empty? A Fire-Resistant Species Triggers Divergent Regeneration in Low-Resilience Pastures

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Fire may divert or arrest natural regeneration in abandoned pastures throughout the tropics, transforming them to low-resilience systems that do not recover even in the absence of disturbances. Understanding regeneration in degraded landscapes is crucial to decision-making and predicting the outcome of passive or active restoration actions. We aimed to understand the effects of intensifying fire regimes on post-fire natural regeneration in sites degraded by logging and fire in the Brazilian Atlantic Forest. We studied five areas with different fire regimes (i.e., different fire frequencies and post-fire regeneration time), dominated by *Moquiniastrum polymorphum* (Asteraceae), a widely-distributed species with fire resistance traits. We analyzed differences in structure, diversity, the amplitude of the species' geographic distribution, and floristic composition. We recorded Leaf Area Index and grass cover to understand the effect of canopy closure on fire exclusion and analyzed functional traits related to succession and response to fire (specific leaf area, height, wood density, bark thickness, seed mass). Post-fire regeneration was slow and fire-prone and dominance by *M. polymorphum* decreased with less disturbance, as other species entered the communities. Structure, diversity, and functional composition recovered along the gradient but did not reach old-growth values. The taxonomic composition was strikingly different in burned areas and forests, irrespective of fire history. Natural regeneration followed a divergent trajectory, marked by the establishment of other widely-distributed species, which suggests a long-term floristic impoverishment. The establishment of *M. polymorphum* allows these pastures to exit grass-fire cycles. Longer post-fire recovery and fewer fire events allow for canopy closure, grass exclusion, and eventually fire suppression. This two-step dynamic breaks a crucial barrier for restoration from degraded pastures and represents a more desirable state than pastures. However, relying only upon natural regeneration results in impoverished secondary forests. Given the pervasive effects of deforestation and fire, natural regeneration observed in tropical landscapes may correspond to impoverished new secondary forests that fail to attain conservation targets for the biome. Preventing future fires and controlling grass cover in the understory is crucial to avoid their retrogression to pastures and to treat them as regeneration templates for active restoration.

Keywords: Brazilian Atlantic Forest, dominance shifts, monodominance, savannization, tropical secondary forests, novel forests, fire in tropical forests

1. INTRODUCTION

Throughout the tropics, many forest areas have been cleared to pastures and are subjected to modified fire regimes as they recover (Cochrane, 2003). Fire affects both anthropogenic pastures and fire-prone degraded forests at varying frequencies and intensities (Nepstad et al., 1999; Barlow and Peres, 2008). In the most extreme cases, repeated fires may trap these pastures in low-resilience points dominated by fire-grass feedbacks (D'Antonio and Vitousek, 1992; Flores et al., 2016). Forest species lack the mechanisms to respond to these modified fire regimes and degraded pastures remain as low-diversity "derived savannas" (Veldman and Putz, 2011) that fail to recover even after long periods without fire (Lamb et al., 2005). These areas have been described as "treeless" states (Hirota et al., 2011), and the processes that create them have been described under the terms "secondarization" (Barlow and Peres, 2008), and "retrogressive succession"—a return to early successional states (Santos et al., 2008; Tabarelli et al., 2008; Ewers et al., 2016). The conversion of forests to such stable degraded pastures has been reported in the Amazon (Barlow and Peres, 2008; Veldman and Putz, 2011; Flores et al., 2016) and tropical dry forests (Cavelier et al., 1998).

Abandoned pastures trapped in fire-grass cycles exhibit opposing fire dynamics to old-growth forests, that have low to null flammability (Uhl et al., 1988; Nepstad et al., 1999; Barlow and Peres, 2008). Transitions between the two extremes may be gradual or abrupt, and they may be composed of a mix of species from both sides of the gradient or have a distinct floristic identity (Pausas, 2015). In some cases, pastures represent anthropogenic stable states alternative to forests, just like natural savannas and forests are considered alternative stable states in savanna-forest ecotones (Hoffmann et al., 2012; Pausas, 2015; Reyer et al., 2015). Considering that anthropogenic pastures cover a substantial portion of tropical forest regions, understanding the main mechanisms and barriers to natural regeneration has fundamental implications for ecological restoration actions.

The most detailed recent survey estimates that 28% of the original area of the Brazilian Atlantic Forest (BAF) corresponds to native vegetation (Rezende et al., 2018). In the BAF, fire severity is one of the most critical processes affecting natural regeneration (dos Santos et al., 2019). Under the scope of fragmentation and edge effects, abandoned pastures are anthropogenic matrices that surround forest fragments (Tabarelli et al., 2010; Melo et al., 2013), but it is more important than ever to treat them as potentially regenerating vegetation. There is a considerable effort to foster natural regeneration as a paradigm for forest cover recovery in the BAF (Crouzeilles et al., 2019). Still, the existence of low-resilience areas may represent a challenge to attain these restoration goals, since a crucial part of the decision-making process regarding restoration is to predict active or passive restoration success and allocate resources accordingly (Suding et al., 2004; de Rezende et al., 2015).

In this study, we analyze the effect of different fire regimes (i.e., different fire frequencies and years since the last fire) on post-fire regeneration in abandoned pastures in lowland areas of the BAF. *Moquiniastrum polymorphum* (Less.) G. Sancho (Asteraceae), is dominant in the secondary vegetation at the interface between pastures and forests in the PABR. This species is common in the *Cerrado* (Brazilian Savanna) and in degraded pastures in the BAF (Sansevero et al., 2017, 2020). It can survive fires and form fire rings, which allows its use in fire history reconstruction (Brandes et al., 2019). Its thick bark allows for survival to frost events as well (Brando and Durigan, 2005). In the PABR, *M. polymorphum* creates areas that appear to have a low resilience to disturbance (Sansevero et al., 2020). The dynamics of natural regeneration and the implications for ecological restoration in this transition from pastures to forests have not been addressed yet.

We analyze the changes in structure, diversity, species, and functional trait composition along the fire gradient. We expect the recovery of diversity, structure, and taxonomic composition along the fire disturbance gradient intensity, with less fire events and more time for post-fire succession. We also expect leaf area index (LAI), a proxy for canopy density, to increase along the gradient, and grass cover, which represents fuel for further fires and increases community flammability, to decrease. We also expect changes in the functional response attributes from traits related to fire resistance (thicker barks, smaller seeds, low SLA) in the most disturbed sites, toward trait compositions related to old-growth forests with milder fire regimes, such as high wood density and high seed mass. We also test whether species entering the secondary vegetation are the same that are already present in nearby old-growth forests, and evaluate if they are forest specialists or not through their geographic distribution area, as a proxy for niche breadth and habitat specialization. Finally, we discuss the implications of our findings for active or passive restoration strategies in these degraded landscapes and discuss the positive (glass-half full) and negative (glass half-empty) effects of the presence of *M. polymorphum* in the post-fire regeneration of abandoned pastures in the BAF.

2. MATERIALS AND METHODS

2.1. Study Area

Poço das Antas Biological Reserve (PABR, 22°30′S, 42°19′W) was created in 1974 to protect lowland fragments of Atlantic Forest in the Rio de Janeiro state and its threatened fauna, including the golden lion tamarin (*Leontopithecus rosalia* L., Callithricidae). The climate in the PABR corresponds to tropical savanna climate with dry winters (Aw) (Köppen, 1936), with mean monthly temperatures between 21.8°C in July and 29°C in February, and mean annual precipitation of 2,160 mm, with a dry season between June and July (38.9 mm) and rainy summers (320 mm in February) (Lima et al., 2006).

PABR has a long history of land use that includes clearing forests for raising cattle and the canalization of rivers to drain swampy areas since the early twentieth century (Brazilian Ministry of the Environment, 2005). Small-scale slash-and-burn practices have existed in the region for at least a century, but large-scale fires began in 1984, following the construction of the Juturnaíba dam that drained and exposed large tracts of highly flammable peatlands (Dean, 1996, p. 374). As a result, only 52% of the PABR is covered by old-growth forest remnants, the rest corresponding to secondary vegetation, anthropogenic pastures, and grass-dominated peatlands (Lima et al., 2006). However, there is no record of fire entering the old-growth forests, even in small insular fragments surrounded by pastures. The transition from pasture to forests comprises secondary vegetation with different fire histories, with structures that vary from almost 100% grass cover with isolated trees to closed-canopy woodlands and secondary forests. *M. polymorphum* is the dominant tree species in these secondary areas.

2.2. Fire History and Area Selection

We established the fire history in the PABR by analyzing maps made since 1990, when the most extensive fire to date happened. This fire covered ca. 1,500 ha and triggered the creation of Prevfogo, the Brazilian program for preventing fires in preserved land, according to the PABR's management plan (Brazilian Ministry of the Environment, 2005). After this large fire event, the staff at the reserve began mapping the extent and perimeter of every fire. We found data for fires that occurred in 1993, 2002, 2010. To recognize the areas affected in 1990, we asked and checked with the PABR staff in the field. For fires that occurred after 1990, we digitalized and georeferenced the maps made by the PABR staff following Prevfogo and the Brazilian Environmental Institute and Chico Mendes Institute (IBAMA/ICMBio) protocols (**Figure 1**). To assess the general state of the studied areas before 1974, we analyzed an aerial photograph taken in 1956. We conducted the present study between July and November 2010 (**Figure 1**).

Peatlands and contiguous anthropogenic pastures have the highest fire frequencies in the PABR. They are treeless areas, and grasses, such as *Imperata brasiliensis* Trin. and *Melinis minutiflora* P. Beauv. dominate and recolonize them rapidly after each fire event. They represent a stable state governed by grass-fire cycles and are part of the fire gradient, but we focus on the subset of pastures that have a few trees breaking this cycle. Overall, this kind of frequently burned abandoned pastures occupy 1,613 ha of the area of the PABR (32.3%), while the early regenerating states occupy 213 ha, 4.3% of its area (Lima et al., 2006).

Following the 2010 fire, we selected five areas according to their fire history:

1. secondary woody scrubs that burned four times, the last of which was 0.5 years before the measurements (in 2010). This area that was subjected to four fire events (1990, 1993, 2002, 2010) and had less time for recovery will be hereafter named **high disturbance** areas;
2. secondary woody scrubs that burned three times (1990, 1993, 2002), the last of which occurred 8 years before the measurements (2002). The areas with this fire history were classified as **medium disturbance** areas;
3. secondary woody scrubs that burned once, 20 years before the surveys (1990). Because of the low number of fire events and the longer time for recovery, we classified the vegetation with this fire history as **low disturbance** areas;
4. **secondary forests**, which were pastures in 1956 according to the aerial photograph, and are regenerating in the absence of fire at least since 1974 (date of the creation of the PABR, 36 years before the surveys);
5. **mature forests**, with no evidence of significant anthropogenic disturbance for at least 54 years, according to the 1956 aerial photograph.

The studied areas have simultaneously different fire frequencies and different recovery times (0, 8, 20, >36, and >54 years). Likewise, distance to the nearest propagule source is also correlated to a higher fire frequency and less time for recovery (**Table 1**). We consider that this gradient does not form a classic space-for-time substitution (a chronosequence) because the areas along it have different disturbance histories (Walker et al., 2010). They instead form a complex fire gradient, in which the number of fire events and time since the last disturbance are inversely related. We consider this gradient as a natural experiment (Legendre and De Cáceres, 2013). The fact that there are no sites in the PABR and its surroundings to complete a full factorial design reinforces the idea that there is an established positive feedback between fire and grasses in these pastures (**Figure 1**).

2.3. Vegetation Survey

In each one of the five kind of areas with the same fire history (High, Medium, Low Disturbance, Secondary Forests and Mature Forests), we marked three 30 × 60 m plots, with at least 100 m between them (**Figure 1**). We divided each plot in three 20 × 30 m blocks and each block in six 10 × 10 m subplots. We sampled randomly two subplots in each block (20 × 30 m), thus surveying six 10 × 10 m subplots (600 m^2) per plot, for a total of 90 subplots in 15 plots.

In each 10 × 10 m subplot, we surveyed all the individuals of trees, shrubs, and palms, with diameter at breast height (dbh) dbh $\geq$5 cm. The dbh was measured at 150 cm from the trunk base and consistently on the downslope-facing side of the trunk. Stems from multi-stemmed individuals were measured and the individuals were included if their equivalent dbh (the equivalent diameter of a circle with the same basal area taken from all the individual stems) was also $\geq$5 cm. We also measured leaf area index (LAI) at the center of each subplot, by analyzing hemispheric photographs taken under overcast weather, 1 m above the ground. The photos were taken by a fisheye lens Nikon FC-08 coupled to a Nikon Coolpix 4500 camera, and LAI was

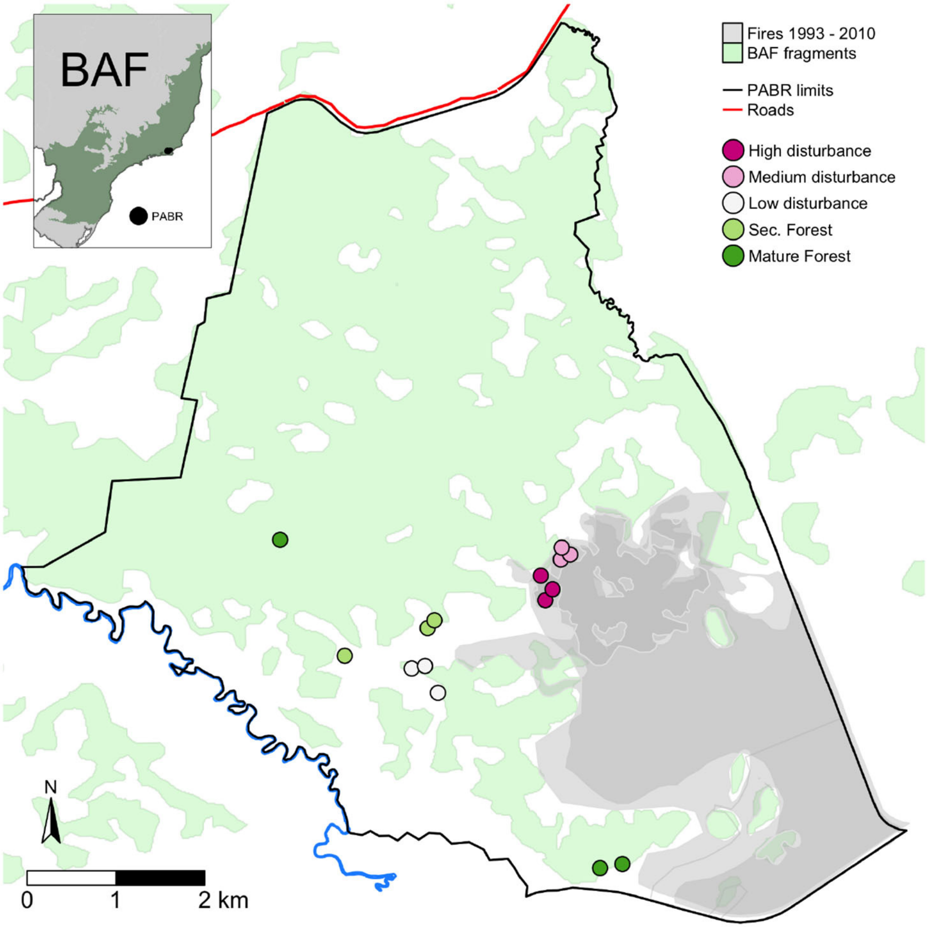

FIGURE 1 | The study area at the Poço das Antas Biological Reserve (PABR, black line), a Biological Reserve located in the eastern portion of the Brazilian Atlantic Forest (BAF). The green area in the inset map corresponds to the official limits of the BAF (IBGE, 2019), and the remaining BAF forest fragments (SOS Mata Atlântica, 2010) are depicted in light green in the main map. We established the fire history since 1993–2010 (overlapping gray areas), from maps made by the PABR staff. An additional fire in 1990 has no official map but it affected the High, Medium, and Low disturbance areas (last burned in 1990). The burned areas are mostly abandoned pastures and peatlands, and we positioned our sampling plots along the pasture-to-forest transition, where vegetation is regenerating. Each point in the map corresponds to a 60 × 30 m plot, subdivided in 10 × 10 m subplots. The fire history is detailed in **Table 1**.

calculated using Gap Light Analyzer Version 2.0 (Frazer et al., 2001). Percent grass cover was estimated visually in two 1 × 2 m quadrats in each 10 × 10 m subplot.

2.4. Response Functional Traits

To analyze the community response to the opposed effect of the fire regimes and secondary succession, we selected five functional response traits related to fire resistance and forest growth (**Table 2**).

- **Specific leaf area** (SLA, cm^2/g) is an indicator of the plant's light acquisition strategy (Weiher et al., 1999; Wright et al., 2004) and is expected to be higher in less disturbed areas (mature forests), for two reasons. On the one hand, it will contribute to maximizing light capture in low-light environments and therefore is expected to be higher in forests; on the other, thicker, heavier leaves with high longevity are expected in harsher environments (Díaz et al., 2016).
- **Wood density** relates inversely to relative growth rate, and lower values relate to fast growth and colonization ability in newly disturbed sites. In mature forests, wood density relates to plant longevity and long-term resistance to decay (Kraft et al., 2010; Larjavaara and Muller-Landau, 2010).
- **Potential height** is related to competitive capacity and light acquisition strategies, but also to plant longevity. We expected canopies to be taller in general in forest environments. We also expected a canopy stratification to appear with forest development, reflected in multimodal distributions or larger variances of this trait (Kunstler et al., 2016).
- **Seed mass** is related to the dispersal vs. survival trade-off and dispersal syndromes (Westoby, 1998), and we expected it to be higher in forests due to the presence of plants with lower number of larger seeds, dispersed by animals, while the presence of smaller seeds-probably dispersed by wind is expected in open environments (Westoby, 1998).

TABLE 1 | Environmental factors that compose the complex fire gradient.

Plot	Time post-fire	Fire events	Distance to the nearest propagule font (m)	Longitude, Latitude	Code
2010A	0.5	4	130	−42.269, −22.557	High
2010B	0.5	4	180	−42.268, −22.556	High
2010C	0.5	4	65	−42.270, −22.555	High
2002A	8	3	55	−42.267, −22.553	Medium
2002B	8	3	50	−42.266, −22.553	Medium
2002C	8	3	30	−42.267, −22.552	Medium
1990A	20	1	75	−42.281, −22.567	Low
1990B	20	1	30	−42.284, −22.564	Low
1990C	20	1	30	−42.282, −22.564	Low
SfA	>36	0	0	−42.282, −22.560	Sec.
SsB	>36	0	0	−42.281, −22.560	Sec.
SfC	>36	0	0	−42.291, −22.563	Sec.
MfA	>54	0	0	−42.261, −22.584	Mat.
MfB	>54	0	0	−42.263, −22.584	Mat.
MfC	>54	0	0	−42.298, −22.551	Mat.

For secondary and mature forests, we chose the last certain date the areas had not burned (1974 and 1956, respectively), although the real time can be higher, especially in mature forest. Secondary forests were considered to be their own propagule source.

TABLE 2 | Functional response traits measured for this study, their units, and hypotheses related to fire resistance and forest growth.

Trait	Unit	Hypothesis	References
Specific Leaf Area (SLA)		Higher in more shaded environment, lower in low-nutrient areas	Poorter et al., 2009; Reich, 2014
Plant height (H)	m	Higher in forests, related to competitive ability, longevity, light acquisition	Westoby, 1998
Wood density (WD)	g/cm^3	Higher in forests, related to longevity, slow growth	Kraft et al., 2010; Larjavaara and Muller-Landau, 2010
Bark thickness (BT)	mm	Higher in areas with harsher fire regimes, related to fire survival, meristem protection	Pausas, 2014, 2017
Seed mass (SM)	g	Higher in forests, zoochory, coupled with lower seed number, higher investment per seed	Westoby, 1998

- **Bark thickness** confers the ability to survive fire events (Hoffmann et al., 2009; Pausas, 2014) and was thus expected to be higher in areas more affected by the fire regime.

Leaf traits were collected from 1 to 8 individuals in the plots along the gradient. We found individuals for 121 of the 137 species present in the original species list, and followed Cornelissen et al. (2003) protocols. Twigs were collected and stored in the dark and refrigerated to avoid water loss. Individual leaves were cut in the laboratory underwater, to avoid cavitation, and their weight and area were measured. Bark thickness was measured from branch twigs (Paine et al., 2010), taking care of controlling for average diameter and position on the plant (i.e., not comparing twigs that were too thick with thinner twigs). We measured wood density from these twigs, by calculating the twig fresh volume following the volume replacement method and dividing it by its dry weight (Cornelissen et al., 2003). Potential height was assessed in the field, after calibration by two experienced persons and using marked leaf-cutter poles. Since most of the collected material was infertile, seed mass was measured from herbarium material. RB herbarium at the Rio de Janeiro Botanical Garden is the principal repository of botanical collections in Brazil, and the PABR has been thoroughly surveyed, therefore for all species it was possible to select botanical samples collected in the previous 10 years in the PABR or its close surroundings. This dataset was previously analyzed in Sansevero et al. (2020).

2.5. Species Geographic Distribution

Occurrence records for each species (see **Supplementary Table 1**) were downloaded from the Global Biodiversity Information Facility (GBIF) using **rgbif** package (Chamberlain et al., 2016) in the R statistical environment (R Core Team, 2016). GBIF returns spatial coordinates of the species as recorded in botanical collections around the world. We removed geographic outliers and suspect coordinates (e.g., at the centroid of countries). We calculated the known area of distribution by rasterizing the occurrence points shapefile to a 2.5-min resolution WorldClim template, and counting the resulting pixels, thus calculating the Area of Occupancy (AOO; IUCN, 2001). Both the weighted and unweighted means of the distribution area (e.g., taking into account the dominance structure of communities or not) were calculated for each area along the gradient and used as a proxy to analyze the extent of the distribution area of the species composing the communities.

2.6. Generalization to Other Sites in the BAF

We reviewed the Neotropical Tree Communities database (TreeCo) and the National Forest Inventory database (http://www.florestal.gov.br/inventario-florestal-nacional) to gather possible occurrences of the species in forest inventories in other regions of the BAF. Guided by these occurrence data, we visited and surveyed forest fragments larger than 0.5 ha, looking especially for the presence of *M. polymorphum* as a monodominant species (relative abundance above 60%, Peh et al., 2011). At sites surveyed, monodominance was assessed visually, by taking into account the proportion of individuals from different species in relation to the total number of *M. polymorphum* individuals in the canopy. To obtain the stand size, we delimited manually the perimeter of each one using high-resolution satellite images (Google Earth) considering their color homogeneity, texture, and canopy pattern. We built a map of *M. polymorphum* monodominant sites in the visited areas in the BAF.

2.7. Data Analysis

To test the hypothesis that harsher fire regimes (e.g., more fire events and less recovery time) simplify forest structure and decrease their diversity, we compared the following variables along the fire gradient: (1) the relative dominance of *M. polymorphum*, (2) Simpson's diversity, (3) forest structure (mean tree height, tree density, mean tree ramification, total basal area, LAI), (4) percent grass cover.

To analyze functional trait composition and the Area of Occupancy (AOO) of each tree species present along the fire gradient, we calculated the community-weighted mean (CWM) of each studied functional response trait and of their AOO according to the following formula:

$$CWM_{trait} = \sum_{n=1}^{S} p_{ij} * q_i$$

where p_i is the relative abundance of species i in plot j and q_i is the mean trait value or the AOO of species i. We obtained thus a mean trait value per plot or subplot for each trait.

Comparisons of structural parameters and of functional response trait CWMs along the gradient were performed using a one-way permutation-based analysis of variance with *post-hoc* pairwise tests as implemented by function `aov.perm()` in Basso et al. (2009), at the plot level (five areas, three plots per area).

A principal components analysis (PCA) was also performed on the vegetation structure data to understand the overall relationships between variables, at the subplot level ($n = 90$). To analyze taxonomic and functional turnover along the disturbance gradient, we calculated the Chord distance from the community matrix (121 species in the 90 subplots) and the Gower distance from the functional community-weighted mean trait matrix. We performed Principal Coordinates Analyses (PCoA) (Legendre and Gallagher, 2001) for both distance matrices. All analyses were performed in the R statistical environment, using the **vegan** community ecology package v.2.3-0 (Oksanen et al., 2016).

3. RESULTS

High disturbance areas were composed of mainly *M. polymorphum* individuals (**Figure 2A**), with a mean canopy height of 4.10 m (s.d. = 0.63), and multistemmed individuals. These areas had the lowest plant densities (**Figure 2C**) and LAI values (**Figure 2D**), and more than half of them had a continuous grass cover in the understory (**Figure 2G**). In consequence, Simpson's diversity was null in most plots (**Figure 2B**). High community-weighted mean (CWM) values for bark thickness and low CWM values for seed mass, wood density, and specific leaf area reflected the attributes of the dominant species.

Medium and Low disturbance areas, with more time since the last fire and less fire events, exhibited a recovery in structural parameters. Plant density (**Figure 2C**), canopy height (**Figure 2D**), basal area (**Figure 2E**), and LAI (**Figure 2F**) also increased at different rates along the fire gradient. However, secondary forests did not attain the canopy height or basal area of the old-growth reference forests. Dominance by *M. polymorphum* also decreased along the gradient, with less fire events and more time since the last fire. However, more than half of the plots in secondary forests still exhibited a relative density higher than 0.5, and monodominance (r.d > 60%) in almost 25% of them. The high dominance of the species along the gradient contrasts sharply with its complete absence from old-growth forests (**Figure 2A**).

Grass cover decreased sharply along the gradient (**Figure 2G**), from 100% cover in the High disturbance areas until the full exclusion of grasses in secondary forests. Reference old-growth forests had no grasses in their understory. Mean plant ramification decreased with milder fire regimes (**Figure 2H**), not only due to the effect of species arrival since the individuals of *M. polymorphum* were also mostly multi-stemmed in more disturbed areas and mostly monopodial (i.e., having only one stem) in less disturbed areas. The PCA of the structural variables (**Figure 3**) reflected the structural recovery in terms of higher plant density, higher LAI, larger basal area and canopy height along the fire gradient, but differentiated the old-growth forests from the rest of the areas by having species with relatively small distribution areas and significantly higher basal areas and mean heights (**Figure 3**).

Likewise, mean community-weighted SLA, woody density, and seed mass increased, while bark thickness decreased along the gradient. In all cases, old-growth forests and secondary forests had significantly different values and larger ranges of CWM variation from High, Medium and Low disturbance areas (**Figure 4**). Values for wood density and seed mass were significantly higher and more variable in mature reference forests than in the rest of the gradient.

Structural changes were accompanied by an increase in Simpson's diversity (**Figure 2B**), but regeneration processes along the gradient included few species present in any of the reference old-growth forests. In fact, reference old-growth areas shared only 11 of the 96 species with any of the other areas (**Supplementary Table 1**). The taxonomic composition was strikingly different between old-growth forests and the rest of the

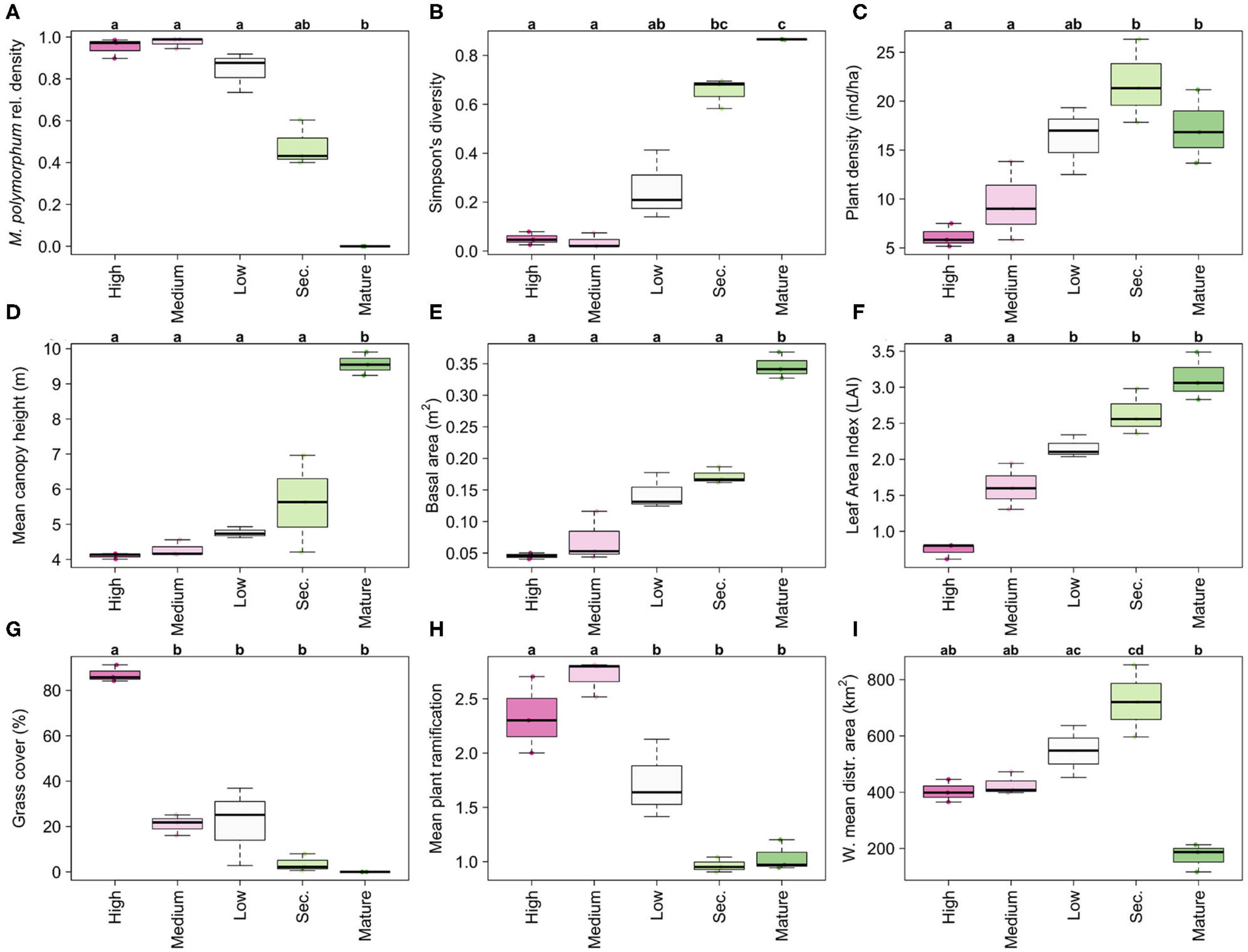

FIGURE 2 | Diversity and structure of secondary vegetation along a fire gradient that combines an increasing number of fire events and less time for recovery. High disturbance: four fire events and 0.5 years post-fire. Medium disturbance: three fire events and 8 years post-fire. Low disturbance: one fire event and 20 years post-fire. Secondary forests: no fire events and at least 36 years of regeneration. Old-growth forests, no fire events and they were confirmed forests since 1956 (at least 54 years of regeneration but possibly more). **(A)** Relative dominance of *Moquiniastrum polymorphum*, **(B)** Simpson's diversity, **(C)** plant density, **(D)** mean canopy height, **(E)** total basal area, **(F)** Leaf Area Index (LAI), **(G)** percent grass cover and **(H)** mean plant ramification increased with lower disturbance intensity, indicating the structural recovery of secondary vegetation. **(I)** The mean area of distribution of the species increased from harsher to milder fire regimes and peaked in secondary forests, but the reference mature forests had the lowest values. Letters indicate significance groups (α = 0.05) following a permutation-based ANOVA with a *post-hoc* pairwise comparison (Basso et al., 2009). The statistics for these comparisons are in **Supplementary Material**.

fire gradient, regardless of their fire regime (**Figure 5A**, 48.52% of the explained variation along the first axis). Species turnover between high, medium, and low disturbance areas followed a linear trajectory that converged toward the composition of secondary forests, but diverged from the composition of mature forests, as shown by the second PCoA axis (10.37% **Figure 5A**). Most of the high and medium disturbance areas had almost the same composition, and variation along this axis came mainly from turnover between low disturbance areas and secondary forest areas.

In addition to the divergence in composition, species recruited in burned and secondary forests had significantly larger geographic distribution than species present in mature forests. The mean distribution area of species in high and medium disturbance areas (weighted or not by community abundance vectors) reflected mostly the geographic distribution of the monodominant *M. polymorphum* (**Figure 2I**). The mean geographic area was the main factor that differentiated the secondary forest structure from the rest of the gradient (**Figure 3**). In contrast to this tendency to recruit widely-distributed species, the species present in old-growth forest areas had consistently lower mean distribution areas than the rest of the species in the area.

Regarding the distribution of *M. polymorphum* in other abandoned pastures in the BAF, we recorded 74 areas of abandoned pastures that exhibited a monodominance of *M. polymorphum* in the visited sites (**Figure 6**).

The functional composition along the fire gradient converged toward the functional composition of some of the mature forests (**Figure 5B**, contrasting with the divergence in taxonomic

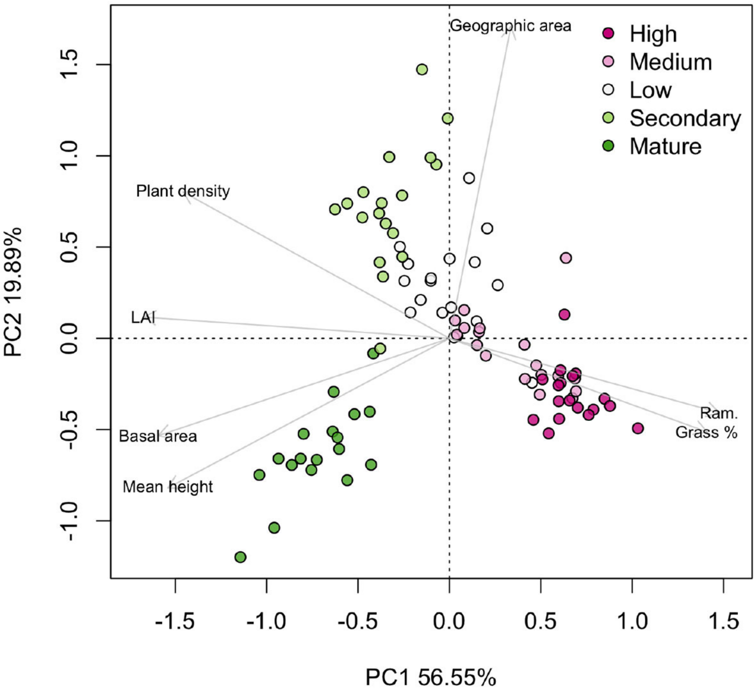

FIGURE 3 | PCA of the structural parameters along a fire gradient that combines an increasing number of fire events and less time for recovery. High disturbance: four fire events and 0.5 years post-fire. Medium disturbance: three fire events and 8 years post-fire. Low disturbance: one fire event and 20 years post-fire. Secondary forests: no fire events and at least 36 years of regeneration. Old-growth forests, no fire events and they were confirmed forests since 1956 (at least 54 years of regeneration but possibly more). Each point represents a 10 × 10 m subplot in three plots per area (*n* = 90). High percent grass cover and plant ramification characterized the areas with harsher fire regimes. Plant density, LAI, basal area, and mean canopy height increased with milder fire regimes. Mature reference forest had the highest basal area and mean canopy height. Large species geographic distribution areas separated the secondary forests from the rest of the gradient.

composition. The functional turnover along the gradient was extremely high, with the first PCoA axis accounting for 83% of the variation in functional composition and corresponding to the differences between all the burned sites and the mature forests. Old-growth functional turnover appears along the second PCoA axis (12.7% of variation).

4. DISCUSSION

Our results show how the establishment of a fire-resistant species helps the system break the fire-grass cycles that dominate the area. Some of the characteristics of the subsequent regeneration point to recovery with milder fire regimes (i.e., longer post-fire time and lower fire frequency), which confirms our initial hypotheses about the effect of less fire events and more time leading to recovery in forest structure and diversity. On the other hand, the presence of *M. polymorphum* generates a divergent pathway toward novel, impoverished forests composed of widely-distributed, generalist species. In the following sections, we analyze this duality in terms of a glass-half-full or glass-half-empty dilemma because success in passive and active restoration activities (i.e., the "desirability" of the outcomes) depends on the specific context in which restoration takes place, especially in human-modified landscapes. If the desired outcome is tree cover or carbon sequestration, some secondary forests may be providing already the sufficient ecosystem services to attain such goals, and no active restoration would be needed. It the outcomes are aiming to the recovery of biodiversity, cultural ecosystem services, or food provision, for instance, the outcome of natural regeneration may be insufficient (Lamb et al., 2005).

The studied areas occur in the transition from abandoned pastures trapped in the fire-grass cycle (*sensu* D'Antonio and Vitousek, 1992) to old-growth forests (**Figure 1**). These areas were pastures in 1956 and their current vegetation corresponds to the outcome of natural regeneration in the presence of different fire regimes. We thus cannot say that either "retrogressive succession" (Tabarelli et al., 2008) or "secondarization" (Barlow and Peres, 2008) happened in this system, since the studied fire gradient does not represent the erosion of standing forest fragments because of fire, as observed for some forests in the Amazon, where selective logging and surrounding fires interact to tip the forests to fire-prone states (Nepstad et al., 1999). Disentangling the specific effects of fire frequency and post-fire recovery time goes beyond the scope of this study and may prove impossible without experimental manipulation. However, the effects of both factors are directly related, so this does not impede the analysis of the regeneration taking place along the fire disturbance intensity gradient.

M. polymorphum is the main species from the regional species pool able to establish and persist in the abandoned

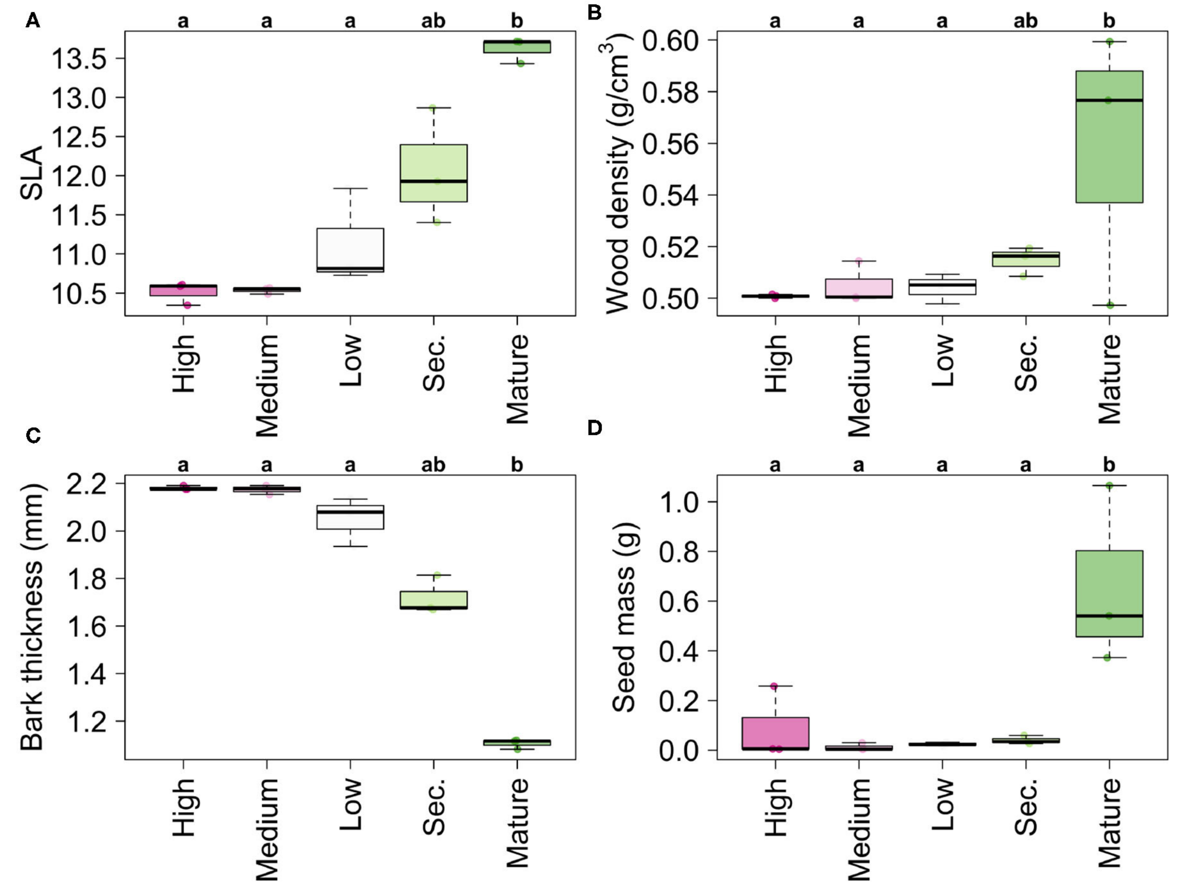

FIGURE 4 | Community-weighted values for the following functional traits: **(A)** Specific Leaf Area, **(B)** Wood density, **(C)** Bark thickness, **(D)** Seed mass along the disturbance gradient, from areas with high disturbance frequency to Mature Forests. Letters indicate significance groups (α = 0.05) following a permutation-based pairwise comparison. The statistics for these comparisons are in **Supplementary Material** (Basso et al., 2009).

pastures. The mechanism by which it establishes deserves further study, since we sampled individuals with dbh $\geq$5 cm and very few juvenile individuals are present among the grasses in the understory. Previous studies have shown that the species can flower and disperse its small, wind-dispersed seeds continuously, even shortly after fire events (Kolb, 1993). Due to the continuous propagule pressure, the species may find opportunities for colonization when grasses are suppressed by fire. Fire-free intervals allow individuals of the species to attain fire-resistance thanks to functional response traits like bark thickness (Pausas, 2014, 2017). This has been observed in tropical savannas, where the first key threshold for savanna-to-forest transitions is that established individuals survive fires and impede further fires to reset the community entirely (Hoffmann et al., 2012).

The vegetation structure in High disturbance areas, burned only 6 months before our measurements, confirms previous observations that the individuals of the species survive fire as reproductive adults (Prieto et al., 2017; Sansevero et al., 2017; Brandes et al., 2019). *M. polymorphum* individuals that attain fire resistance and survive fire events act as a template for regeneration. In the PABR, another species that can establish in the repeatedly burned pastures is the palm *Attalea humilis* Mart. ex. Spreng., but the species is not resistant to fire but resprouts after fire events (it occupies the "persistence niche" *sensu* Bond and Midgley, 2001). Therefore, it does not confer structure to the vegetation or facilitates the establishment of other species, as a remnant tree would do. Remnant trees play a key role in triggering regeneration following disturbance in some tropical forests (Holl et al., 2000; Hooper et al., 2005), but in the case of repeatedly burned pastures, species without fire-resistance traits are unable to survive (Bond and Midgley, 2001; Hoffmann et al., 2003), which forces a shift in composition after the fire. This would explain the absence of fire-sensitive pioneer species that are common in other regions of the BAF, such as *Trema micrantha* (L.) Blume and *Cecropia* spp. (Silva-Matos et al., 2005). In the *Cerrado* (Brazilian savanna), where fire is an endogenous disturbance, the transition from burned grassland to fire-resistant forests also depends on the establishment of fire-resistant species (Hoffmann et al., 2012). In highly-modified landscapes, pioneer, widely-distributed species and even allochthonous species can be favored for having functional response traits that are key for survival under the modified

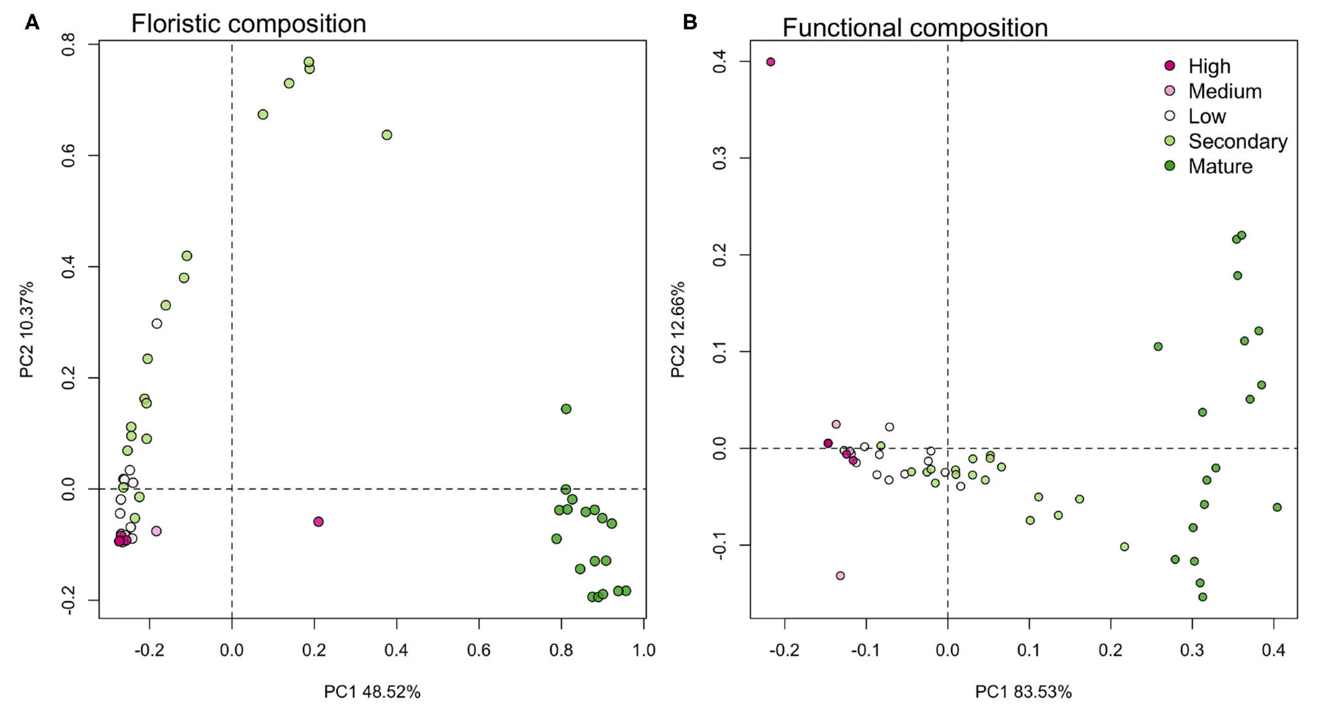

FIGURE 5 | (A) Taxonomic turnover along the fire gradient showed divergent floristic compositions between recovering burned areas and old-growth areas. Along the gradient, burned areas remained strinkingly different from reference old-growth areas (PC1), and their floristic composition diverged orthogonally, along the PC2. **(B)** Functional composition reflected the structural recovery of the vegetation along the gradient, in spite of the lack of floristic affinity, from High disturbance areas to Secondary Forests along PC1 and toward the functional composition of reference old-growth forests. Variation in the functional composition among mature forests is independent from this recovery and can be seen along PC2 axis. Each point represents a 10 × 10 m subplot in three plots per area (*n* = 90).

disturbance regime (Carpenter et al., 2004). Similar shifts in dominance have been discussed previously on several occasions, for example by Uhl et al. (1988) and Mesquita et al. (2001) for post-fire *Vismia* dominance in Amazonian forest and Santana et al. (2010) for *Rosmarinus officinalis* in temperate forests.

High disturbance areas have the lowest LAI values, that fail to exclude grasses in the understory and suppress fires. In addition to mortality due to fires, other species arriving in the areas are subjected to increasing competition with grasses during fire-free intervals and an excess light environment unsuitable for shade-dependent species. This hinders the early establishment of other species in these pastures, and perpetuates the monodominant state for a long time, as seen in the lack of significant differences between high and medium disturbance areas and the high dominance of the species even in the low disturbance areas. Studies on tropical forest succession have demonstrated that the first decades of succession can indeed be very slow (Uhl et al., 1988; Finegan, 1996), and the presence of continuous fires may delay regeneration even more.

With a longer time without fire, sites dominated by *M. polymorphum* gradually turn into more benign environments for the establishment and survival of other species. LAI almost doubles, and grass cover falls from ca. 100% to ca. 4% along the gradient, which explains the lower fire frequency. The step where canopy closes, grasses are excluded, and fuel accumulation stops is the "fire suppression" threshold described in pasture-to-forest transitions in the *Cerrado* and leads the herbaceous state toward a forested one, mostly uninfluenced by fire (Hoffmann et al., 2012). An increase in Simpson's diversity and basal area was observed between low disturbance sites and secondary forests, marking the stage at which most of the recruitment happens. Despite the milder environmental conditions, few species present in mature forests establish in these areas, and most of the species that enter the communities have significantly larger distribution areas than species present in old-growth areas. This floristic impoverishment reveals that fire has long-term effects, modifying the community assembly processes in pastures and diverting successional trajectories.

The appearance of *M. polymorphum*-dominated communities in the repeatedly burned pastures poses a glass-half-full/glass-half-empty situation, in which the outcomes are perceived as positive or negative depending on the observer's perspective and aims (Arroyo-Rodríguez et al., 2017). On the one hand, pastures caught in the fire-grass feedback represent an undesired state for biodiversity conservation, carbon emissions, and soil integrity, among others (D'Antonio and Vitousek, 1992; Veldman and Putz, 2011). Any natural process that breaks this feedback is significant, and in this sense *M. polymorphum*-dominated stands constitute more desirable states than abandoned pastures. Monodominated stands of the species can act as shelter and

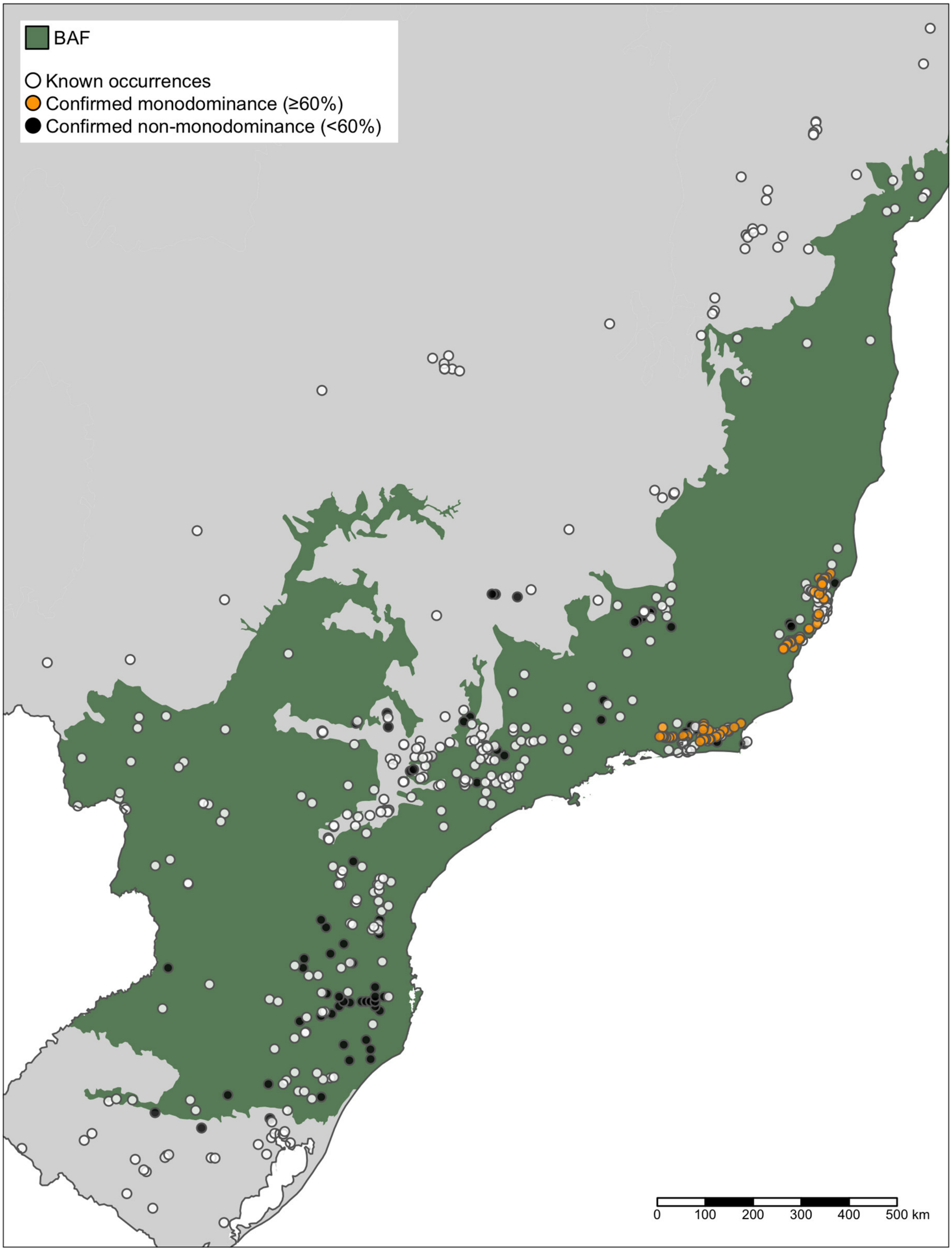

FIGURE 6 | Occurrence records for *Moquiniastrum polymorphum* along its whole area of distribution. We visited the areas with symbols in black and orange. Orange symbols indicate sites where the species was present as a monodominant (more than 60% relative abundance) and black symbols indicate sites where the species was present but not monodominant. The shaded green area corresponds to the official limits of the Brazilian Atlantic Forest (BAF; IBGE, 2019).

perches for fauna, promoting the dispersal of other plant species, and they can provide resources for pollinators. On the other hand, succession in these areas is very slow, monodominated stages persist for a long time, and the secondary forests are composed mainly of widely-distributed species, with a few forest and fire-adapted elements. A previous study carried out in low and medium disturbance sites showed low biomass and species richness resilience compared to other Neotropical secondary forests (Sansevero et al., 2017).

Many succession studies have concluded that floristic composition is one of the hardest parameters to recover and it should not be expected beforehand (Chazdon et al., 2007; Norden et al., 2015; Rozendaal et al., 2019). Choosing reference areas is also a key part of this comparison, since succession proceeds in idiosyncratic ways (Norden et al., 2015) and beta diversity is high in high-diversity regions, such as the BAF. Here, we have coupled comparisons regarding floristic composition with the size of the species' distribution area and the functional composition recovery, to avoid focusing in floristic composition as a target *per se*.

In the PABR, *M. polymorphum* is the only species in the regional species pool that can establish in repeatedly-burned areas, and it is totally absent from old-growth forests. The species is also widely distributed across the BAF (**Figure 6**) and the Brazilian Savanna (*Cerrado*). The BAF is heterogeneous and not covered fully by tropical rainforest, and the transition from *Cerrado* to BAF comprises semi-deciduous vegetation fragments that may act as corridors for *Cerrado* species, therefore the mere presence of *M. polymorphum* should not be taken as proof of modified fire regimes. However, the BAF has been severely degraded and the shifts from presence to monodominance were found in tropical rainforest portions, away from the ecotones from BA to *Cerrado*, which suggests that similar patterns of species assembly could be happening in these regions.

Our results highlight the need to assess regeneration processes at the local scale, in a qualitative way and not only in a quantitative way. Some studies have documented an increase in forest cover in the tropics (e.g., Aide et al. 2012 in Costa Rica and de Rezende et al., 2015; Rezende et al., 2018; dos Santos et al., 2019, in the BAF) but the nature of the regeneration pathways is frequently ignored. Observing community composition directly and assessing both the functional composition and the provision of ecosystem services would also be helpful to understand if the observed secondary forest are recovering or stuck in low-functioning secondary forests.

Dominance-shifts and divergent successional trajectories, such as these may be occurring along the whole Atlantic Forest, given the long time degradation history of the biome (Dean, 1996; Joly et al., 2014), the increasing fire frequency (dos Santos et al., 2019; de Jesus et al., 2020), and the existence of many more areas dominated by *M. polymorphum* in several degraded areas in the biome (**Figure 6**). If no action is taken (i.e., if ecological restoration relies solely in natural regeneration in these areas), the system can swing between two stable states, depending on the fire regimes. Especially, further fires can reset the communities back to *M. polymorphum* monodominance. However, the resulting secondary forests may serve as templates for future forest recovery, especially for restoration by enrichment planting to increase species richness and to guide the natural regeneration toward a composition that aligns with biodiversity conservation (Jakovac et al., 2015). This would require (1) a better understanding and mapping of the fire regimes across the Biome, (2) actions to prevent further fires, (3) the control of grasses under the canopies to lower their flammability, and (4) the active restoration of these sites, as enrichment plantations, to help increase the LAI and guide the recovery of taxonomic composition. We make a call for forest restoration practitioners to go beyond the simplistic approach of deciding between passive or active restoration, and to combine available techniques when possible, to fulfill the large-scale targets for biodiversity conservation and ecological restoration in the biome.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://github.com/AndreaSanchezTapia/sanchez-tapia_ffgc_2020.

AUTHOR CONTRIBUTIONS

AS-T, JS, and FS conceived the research idea. AS-T and JS collected the data. AS-T performed the statistical analyses and wrote the manuscript, with contributions from JS, MG, and FS. JB made the taxonomical determination of all plant species in the area. PF made the field surveys and dominance calculations in other BAF sites. All authors discussed the results, commented, and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2020.560912/full#supplementary-material

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Species Selection and Management Under Farmer Managed Natural Regeneration in Dodoma, Tanzania

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Farmer managed natural regeneration (FMNR) is promoted as a cost-effective technique to restore degraded arable drylands. Evidence comes mainly from the West-African Sahel, where it is a traditional practice, and it is now being promoted across the African continent. In this study, we evaluated the role of the farmer affecting natural regeneration under farmer managed natural regeneration in the highly degraded Dodoma region in Tanzania. We systematically assessed the linkages between species selection, perceived benefits and management practices as reported by 57 farmers in 13 villages involved in FMNR. On average, farmers list 2.8 species to be promoted on their farms as part of the practice of FMNR. In total, a list of 69 species was promoted by the practice, of which most (51) were only mentioned by one or two farmers, indicating that FMNR may contribute substantially to on-farm regional diversity. Most species selected were associated with a range of benefits and the diversity of benefits, not any single benefit, explained species selection under FMNR. Management of FMNR species goes beyond pruning, a practice promoted within FMNR, and is characterized by 10 different practices that are differentially applied to the selected species and individuals. We conclude that species selection and management under FMNR is driven by farmers autonomous decisions, making FMNR both diverse and complex and complicates predicting the extent to which FMNR may successfully contribute to achieving specific restoration outcomes. Monitoring farms over extended periods may increase outcome prediction capacity.

Keywords: farmer-managed natural regeneration, drylands, Tanzania, Africa, farmer, restoration, Dodoma

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INTRODUCTION

Communities worldwide are affected by land degradation, particularly in developing countries, because of high population pressure, reliance on charcoal and woody resources as the main energy sources and livestock overgrazing (Sabogal et al., 2015). Subsistence farmers face decreasing food security resulting from loss of soil quality and declining land productivity (Pimentel and Burgess, 2013). Land degradation not only negatively impacts local livelihoods but also increases the vulnerability of agro-ecosystems to climate change (Webb et al., 2017). Integrated approaches to land restoration can improve livelihoods, enhance biodiversity and increase climate mitigation by enhancing carbon sequestration in soil and vegetation (Benayas et al., 2009; Carey, 2020). The long-term success of restoration efforts generally depends on factors such as climate, soil characteristics, availability of materials, disturbance regimes, socio-economic circumstances, and local engagement (Holl et al., 2003; Chazdon, 2008; Crouzeilles et al., 2019). Dryland systems, which include arid, semi-arid and dry-sub humid ecosystems, are particularly vulnerable to land degradation and disturbances (James and Carrick, 2016; Hulvey et al., 2017). Most restoration opportunities for dryland subsistence farming exists in landscapes with moderate to high population pressure (Minnemeyer et al., 2011). Here, integrating trees on farms and grazing land is often a suitable restoration strategy. Research has shown that agroforestry can increase productivity (Schroth and Sinclair, 2003; Glover et al., 2012) and other ecosystem services (Jose, 2009). Agroforestry practices can have a positive impact by controlling pests and diseases, regulating the microclimate and affecting the nitrogen and phosphorus content in the soil (Kuyah et al., 2016; Hoosbeek et al., 2018). In addition, integrating trees can improve household nutrition (Reed et al., 2017) and contribute to both climate change adaptation and mitigation (Roshetko et al., 2007; Zomer et al., 2016). However, planting trees in dryland systems is challenged by low survival rates, in combination with the high costs of planting (Tougiani et al., 2009; Reij and Garrity, 2016; Holl and Brancalion, 2020).

Farmer-managed natural regeneration (FMNR) is considered one of the more promising techniques to restore degraded agricultural landscapes in dryland systems (Weston et al., 2015; Reij and Garrity, 2016). Under FMNR, farmers actively revegetate their fields by nurturing spontaneous/natural woody regeneration, while keeping crop production as their priority (Weston et al., 2015). Farmers make a decision based on what they expect is beneficial for their farmland and which services the woody vegetation provides (Reij and Garrity, 2016). This technique is different from other agroforestry techniques since it does not include the planting of seeds or woody vegetation (Tougiani et al., 2009). As naturally regenerating species are well-adapted to local conditions, they have a higher survival rate than planted species in semi-arid regions (Tougiani et al., 2009). FMNR was shown to be effective in agroforestry parklands of Niger, where three million hectares have been revegetated since the 1980s (Rinaudo, 2007). Examples from Niger, more recently also from Burkina Faso, Mali, Senegal, and Ethiopia, show that FMNR can reverse the loss of tree cover and diversity in dryland systems (Garrity et al., 2010), increase crop diversity and raise household income (Haglund et al., 2011; Weston et al., 2015). These examples have led to high expectations toward FMNR as a low cost and effective method for restoration, and it is now being promoted across different regions in Africa, Asia, and the Pacific (Birch et al., 2016). One of the main elements of FMNR is that farmers stay in control over their land and what they grow on it and build on their own past experiences. This is a condition for FMNR to be successful, and at the same time, continued empowerment of farmers is an outcome of the practice (Francis et al., 2015). However, little is known about what farmers select, how they manage natural regeneration and for what reasons.

Different management practices can be applied to select and promote useful woody species, including protection, removal of unwanted plants and soil improvement (Levis et al., 2018). Here the benefits of the woody species and the main purpose of the land will determine the selection and management activities and the extent to which the farmer can promote regeneration. Farmers adapt FMNR to their own needs and have different reasons for their choices (Rinaudo, 2007). Although FMNR is now being scaled out beyond its original range in the Sahel, many unknowns remain regarding the selection and management of natural regeneration by farmers, and how this influences the social and environmental restoration benefits that can be derived from the technique (Chomba et al., 2020). Specifically, there is a lack of studies that allow for a more in-depth understanding of what species farmers promote and manage and for what reasons (but see Ndegwa et al., 2017). Understanding what natural regeneration farmers select and promote is of importance because species differentially affect ecosystem functions, having large consequences for restoration outcomes that can be achieved with FMNR (Lohbeck et al., 2020). To get more insight into these farmer decisions, we consider the role of the farmer based on three pillars that are strongly interlinked and that are expected to eventually determine FMNR outcomes. These three pillars are species selection, perceived species benefits and management practices.

Here we report on the role of the farmer affecting regeneration under FMNR in the Dodoma region in Tanzania. The region has a long history of problems with land degradation, mainly caused by cultivation, overgrazing, cutting down trees for firewood, charcoal and timber and an increasing population (Östberg, 2000). In this region, FMNR has been supported since 2015. We systematically assessed species selection, perceived benefits and management practices by farmers that are involved in the FMNR program. Differences between the districts may also influence the choices farmers make; therefore, we also compared the species that farmers select at the district level. Understanding the role and preferences of the farmer within the practice of FMNR is central to evaluating the success of these projects in the long term, and for improving the implementation of FMNR as a restoration strategy.

Specifically, we asked

(1) What species do farmers select under FMNR and is there a difference between the (number of) species selected in each district?
(2) How do the perceived benefits of species influence whether they are selected under FMNR?
(3) What management practices are being applied across species, and how do these reflect their selection and perceived benefits?

MATERIALS AND METHODS

Study Region

For this study, we draw from an ongoing project in the Dodoma region in Tanzania where FMNR has been supported on a small scale since 2015 and more widely since 2018. Dodoma is a semi-arid region with an average annual rainfall of 400–570 mm per year (Mayaya et al., 2015). Most households in Dodoma depend on rainfed agriculture (Mayaya et al., 2015) and grow cereals (maize, sorghum and millet) and pulses (beans) (Brüssow et al., 2017). Fuelwood is their main energy source (Scheid et al., 2018). The FMNR practice is not considered traditional across these smallholder farming systems.

FMNR is being promoted through the Regreening Dodoma Program, which is jointly implemented by the organizations Justdiggit and LEAD Foundation and started on a larger scale in 2018. Farmers are trained in the practice of FMNR based on four steps which are (1) selecting, (2) pruning, (3) marking, and (4) protecting woody regeneration (see **Supplementary Material** for detailed project description). No recommendations are given as to which tree species should be promoted; the idea is that the farmer makes his or her own decisions, which is also core to the FMNR practice. Farmers don't receive compensation from the Regreening Program, and participation is on a voluntary base.

Data collection took place in November 2019. We visited 13 villages in six districts and 57 farms across the Dodoma region (**Figure 1**). One district, Dodoma urban, was not visited since it is not part of the program. All farmers practiced FMNR and were pre-selected randomly based on when they started with FMNR. If the selected farmers were not present at the introduction meeting, other available farmers were randomly selected. For answering the three research questions, we used interviews in which we asked four questions regarding the selection and management of regeneration (1) What species were selected to be promoted under FMNR on the farm? (2) For what reasons did the farmer select each species listed? (3) What management activities did the farmer apply to the species? (4) Why did the farmer perform these management activities? (see **Supplementary Material** for the interview form). Species were listed using local names, and the corresponding scientific names were derived from floras and online sources which was then cross-referenced with local experts who accompanied us in the field (see **Supplementary Table 1** for a list of identified species and references). Full identification was achieved for 46 of the 69 species.

Indicators of Species Characteristics

Perceived Species Benefits

To understand how farmers value the species selected for FMNR, we categorized the mentioned benefits post-data-collection into seven benefits: food, medicinal use, microclimate, products (e.g., timber, hoe handles, beehives), fuelwood, fodder, and soil nutrients (see **Supplementary Table 2** for a complete description of each category). The number of mentions of each benefit per species was divided by the number of farmers that listed this species in the interview. This resulted in a species-level score that ranges between zero and one per species for each of the seven benefits. The diversity of benefits per species was calculated by taking the frequency of mentions per service and dividing it by seven (maximum possible score) to come to a score between zero and one. If the score equals zero, no benefits were mentioned for that species, and if the score equals one, all benefits were listed for that species by all farmers.

Species Management Practices

The farmer listed the management they applied to each species, including if they applied no management. We categorized the management practices post-data-collection into 10 practices: pruning, competition removal, hang iron sheets, fencing, dig a base around the tree, structural support, apply insecticides, watering, marking, and no management (see **Supplementary Table 3** for a complete description of each category). No management was included as a category because it is also a conscious management decision taken by farmers. For further analysis, we only included management practices mentioned by more than five farmers. This resulted in four management practices being used; pruning, weeding, fencing and no management applied. Then, for each management practice per species, the count of mentions of each management practice was divided by the number of farmers that listed this species. This resulted in a score between zero and one for each of the 10 management practices per species. The diversity of practices per species was based on all 10 management practices and was calculated by taking the frequency of mentions per service and dividing it by 10 (maximum possible score) to come to a score between zero and one. With a score of zero, the management practice was not applied to that species and with a score of one, the management practice was mentioned by all farmers to be applied to that species.

Statistical Methods

Statistical analyses were carried out at the species level and only those identified to scientific species names and mentioned by at least three farmers were included. This led to a total frequency of 98 mentions across 18 species. After transformation to improve parametric model fit, we performed an analysis of variance (ANOVA) to understand if there were differences between the numbers of species mentioned by farmers across districts.

We performed a Moran's I test to test for spatial autocorrelation underlying species mentions across the region. This was tested separately for all 18 species with at least three mentions. We found no spatial autocorrelation underlying the abundances of 15 species, the species that did show a spatial pattern in their number of mentions were: *Leucaena leucocephala*, *Senna siamea*, and *Terminalia sericea*. Since most species showed no spatial autocorrelation, we assume independence of our data points.

To evaluate how the perceived benefits affected whether species are favored for FMNR, we used generalized linear models with a Quasi-Poisson distribution. Quasi-Poisson is suitable for non-parametric and over-dispersed count data. Eight separate models were created for each benefit plus the diversity of benefits as the independent variable and the frequency of mentions by farmers as the dependent variable. To understand how management reflects species selection, we also used generalized linear models with a Quasi-Poisson distribution. Five models were created for each management practice plus the diversity of management as the independent variable and the frequency of mentions as the dependent variable. We then correlated species management practices to the perceived benefits using a Kendall distribution to account for non-parametric distributions and small sample size. All statistical analyses were carried out using R version 3.3.2 (R core team, 2014).

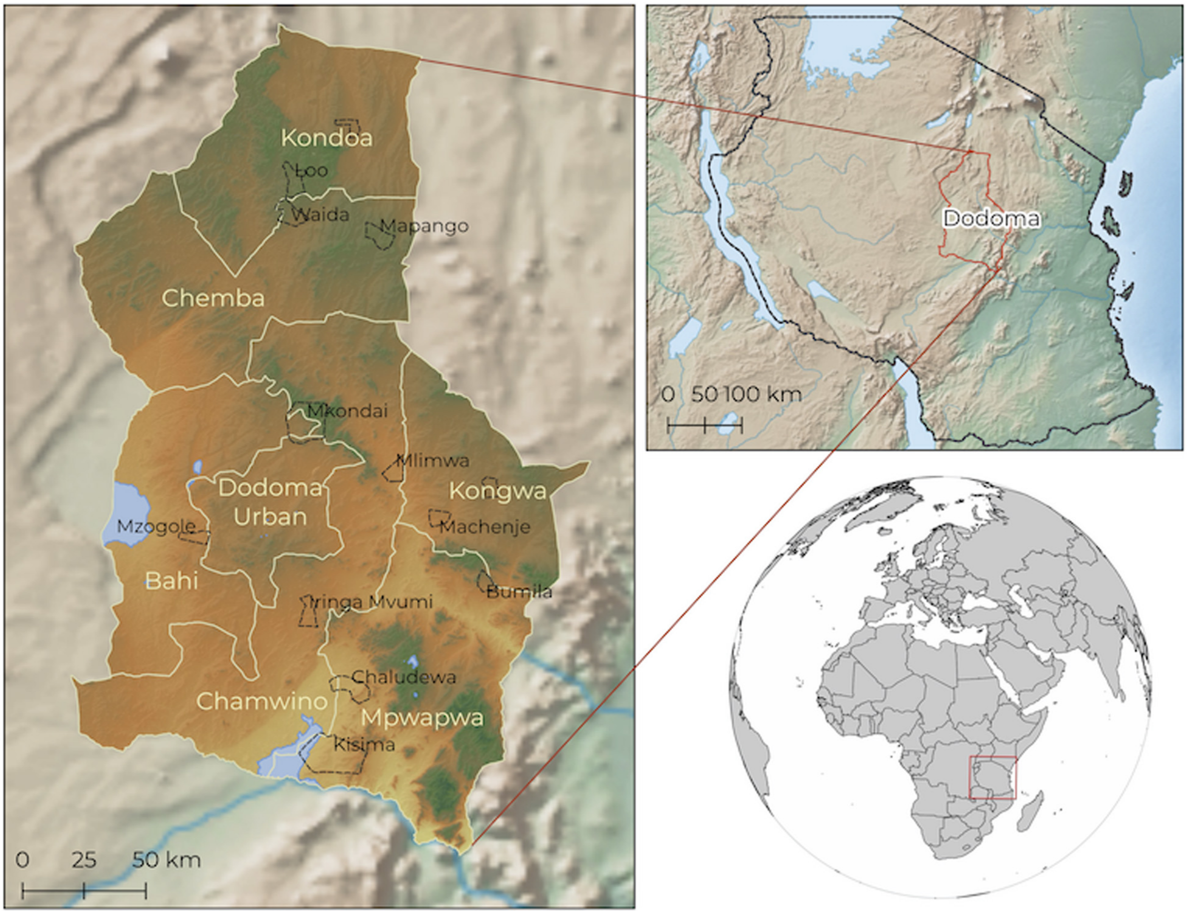

FIGURE 1 | A map of the study region. The districts are written in yellow, and the villages are written in black.

RESULTS

Species Selection

A total of 69 species were mentioned to be managed under FMNR, of which 18 species were mentioned three times or more. On average, farmers promoted 2.8 species on their farms. About half of the farmers (52%) listed that *Vachellia tortilis* was promoted on the farm as part of FMNR, followed by *Dichrostachys cinerea*, *Senna siamea, Senna singueana* (7%). There were no significant differences between the number of species mentioned by farmers across districts (**Figure 2**, $p > 0.05$, $F = 0.644$, $df = 5$). Despite this lack of differences, no species were found across all districts. Only *V. tortilis* and *D. cinerea* were found across five of the six districts, and 45 species were only mentioned in one district.

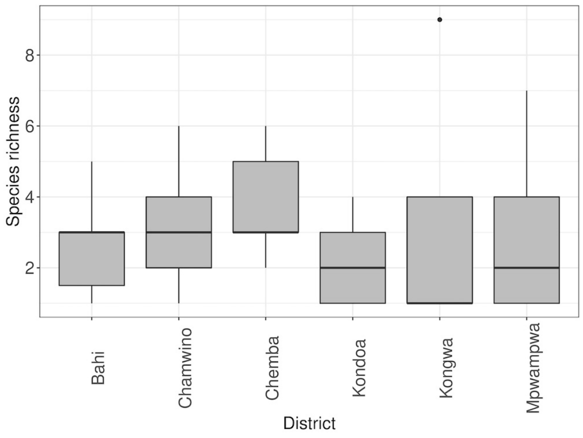

FIGURE 2 | The number of species chosen for FMNR by each farmer throughout each of the six districts sampled throughout Dodoma (*n* = 57).

Perceived Species Benefits

Farmers mentioned 24 different reasons for selecting individuals under FMNR, which we categorized in seven benefits the most common being fuelwood (91%), products (54%), and fodder (48%) (**Supplementary Figure 1**). Fuelwood was given as a reason by at least one farmer for 78% of species, products 52%, fodder for 42%, soil nutrients for 39%, and food for 30% of species (**Figure 3**). The frequency of species

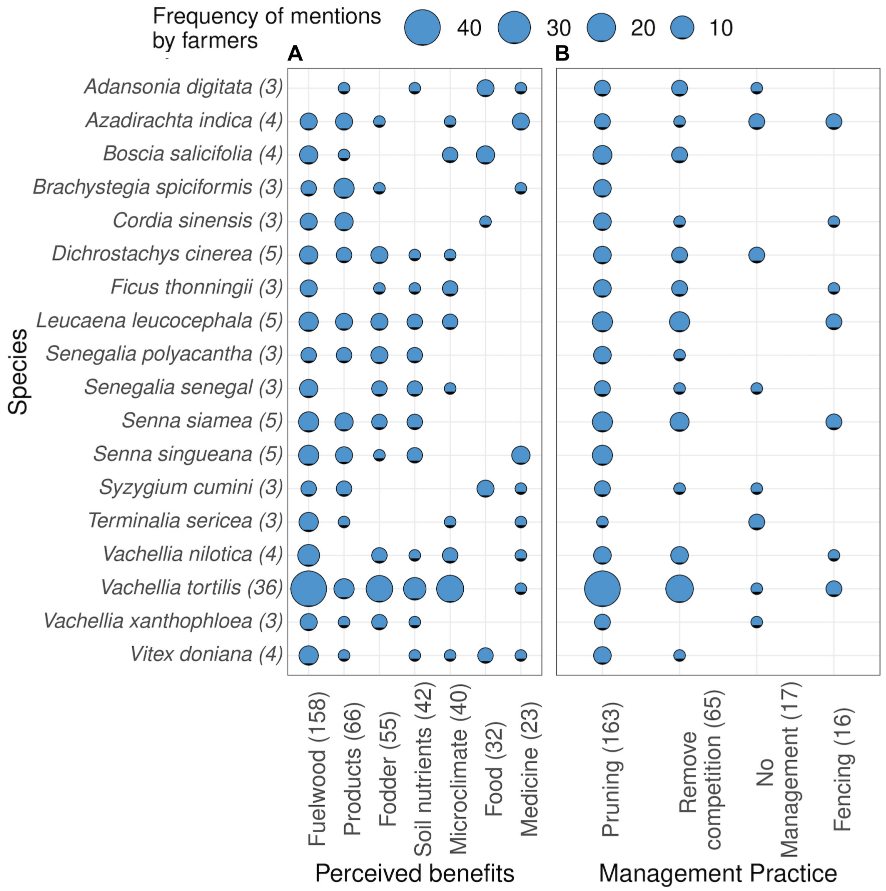

FIGURE 3 | The **(A)** perceived benefits and **(B)** management practices by species selected under FMNR as listed by the 57 farmers. The frequency of mentions (max 57) is given by the size of the blue circles. To the right of the species name is the number of mentions for that species (max 57). To the right of the perceived benefits and management practices is the total frequency of mentions, these are ordered in decreasing number of mentions. Only 18 species with more than two mentions are shown, see **Supplementary Figure 3** for all species.

mentions was not explained by any single species benefit. However, species more frequently used for FMNR provided significantly higher diversity of benefits (beta = 5.2, $R^2 = 0.5$, $p < 0.05$).

Management Practices

Pruning was the most important management practice, applied to 90% of species, followed by competition removal (49%) (**Figure 3**). Also "no management" was indicated by farmers and applied to 19% of the FMNR species followed by fencing, which was applied to 17% of species. **Figure 3** shows the frequency of mentions for management practices by species (see **Supplementary Figure 2** for the total frequency of mentions, and **Supplementary Figure 3** for the frequency of management practices for all listed species). Species more frequently used for FMNR had a significantly higher diversity of management practices applied to them (beta = 4.9, $R^2 = 0.48$, $p < 0.05$). We found no significant correlations between the management practices applied to species and the perceived benefits (**Figure 4**, see also **Supplementary Table 4**).

DISCUSSION

In this study, we evaluated farmers selection and management of natural regeneration when applying farmer-managed natural regeneration in the highly degraded Dodoma region in Tanzania. Here FMNR has been widely supported and promoted since 2018. We systematically assessed the linkages between species selection, perceived benefits and management practices as reported by farmers that are involved in FMNR. We found that farmers list a total of 69 species to be promoted under FMNR, of which most (51) were only mentioned by one or two farmers, indicating that FMNR may contribute substantially to on-farm regional diversity. Farmers mention a range of benefits associated with species they select, and, although no single benefit could explain what species are selected, the diversity of benefits was associated with species selection. Also, the management of FMNR individuals is characterized by 10 different practices that are differentially applied to the selected species and individuals. We found that the practice of FMNR is complex because of the diversity of reasons to select individuals and because of a wide range of management practices applied. This suggests that

FIGURE 4 | Correlations between management practices (rows) and the species scores for benefits (columns). Reds are negative relations, and blues are positive relations with the darkness of the color indicating the strength of the relation. Asterisks in the cells indicate significant relations (**$p < 0.01$, *$p < 0.05$, $N = 69$), see also **Supplementary Table 4** for test statistics.

FMNR promotes species with multiple benefits and is driven by farmer's autonomous decisions. It is characterized by diversity and complexity, which complicates the potential of predicting restoration outcomes in the long term. Nevertheless, we stress that understanding the role and preferences of the farmer within the practice of FMNR is central to evaluating the success of these projects on the long term, and for improving the implementation of FMNR as a restoration strategy. Further research into the species preferences of farmers may give insight as to how to promote the use of less common species for FMNR, further increasing on-farm biodiversity.

Species Selection Under FMNR

On average farmers report to promote 2.8 species on their farms. There was no significant difference in the number of species mentioned on the farms across the six districts. 51 out of 69 species were mentioned only once or twice, highlighting the range of different species farmers are selecting for FMNR and supporting findings that FMNR can increase the diversity of woody species on farmland (Haglund et al., 2011). In particular, our result indicates that farmers make very different choices in what species they select and promote, and thereby FMNR may be specifically beneficial for on-farm regional (or gamma) diversity. Increasing biodiversity not only makes systems more resilient but also increases the diversity of resources to the smallholder farmers (Francis et al., 2015).

The species *Vachellia tortilis* was selected most often by the farmers. Research by Krog et al. (2005) in a nearby region, shows that *V. tortilis* is an important tree for farmers livelihood in Tanzania. In addition, this species is very common in the area (Komwihangilo et al., 1995) and in our study, it was used for FMNR in five of the six districts sampled.

Species Benefits

Although we found no relation between species selection and any single perceived benefit (**Table 1**), species more frequently chosen for FMNR provided a higher diversity of benefits. This result highlights that species are valued for a range of different benefits (**Figure 3**). This is typical for smallholder farming systems where farmers depend on their land for a wide range of services (Ango et al., 2014). Moreover, under FMNR management, the primary purpose of the field remains crop production. Therefore, it may be more suitable for farmers to favor species that provide a wide range of benefits because it reduces the number of species and/or individuals needed in the field, perhaps reducing competition with crops and making it easier for the farmer to manage. This may also explain why we found no relations between any single benefit and species selection. Instead, it is likely that species selection under FMNR may be driven by a more holistic strategy, where the diversity of species is considered at the whole farm level and how these together provide for the different needs of the smallholder farmer.

The species listed most often by farmers, *Vachellia tortilis*, may be a popular choice for the farmer since it is a common species in the area and provides many benefits: fuelwood, fodder, soil nutrients, microclimate, products and medicine (**Figure 3**). Species in the *Vachellia and Senegalia* genera have the ability to fix nitrogen and make it available to other plants in the system (Tedersoo et al., 2018). This can have direct impacts on the productivity of crops. Soil fertility benefits of N_2 fixers can be very local, highlighting the need to preserve these in the field with

TABLE 1 | Summary of test results relating (A) the frequency of species mentions to the benefits per species, as tested with regression analyses and (B) the frequency of species mentions to management practices, as tested with regression analyses.

(A)		Frequency of mentions		(B)		Frequency of mentions	
Benefits	**Beta**	**R^2**	***p*-value**	**Management practices**	**Beta**	**R^2**	***p*-value**
Food	−0.68	0.06	0.52	Pruning	1.22	0.06	0.466
Medicine	−0.82	0.04	0.58	Remove competition	0.24	0.006	0.83
Microclimate	1.65	0.15	0.19	No management	−1.22	0.07	0.47
Materials	−0.8	0.07	0.44	Fencing	−0.56	0.011	0.77
Fuelwood	1.2	0.06	0.51	Diversity of practices	4.9	0.38	< 0.05
Fodder	0.42	0.02	0.7				
Soil nutrients	0.06	0.00	0.97				
Diversity of benefits	5.2	0.5	< 0.05				

Given are the beta, R^2 and p-value for each test.

the crops (Giller and Cadisch, 1995). These results are similar to a study in Kenya where *V. tortilis* as well as a number of other *Vachellia and Senegalia* spp. (*V. gerrardii, Senegalia mellifera, V. nilotica, V. lahai, S. senegal, V. seyal*) were also favored under the practice of FMNR and were valued mainly for charcoal, fodder and microclimate (including shade) (Ndegwa et al., 2017).

The majority of species are mainly valued for fuelwood and fodder. The dependency on fuelwood is unsurprising because it is essential for households daily cooking, and there are documented fuelwood shortages in the region (Scheid et al., 2018). Fuel and fodder production were also the main reasons for selecting and managing FMNR trees in Kenya (Ndegwa et al., 2017).

Tree Management

The first core principle of FMNR as given by Rinaudo et al. (2018) is: "The systematic pruning and management of existing indigenous trees and shrubs by the land user." Pruning, as such, is a core principle and practice to FMNR and other management practices are allowed but not specified. Also, in the Regreening Dodoma program, pruning is identified as a core practice (see detailed project description in **Supplementary Materials**). This is confirmed by our results: pruning was applied to 90% of the species selected under FMNR. Pruning is a way to influence the growth form of an individual and can be used to reduce competition for light and water with crops (Jackson et al., 2000). In addition, pruning can increase the light within the crown and affect flower and fruit production (Timmer et al., 1996; Bayala et al., 2008). Pruning is also a consequence of harvesting leaves and branches that can then be applied to the soil as green manure, as mulch, or fed to livestock (Bayala et al., 2012; Cuni-Sanchez et al., 2018). We, therefore, expected that pruning would be associated with the benefits of fodder and soil, which we did not find (**Figure 4** and **Supplementary Table 4**).

Interestingly, when farmers are openly asked for management practices, the list is much longer than only pruning; 10 different management practices are given, although some are rarely applied. No management, the deliberate lack of management, was explicitly mentioned. Although under some stricter definition of FMNR this may be excluded, we included it as it is a deliberate decision by some farmers and they see it as part of FMNR. No significant relations between species more frequently used for FMNR and individual management practices were found, although we did find a significant positive relation with the diversity of management practices applied (**Table 1**). However, this result was strongly influenced by the popularity of *V. tortilis,* and the relation disappeared once this species was removed. This may be because farmers have more knowledge on such a common species to the region (Komwihangilo et al., 1995). In addition, *V. tortilis* is a fast-growing species, which may require the application of several different management practices.

Duration of This Restoration Project and the Need for Long-Term Studies

Although the diversity of benefits underlies farmers reasons for selecting species, many (51) species were only selected by one or two farmers. This highlights that individual farmers have their own reasons for species selection, and that part of this variation is unpredictable. We expect this may have been caused by the short duration of the FMNR project in Dodoma, which had only started intensively 2 years prior to this study. Probably farmers are still experimenting with the technique and with different species, which over time will show the result of their accumulated experiential knowledge. However, the project in Dodoma has a total duration of only 3–4 years. A recent review highlighted that widespread adoption of FMNR beyond project localities is yet to be evidenced and that the success of these projects depends on intense, long-term external interventions (Chomba et al., 2020). Our results thus highlight the need for long-term studies to monitor the persistence of selected species, and the development of farmers' perceptions and decisions, also beyond project durations. This, to our best knowledge, has not been done yet in studies on FMNR farms and is vital for predicting restoration outcomes in the long term.

Synthesis and Implications for Restoration

As we are entering the UN decade of ecosystem restoration, there are high expectations for restoration techniques based on natural regeneration as they are considered cheap and effective. Farmer-managed natural regeneration is one such technique. This is to our knowledge among the first studies to systematically assess the role of the farmer in promoting regeneration under FMNR. Regeneration is the basis for the benefits that can be achieved with FMNR as a restoration practice and predicting what can regenerate and where is crucial for predicting its success and thus for restoration planning (e.g., Lohbeck et al., 2020). We found that farmers have a broad knowledge of species and their benefits and promote many different species on the farm. Moreover, FMNR encompasses many different management practices. Species with more diverse benefits were selected more often although many species were only selected by one or two farmers. This highlights that species selection and management under FMNR are driven by farmers autonomous decisions, making it diverse and complicates predicting the extent to which FMNR may successfully contribute to achieving specific restoration outcomes.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

ML directly contributed through both advice and written work regarding the manuscript. FB, AA, FS, and EV gave valuable feedback as co-authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2020.563364/full#supplementary-material

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Enhancing Plant Diversity in Secondary Forests

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Dispersal, recruitment and establishment limitations are crucial processes shaping forest composition. In secondary forests these mechanisms may operate differently than in mature forests, because young and isolated secondary forests may suffer stronger limitations due to a lack of suitable dispersers and harsh environmental conditions—such as the elevated competition of exotic grasses. To assess establishment limitations in these forests, we undertook transplant experiments involving seeds and seedlings along a chronosequence of secondary forests in tropical Australia. The experiments included six species that varied in seed size (6–50 mm in length) and successional status (early to late successional). Seeds of five species were placed in one of three treatments: (1) exposed seeds, (2) fenced seeds, and (3) buried seeds, and multiple seedlings of six species were transplanted in block treatments. After 14–17 months, seed from all plant species germinated across all ages of secondary forests. However, in young secondary forest sites (4–12 years) fewer germinated seeds survived. The highest survival rates were observed for buried seeds (27.2%) compared to the low survival of exposed seeds (6.0%). Planted seedlings (6 spp) had the greatest overall survival (63.1%) and the highest growth rates in older secondary forests. We found that species identity was important for growth and survival in both experiments, but detected no effect of successional status or seed size. A crucial finding of this study was that the buried seeds of all species germinated and had relatively high survival irrespective of variation in site conditions or successional status, suggesting that seed availability may be a greater barrier to recovery of secondary forests in the region than the establishment limitations imposed by environmental conditions.

Keywords: chronosequence, dispersal limitations, establishment, forest succession, seeding experiments, seedling plantings, secondary forest

INTRODUCTION

Rapid transformation of mature tropical forests puts at risk the high biodiversity and the varied ecosystem services these forests provide. Approximately 70% of the tropical rainforest biome has been modified into a matrix of mature forest remnants, agricultural fields, and secondary forests of different ages (Dent et al., 2013; van Breugel et al., 2013). Secondary forests are essential to biodiversity conservation, carbon sequestration and landscape connectivity, and understanding limitations to their recovery is vital to ensure best-practice management in the future (Faria et al., 2009; Dent et al., 2013; Chazdon, 2014; Rozendaal et al., 2019).

Models of forest succession explain and predict changes in species composition specifying interactions among species, and how plant traits affect such interactions through time (Pickett et al., 1987; Meiners et al., 2015; Pulsford et al., 2016). Some models focus on the physiological and morphological traits of the first colonists (e.g., Egler, 1954; Connell and Slatyer, 1977) and highlight that most of the species that will dominate later in succession are present since the onset of succession (Egler, 1954). These species will either prevent or facilitate the colonization of other species according to their life-spans and stress tolerances (Drury and Nisbet, 1973; Connell and Slatyer, 1977). Other models propose that changes in species composition depend on tradeoffs between life history traits, that differentiate species in their ability to acquire resources (Pulsford et al., 2016). For example, the tolerance-fecundity tradeoff model (Muller-Landau, 2010) that also explains tropical succession assumes that species vary inversely in fecundity and stress-tolerance; species with high fecundity and small seeds are unable to tolerate environmental stress (e.g., low soil moisture) whereas species with low fecundity and large seeds are able to tolerate environmental stress. Nonetheless, small seeded species tend to dominate early in succession because they are highly fecund and can be dispersed widely (Coomes and Grubb, 2003) and long-lived pioneers (usually small-seeded) are an important component of tropical forests (Rüger et al., 2020). However, species with larger seeds present at the onset of succession should outcompete small-seeded plants because larger seed reserves provide higher per capita recruitment and survival (Moles and Westoby, 2004) increase resource provisioning (Westoby et al., 1996), stress tolerance (Muller-Landau, 2010) and improve seedling performance (Moles and Westoby, 2002, 2004).

Multiple mechanisms affect and shape forest regeneration in both mature and altered ecosystems (Benitez-Malvido and Martinez-Ramos, 2013). Dispersal and establishment limitations are two key processes that shape forest composition. Dispersal limitation is the "failure of the propagules of a given species to arrive at an available site" (Terborgh et al., 2011), whereas establishment limitation is the failure of a species to be present in all sites favorable for its growth and survival (Hubbell et al., 1999; Muller-Landau et al., 2002; Schupp et al., 2002). Therefore, although overcoming dispersal allows species to reach different sites, establishment limitations may prevent the germination and/or survival of the species. Both mechanisms not only play a fundamental role in maintaining the high biodiversity of mature tropical forests (Terborgh, 2012; Vargas and Stevenson, 2013), but also affect the recovery of regenerating forests, where long distances to seed sources and harsh or unfavorable environmental conditions may delay forest recovery (Guariguata and Ostertag, 2001; Norden et al., 2009). Although recruitment cannot occur without seeds, seeds are no guarantee of recruitment (Clark et al., 2013). Therefore, studying recruitment limitations in tropical secondary forests can provide insights into the barriers for the recovery of these ecosystems.

Although multiple factors preventing forest recovery are well known such as: lack of nutrients and limited water (Carrasco-Carballido et al., 2019), competition with grasses and adverse microhabitats (González-Tokman D.M. et al., 2018) and the recovery of taxonomic and functional diversity of indicator groups (González-Tokman D. et al., 2018), increased knowledge regarding the strength of the processes that influence recovery in different landscapes is required (Rozendaal et al., 2019). Experimental research may assist in providing the necessary information to understand natural regeneration in secondary forests and develop management strategies to aid their recovery (Bentos et al., 2013).

Direct seeding and planting of seedlings have been widely investigated in different ecosystems to examine the potential of species in forest restoration, their potential economic value to forestry, their use by wildlife or to investigate how functional traits (e.g., seed size) influence performance (Palma and Laurance, 2015). In this study, we used direct seeding and planting of seedlings to investigate whether establishment limitation is a major barrier to forest succession and recovery.

Our experiments tested one main hypothesis establishment limitation plays a major role in slowing down succession in secondary forests. We predicted that germination, survival and growth rates would vary among seeds and seedlings in a successional forest chronosequence because they may experience different establishment limitations. We expected lower germination, survival and growth rates in young secondary forests compared to older forests. We used large and small-seeded species and predicted that if secondary forest age and/or seed size does not affect establishment then there would be no difference in germination, survival and growth rates among treatments. The different seed treatments (exposed, fenced, buried) helped us understand establishment limitations in the different sites. If predation and/or desiccation were limiting establishment, buried seeds would be more successful in all age categories. Alternatively, if these establishment limitations do not constraint the germination of exposed or fenced seeds, all treatments would have equal germination, and just placing seeds directly in the soil would be a fast and easy approach to enhance biodiversity recovery in these regenerating forests.

Planted seedlings of the same species provided insights on how the environment could limit growth and survival. If high rates of herbivory, mortality, and slow growth were found in all forests, establishment limitations could be strongly influencing the recovery of these tropical forests. Experiments like these ones that evaluate establishment limitations could provide guidance for successful management strategies (de la Peña-Domene and Martínez-Garza, 2018).

MATERIALS AND METHODS

Study Area and Site Selection

The study was carried out on the southern Atherton Tableland (17°23.3′S 145°35.8′E–17°27.0′S 145°38.2′E), a highly fragmented landscape in north-eastern Australia. The climate is tropical, with mean annual rainfall ranging from 1700 to 2600 mm, and a distinct dry season from July to October (BOM 2019). Mean monthly temperatures range from a mean minimum of 10°C in the drier months to a mean maximum of 29°C during the wet season.

In the 1920s much of the region was cleared of continuous rainforest and converted to pasture for the dairy industry (Frawley, 1987; Gilmore, 2005). Some pastures were abandoned in the 1940s and others in the 1980s as economic conditions changed (Gilmore, 2005). Following pasture abandonment, forest regenerated and now secondary forests of different ages dominate the landscape. Interpreting a time-series of aerial photographs and satellite imagery, we selected different sites that would provide us with a chronosequence of secondary forest age from 4 to 34 years since canopy formation. This study encompassed 12 secondary forest sites that were not directly adjacent to large tracts of mature rainforest (**Figure 1**). Our study sites varied in size from 0.7 to 4.6 ha, with an average size of 2.6 ± 0.92 ha, and are embedded in a matrix of secondary forests, active pastures and forest remnants. Sites were >100 m from primary forest remnants with an average distance of 2.8 ± 1.3 km (range 1.1–4.8 km) from continuous primary forest.

The study sites are located on soils derived from the two dominant soil types in the region: granite (Tully Granite) and basalt (Atherton Basalt). In our study area, basalt soils have higher clay content, total N and total P compared to sites in granite. Nonetheless, clay content, total N and total P are unrelated to soil pH and soil C:N and soil acidity is not strongly associated with nutrient concentration (Pandolfo Paz et al., 2016).

Chronosequence studies have been criticized because calculating age since abandonment and determining previous land uses are major challenges (Chazdon, 2014), and their explanatory power may depend on the scale of study design (Chazdon, 2008; Lebrija-Trejos et al., 2008; Dupuy et al., 2012). We have addressed these challenges through extensive aerial photography interpretation, replication of independent sites that are within the same climatic region and share similar past land use. Additionally, we used age since canopy formation instead of age since abandonment as a proxy of forest age to limit variation between the initial conditions of different sites.

Site Ages and Categories

We selected our studies sites using a range of Queensland State Government aerial photography, satellite images from Google Earth (©2014 Google Image, ©2014 DigitalGlobe), and imagery from Queensland Globe (©State of Queensland 2013, ©CNES 2012, Spot Image S.A. France, ©2013 Pitney Bowes), detailed methods in Goosem et al. (2016). Secondary forests were classified into three age categories using the number of years since canopy formation as a proxy of forest age: Young: forests of 4–12 years; Intermediate: forests of 16–20 years; and Old: forests of 23–34 years. We used four sites for each age category.

Species Selection

Six rainforest tree species were selected, based on previous information regarding the species composition of secondary and mature forest sites in this region (Goosem et al., 2016; Palma et al., in review). For the direct seeding experiments, we chose three large-seeded (> 20 mm in length) rainforest tree species (*Beilschmiedia tooram*, *Cryptocarya oblata,* and *Endiandra bessaphila*), which were absent from our regenerating forest but present in mature forest sites in the region; and two small-seeded (<15 mm in length) rainforest tree species (*Litsea leefeana* and *Guioa lasioneura*) that are present in both secondary and mature forest sites. For the planting experiment an additional small-seeded late successional species (*Synima cordierorum*) was included. This species is present in both secondary and mature forest sites in the region, but was unavailable as seed for the seed experiment. We collected seeds of *C. oblata*, *E. bessaphila*, *L. leefeana,* and *G. lasioneura* from at least four rainforest remnants and parental trees scattered within the region and purchased seeds of *B. tooram* and seedlings of *S. cordierorum* from local nurseries.

Seed Experiments

We established the seed experiments during the wet season (November 2013–February 2014). After collection, seeds were soaked in water for 48 h, the pulp removed and placed in the secondary forests within 60–72 h. The three seed treatments included: (1) exposed seeds (litter removed and seeds placed on the soil); (2) fenced seeds (litter removed, seeds placed on the soil within a plastic fence, 50 cm in height; and (3) buried seeds (litter removed, seeds sown to a depth of 2 cm). We used five species and 20 seeds per treatment per site for a total of 3,600 seeds. In each site, we established a seed experimental plot (3 m × 2.5 m) divided into 15 (1 m × 0.5 m) quadrats, randomly allocating one of the three different direct seeding treatments and species to each quadrat.

Seedling Experiments

All seedlings were germinated and grown for 1–3 months in a greenhouse, with 1 month of "hardening" outdoors with no extra watering (except *S. cordierorum,* bought at 8 months of age). Seedlings were planted during the wet season (March of 2014) at the same sites used for the direct seeding experiments. We planted six species and 30 seedlings per species per site (except *C. oblata*, 24 seedlings per site) for a total of 2,088 seedlings. Species were randomly allocated into 6 quadrats (3 m × 3 m) within an experimental planting plot (9 m × 6 m) at each site.

Data Collection and Analysis

Seed Experiments

All seeds were monitored weekly during the initial 5–10 weeks after placement in the secondary forest sites. During each census, we recorded seed number, status (five categories: eaten, removed, desiccated, rotten, germinated) and height of each uniquely tagged germinated seedling. After week 10, seeds were monitored once a month for 3 months and then every 3 months until April 2015. We calculated the relative growth rate of seedlings (RGR) in mm per day from the difference between initial and final heights of each seedling divided by the growth period [(ln (height final)−ln (height initial)/(growth period in days)]. The total height of each seedling was measured from the ground to the most distant part of the main stem.

Seedling Experiments

Planted seedlings were monitored 2 weeks after planting and all individual seedlings tagged with a unique number.

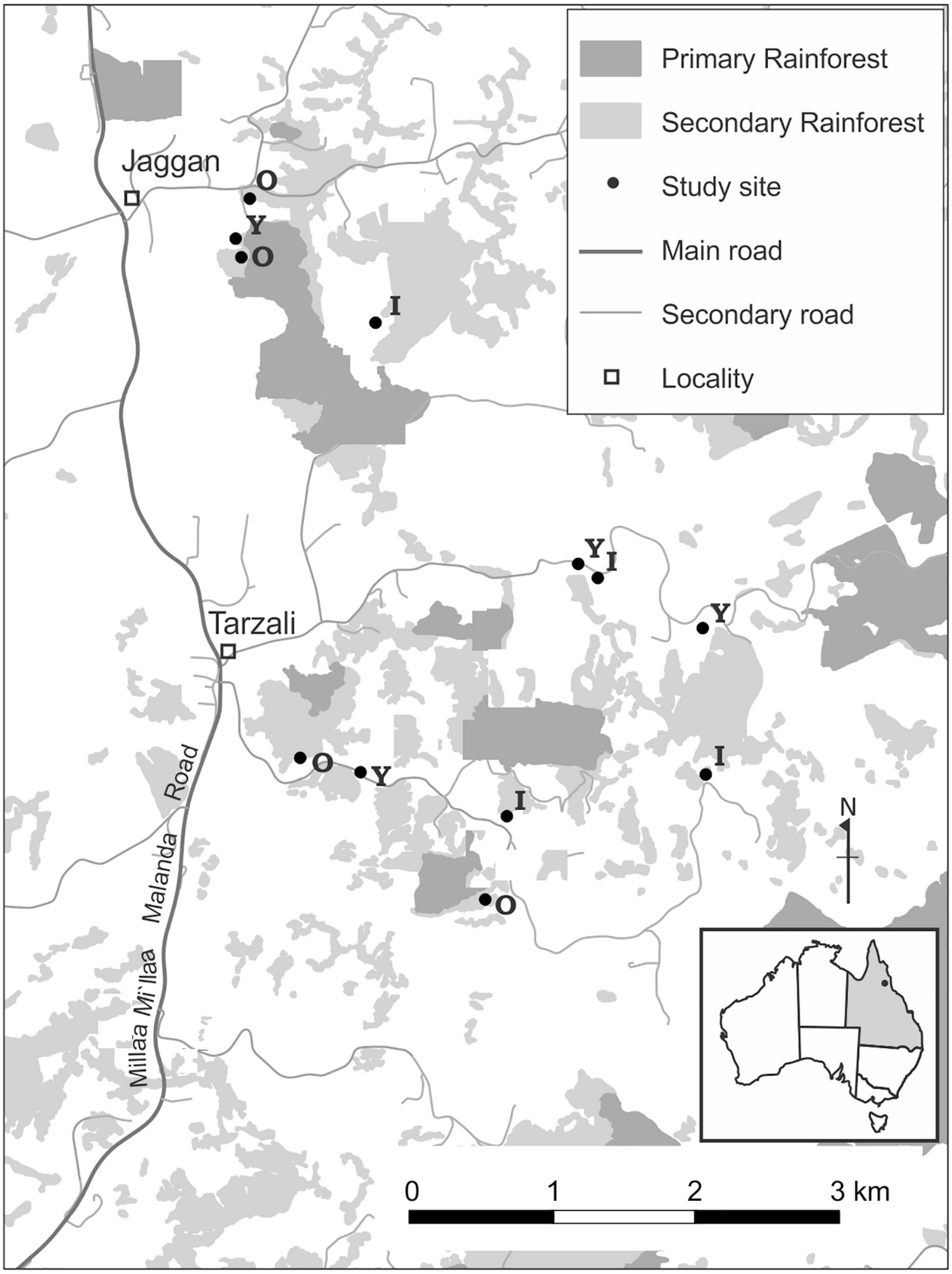

FIGURE 1 | Map of the study area, southern Atherton Tableland, North Queensland, Australia. Letters represent the age of secondary sites. Y, Young secondary forests (4–12 years); I, Intermediate-aged (16–20 years); O, Old (23–34 years).

Subsequently, seedlings were monitored every 3 months for 13 months. In each census, we recorded for each seedling status (four categories: eaten, removed, dry, dead) and height. We calculated relative growth rate (RGR) using the same method described above.

Statistical Analyses

We assessed the effects of secondary forest age and planting method (seed or seedling) and their interactions on survival, growth and species identity using nested analysis of variance models (ANOVA), with site nested within forest age. Our data met the assumptions of the nested ANOVA. Tukey's tests were used for *post hoc* analysis. We analyzed survivorship for both experiments using the "survival" (Therneau, 2020) and "survminer" (Kassambra et al., 2019) packages and pairwise comparisons using Log-Rank Test (*p*-value adjustment method for multiple comparisons: BH). Analyses were performed using R (R Development

Core Team, Version 1.1.1335) and IBM SPSS Statistics Version 21.

RESULTS

Seed Experiments: Survival and Growth

Seeds that survived, were those seeds that germinated, grew into seedlings and were alive at our last census. We transplanted a total of 3,600 seeds, out of these 872 germinated (24.2%) and by the end of the experiment only 516 (14.3%) survived (i.e., remained as seedlings). Seed survival was very low in young forests compared to intermediate and old secondary forest sites (**Figure 2A**), with significant differences between young and intermediate forests ($p < 0.0001$) and between young and old forest sites ($p < 0.0001$). Seeding treatments also had a significant effect on seed survival (**Figure 2B**), with the greatest survival rates recorded when seeds were buried compared to both exposed and fence treatments ($p < 0.0001$ for both comparisons).

Species identity was also important for seed survival (**Figure 2C**). The highest survival was recorded for *B. tooram* and *L. leefeana* both of which differed significantly from all other species ($p < 0.0001$). We found interaction effects between secondary forest age, direct seeding method, and species identity on seed survival [$F_{(16,\ 126)} = 1.82$, $p = 0.034$]. Overall, seed survival was greater in old secondary forests than in young forest for all species and treatments. Survival for *B. tooram*, *E. bessaphila* and *L. leefeana* was greater when seeds were buried in old secondary forests (43.75 ± 27.51, 33.75 ± 16.52, and 53.75 ± 19.31, respectively), whilst *C. oblata* and *G. lasioneura* were more successful if sown in intermediate-aged forests (12.5 ± 15.54 and 8.75 ± 6.29, respectively). We did not find a clear pattern relating to functional traits such as seed size or successional status.

Growth of germinated seeds was not significantly affected by secondary forest age, or direct seeding method [$F_{(2,\ 17)} = 1.49$, $p = 0.25$, and $F_{(2,\ 23)} = 0.12$, $p = 0.88$, respectively, **Figures 2D,E**]. Species identity was important [$F_{(4,\ 23)} = 6.69$, $p = 0.001$], with highest growth in *G. lasioneura* and *L. leefeana*. *G. lasioneura* grew significantly more than *B. tooram* ($p = 0.013$) and *L. leefeana* grew more than *B. tooram*, *C. oblata* and *E. bessaphila* ($p < 0.0001$; $p = 0.006$, and $p = 0.015$, respectively, **Figure 2F**). We did not find interaction effects between secondary forest age, direct seeding method, and species identity on growth of the germinated seeds [$F_{(2,\ 23)} = 0.57$, $p = 0.57$].

Across all age categories and treatments (**Table 1**) the highest loss of seeds was due to seed removal (seeds that were no longer found, average: 65.1%); followed by seeds that were rotten, eaten, desiccated and finally seeds with visible fungal damage. For the germinated seedlings, the highest cause of death was also removal (seedlings that were no longer found, average: 63.1%), followed by seedlings that were desiccated, showed visible fungi damage, suffered from stem breakage, showed clear signs of herbivory, and finally unearthed seedlings. Out of the 3,600 seeds only 872 germinated and at the time of our last census only 516 had established as seedlings (14.3%).

Seedling Experiments: Survival and Growth

Secondary forest age had a significant effect on the survival of transplanted seedlings (**Figure 3A**). Survivorship was significantly higher in old forest compared to young and intermediate secondary forests ($p < 0.0001$ for both comparisons). Species identity also influenced seedling survival (**Figure 3B**), with *S. cordierorum* showing the highest survivorship and surviving better than all other species ($p < 0.0001$, for all comparisons). Seedlings of *G. lasioneura* had the lowest survivorship and differed from all other species ($p < 0.0001$, for all comparisons). We did not find interaction effects between secondary forest age and species identity on seedling survival [$F_{(10,\ 45)} = 1.13$, $p = 0.35$].

Secondary forest age did not influence growth in the planted seedlings [$F_{(2,\ 13)} = 2.32$, $p = 0.13$, **Figure 3C**]. Species identity had a significant effect on seedlings growth [$F_{(5,\ 35)} = 17.51$, $p < 0.0001$] with *G. lasioneura* growing more than all other species ($p < 0.0001$ for all comparisons, **Figure 3D**). In contrast, *C. oblata* showed the lowest growth rate and differed significantly from *E. bessaphila*, *L. leefeana,* and *S. cordierorum* ($p = 0.00$, $p = 0.005$, and $p = 0.026$, respectively). We did not find interaction effects between secondary forest age and species identity on seedling growth [$F_{(10,\ 35)} = 1.68$, $p = 0.12$]. We did not find a clear pattern relating to functional traits such as seed size or successional status.

Across all age categories, removed seedlings (seedlings that were no longer found) accounted for the highest amount of mortality (71.69%), followed by desiccation, signs of herbivory, unearthed seedlings, and finally broken stems (**Table 1**).

DISCUSSION

Along a chronosequence of secondary forests, seed and seedling experiments provided important insight into processes that may delay forest succession and recovery. We found that seeds from all study plant species germinated in all sites from our secondary forest chronosequence, regardless of forest age. This result highlights the importance of seed availability in these recovering forests.

We found that seeds of three late successional species of mature rainforest, that were naturally absent from secondary forest germinated and grew when placed in these recovering forests. These results provide evidence that the absence of these species is due in part to lack or limited seed supply of large-seeded species in this highly fragmented landscape. Additionally, we observed that introduced seeds and seedlings suffered from very high removal rates which we assume is due to predation or herbivory, and demonstrates the constraints to establishment in tropical forests.

Our results show that species identity was as important as forest age for growth and survival, but we did not find a clear pattern relating to functional traits such as seed size or successional status. For example, *L. leefeana* and *B. tooram* showed the greatest survival for the direct seeding experiment. *L. leefeana* is a small-seeded early successional species that is

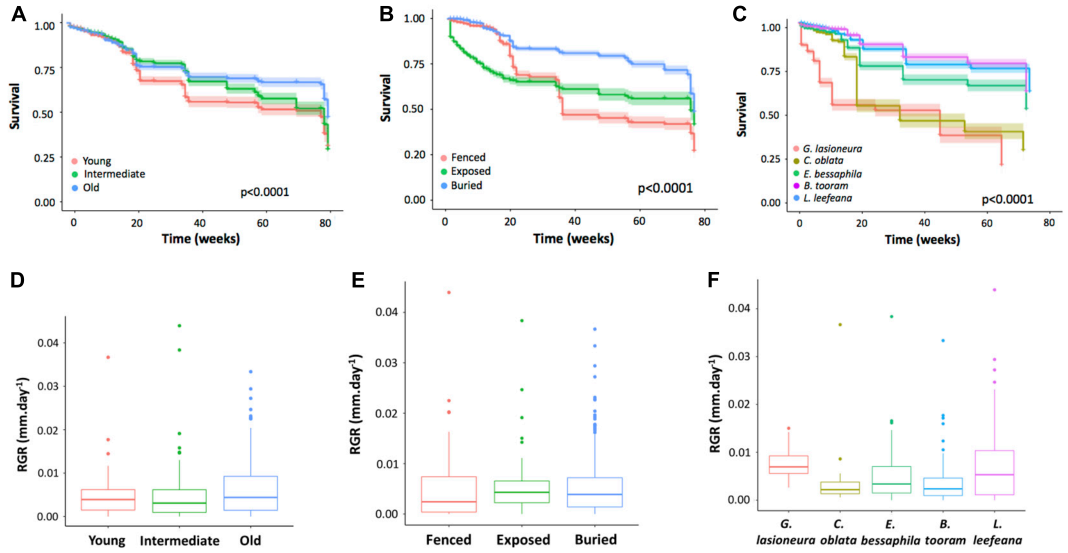

FIGURE 2 | Survival and growth of seeding experiments in three secondary forest ages. **(A)** Secondary forest age had a significant effect on seed survival, with younger forests loosing significantly more seeds than old and intermediate forests ($p < 0.0001$ for both comparisons). **(B)** Direct seeding treatment affected seed survival, buried seeds had highest survival than both exposed and fenced seeds ($p < 0.0001$ for both comparisons). **(C)** Species identity was important for seed survival, *B. tooram* and *L. leefeana* had the highest survival and both differed significantly from *C. oblata* and *G. lasioneura* ($p < 0.0001$ for all comparisons); seeds of *L. leefeana* also survived better than seeds of *E. bessaphila* ($p = 0.029$). **(D)** Secondary forest age did not affect the growth of germinated seeds [$F_{(2,\ 17)} = 1.49$, $p = 0.25$]. **(E)** Seeding treatment did not affect growth either [$F_{(2,\ 23)} = 0.12$, $p = 0.88$]. **(F)** Species identity was important [$F_{(4,\ 23)} = 6.69$, $p = 0.001$], with highest growth in *G. lasioneura* and *L. leefeana*; *G. lasioneura* grew more than *B. tooram* ($p = 0.013$) and *L. leefeana* showed higher growth when compared to *B. tooram, C. oblata,* and *E. bessaphila* ($p < 0.0001$; $p = 0.006$, and $p = 0.015$, respectively). For all box plot graphs, the tick line represents the median, the outer limits of the box the first and third quartiles. Whiskers extend to cover any data point <1.5 times the interquartile range. Circles represent outliers.

TABLE 1 | Seed and seedling mortality across all ages and treatments.

Cause of mortality	Seeds (%)	Seedlings (from germinated seeds) (%)	Seedlings (planted) (%)
Removal	65.09	63.12	71.69
Desiccation	4.21	29.01	21.56
Eaten	13.75	–	–
Herbivory	–	0.72	2.57
Fungi	2.44	5.67	–
Unearthed	–	0.37	2.09
Broken stem	–	1.11	1.91

common in all sites, whereas *B. tooram* is a large-seeded late successional species rarely encountered in secondary forests. Alternatively, in the same experiment survival was lowest for *C. oblata*, a big-seeded late successional species and *G. lasioneura* a small-seeded early successional species. Although our sample size is small and multiple mechanisms limit recruitment, our data shows that seed size might not be enough to predict seed predation or establishment. Species with low dispersal limitation, generally small seeds, may have high recruitment limitations (de la Peña-Domene et al., 2018).

When planted as seedlings, *S. cordierorum*, a small-seeded late successional species survived the best. However, these seedlings were bought from a local nursery and they were 8 months older than all other seedlings. It is possible that *S. cordierorum* might actually survive better at these sites, or that their higher survival might just be an artifact of their greater age increasing their resilience (Vandendriessche, 1992; Herman et al., 2012; Palma and Laurance, 2015). Since over 20% of dead seedlings showed signs of desiccation, these older seedlings may have had a greater advantage establishing in these secondary forests. Since small seeds can be drought tolerant (dormant for longer) (Westoby et al., 1992), but small-seeded seedlings are vulnerable to drought because they lack reserves from the large cotyledons (Westoby et al., 1992; Harrison and LaForgia, 2019), using older seedlings from small-seeded species may be an alternative to overcome these limitations.

The small-seeded, early successional species *G. lasioneura* and *L. leefeana* showed the highest growth in seed and seedling experiments. These species are very common in these secondary forests and such fast growth is a typical characteristic of early successional species (Finegan, 1996), while large-seeded, late successional species such as *B. tooram* and *C. oblata* have relatively slower growth rates. Large seed size might not confer an advantage in the rate of seedling growth yet it has been demonstrated that large-seeded species can resprout more often after plant loss compared to small-seeded species (Green and Juniper, 2004).

Buried seeds had the greatest survivorship (average: 27.25%) with a three to fourfold higher persistence than exposed (6.0%) and fenced (9.75%) seeds. Burial appears to protect seeds from predators, desiccation, heavy rains or movement of leaf-litter by foraging wildlife which may be important to increase germination

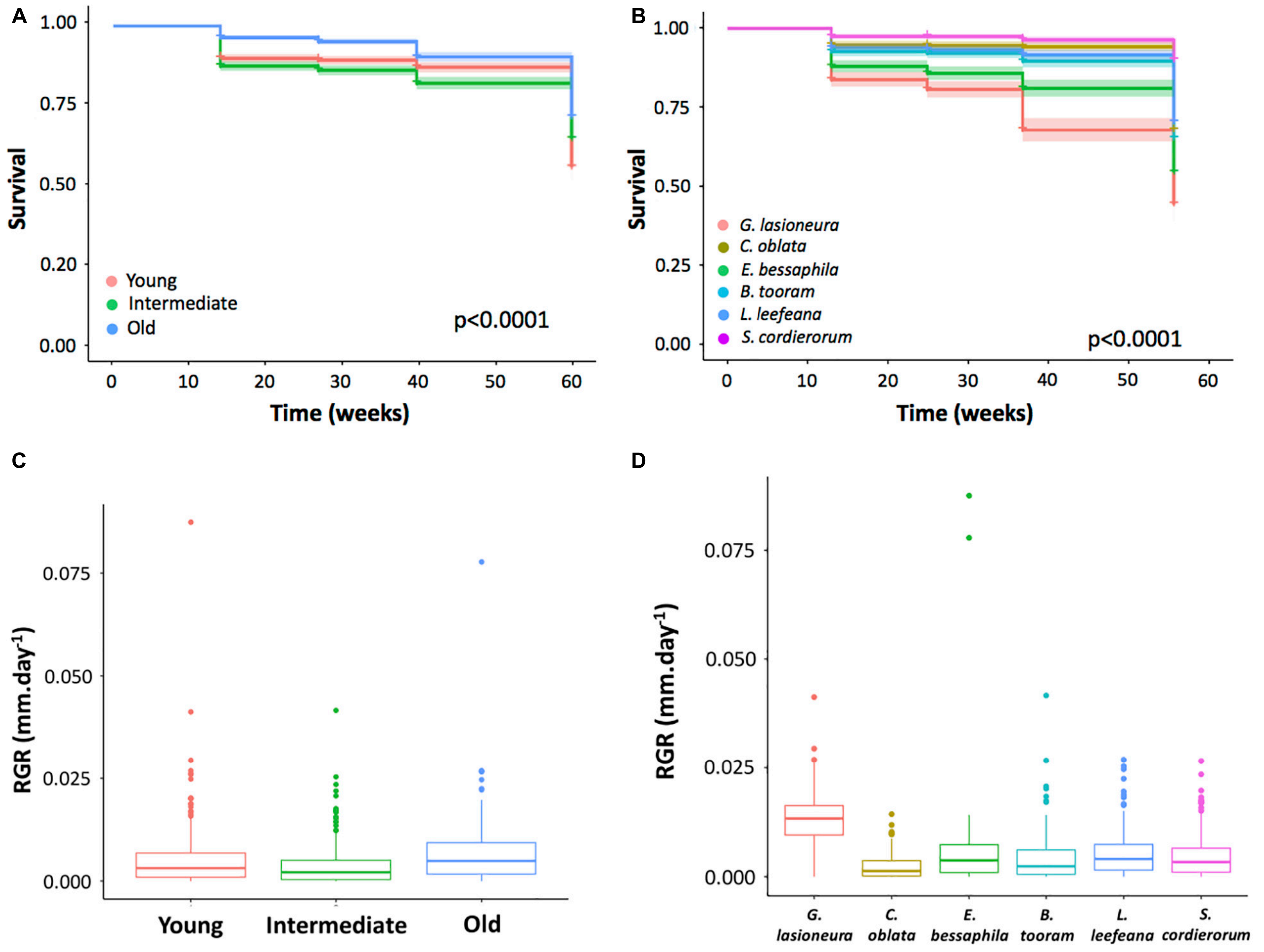

FIGURE 3 | Survival and growth of planted seedlings in secondary forest of three different ages. **(A)** Secondary forest age had a significant effect on seedling survival, seedlings planted in old forests had the greatest survival. **(B)** Species identity influenced seedling survival, *S. cordierorum* had the highest survival, differing from *B. tooram*, *E. bessaphila,* and *G. lasioneura* ($p < 0.0001$ for all comparisons). Seedlings of *G. lasioneura* had the lowest survivorship and differed from all other species. **(C)** Secondary forest age did not influence seedlings growth [$F_{(2,\ 13)} = 2.32$, $p = 0.13$]. **(D)** Species identity had a significant effect on seedlings growth [$F_{(5,\ 35)} = 17.51$, $p < 0.0001$] with G. *lasioneura* growing more than all other species ($p < 0.0001$ for all comparisons. *C. oblata* showed the lowest growth rate and differed from *E. bessaphila*, *L. leefeana,* and *S. cordierorum* ($p < 0.001$, $p = 0.005$, and $p = 0.026$, respectively). For all box plot graphs, the tick line represents the median, the outer limits of the box the first and third quartiles. Whiskers extend to cover any data point <1.5 times the interquartile range. Circles represent outliers.

in these forests. We assumed that removed seeds were eaten or damaged and did not germinate, but it is possible that they were cached by small mammals such as white-tailed rats (Harrington et al., 1997). Overall, the direct seeding experiments showed a ca. 14% survival of seeds which is a very similar result to other direct seeding experiments in different ecosystems which average an 18% survival (Palma and Laurance, 2015).

Planting experiments provided further insight into recruitment limitations. We found the highest survival of transplanted seedlings in old secondary forest sites (average: 63.08%) where fewer grasses and exotic species may favor establishment (Chazdon, 2014). As with the direct seeding experiment, the main cause of mortality was seedling removal. These removed seedlings could have been eaten whole or unearthed and then washed away during rainstorms. Desiccation was the next most common cause of mortality. Droughts and desiccation are a commonly cited cause of death in planting experiments (Palma and Laurance, 2015).

Previous studies on seed germination and seedling survival of species planted into secondary forests have also found that species identity is more important for survival than variations in habitat (Camargo et al., 2002; Cole et al., 2011). However, early growth and survival are not always an indicator of the species persistence in the long-term (Benitez-Malvido and Martinez-Ramos, 2013). Extended monitoring of these experiments could provide more information on the success of each species and whether their relative success in establishment and growth changes over time and in response to changing biotic and abiotic environments (e.g., increased competition and decreasing light).

Our study demonstrated that some of the missing plant species in secondary forests of tropical Australia will germinate and grow when they are introduced as seeds and/or seedlings.

With seed removal rates so high, direct seeding without burial is not recommended. Sowing seeds might be an effective way to reintroduce much of the plant diversity that is currently missing from secondary forests while avoiding potential seed predation by rodents (e.g., white-tailed rat, and the fawn-footed melomys), possums (i.e., common brushtail possum) and birds (i.e., common emerald dove and the Australian brush turkey) (Osunkoya, 1994; Doust, 2011). Planting of seedlings yields better results and older seedlings are more successful, however with the higher costs involved (e.g., greenhouses, transportation, and more labor) this approach should be used for highly isolated sites, for sites with high conservation value such as wildlife corridors (Tucker, 2000), with arrested succession or for the expansion of rare habitats and connectivity between fragments.

Restoration efforts are important to accelerate biodiversity gains in isolated sites, or to reintroduce endangered plant species. However, we need to keep in mind that even if restoration efforts are successful, 25 years after restoration plantings key features of mature rainforest are still lacking (Shoo et al., 2015). Although dispersal limitation lessens over the first years of recovery, with seed rain including more species, mature forest species continue to be limited (Reid et al., 2015), stressing the importance of actively introducing these species when possible.

In our experiments, forest age had a significant effect on seeds and seedling survival, with old secondary forest showing higher survival rates, nevertheless seeds and seedlings of all species were present at all sites until the end of the study. This shows that once succession has started and some canopy has formed, reintroduction of different species to accelerate forest recovery can be successful even in young secondary forests. Since species identity was important, testing different species at small scales before embarking in large-scale restoration projects is necessary. Hence we recommend, direct seeding experiments and planting of seedlings as an effective way to assess recruitment limitations in different habitats and for different species.

Our results highlight the significance of establishment limitations for the recovery of tropical secondary forests. We found that all the species included in the study germinated and grew even in young secondary forest sites. This shows that establishment limitation is not a major barrier for the recovery of these secondary forests, but that seed availability might be the biggest obstacle to forest recovery in this region. Our study sites are small in size (average 2.6 ha), embedded in an agricultural matrix and relatively far from seed sources (average distance to continuous forest: 2.8 Km). Enrichment planting in sites with similar conditions may accelerate forest recovery by providing food sources for seed dispersers and improving habitat conditions.

Planting clusters of different species has been a successful technique that enhances seed rain and seedling establishment with lower costs than tree plantations (Zahawi and Augspurger, 2006; Cole et al., 2010; Zahawi et al., 2013). These small clusters can also be used to plant different species, include a broader range of functional traits and test their resilience to desiccation or heavy rains. These types of experiments are important as they may help us to plan restoration efforts for future climatic scenarios (Palma and Laurance, 2015).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

AP developed the idea, conducted fieldwork, analyzed the data, and wrote the manuscript. MG helped with fieldwork and editing the manuscript. PS helped editing the document and providing ecological advice. SL helped with fieldwork, developing the idea, writing the manuscript, and statistical advice. All authors contributed to the article and approved the submitted version.

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Opportunities and Constraints for Using Farmer Managed Natural Regeneration for Land Restoration in Sub-Saharan Africa

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Farmer Managed Natural Regeneration (FMNR) comprises a set of practices used by farmers to encourage the growth of native trees on agricultural land. FMNR is reported to deliver a number of positive impacts, including increasing agricultural productivity through soil fertility improvement and feed for livestock, incomes, and other environmental benefits. It is widely promoted in Africa as a cost-effective way of restoring degraded land, that overcomes the challenge of low survival rates associated with tree planting in arid and semi-arid areas. Despite being widely promoted, the evidence for these bold claims about FMNR has not been systematically analyzed. This paper reviews the scientific evidence related to the contexts in which FMNR is practiced across sub-Saharan Africa, how this influences the composition of regenerating vegetation, and the resulting environmental and socio-economic benefits derived from it. This reveals that quantitative evidence on FMNR outcomes is sparse and mainly related to experience in the Maradi and Zinder regions of Niger. There is little mechanistic understanding relating how context conditions the diversity and abundance of regenerating trees and how this in turn is related to ecosystem function and livelihood benefits. This makes it difficult to determine where and for whom FMNR is an appropriate restoration technique and where it might be necessary to combine it with enrichment planting. Given the need for viable restoration practices for agricultural land across Africa, well beyond the climatic and edaphic contexts covered by existing FMNR studies, we recommend research combining functional ecology and socio-economic assessments, embedded as co-learning components within scaling up initiatives. This would fill key knowledge gaps, enabling the development of context-sensitive advice on where and how to promote FMNR, as well as the calculation of the return on investment of doing so.

Keywords: agroforestry, restoration, ecosystem, livelihoods, FMNR, tenure

INTRODUCTION

It is estimated that up to 65% of productive land in Africa is degraded, exacerbating poverty, food and nutrition insecurity, loss of biodiversity, conflicts and insecurity (UNCCD, 2013; ELD-UNEP, 2015). Land restoration has the potential to increase food and nutritional security, sequester carbon, recharge groundwater and reverse biodiversity loss (UNCCD, 2013; Nkonya et al., 2016). The United Nations General Assembly declared 2021–2030 the decade of ecosystem restoration (UN, 2019). African governments, under the AFR100 initiative, voluntarily committed to restore at least 100 million ha by 2030 as their contribution to the Bonn challenge (which targets restoration of 100 M ha by 2020 and 350 M ha by 2030); the 2010 Aichi Convention on Biological Diversity (which targets restoration of at least 15% of degraded ecosystems globally) and the Paris accords (CBD, 2010; UNFCCC, 2015). Questions have been raised about how realistic these restoration targets are, considering that annual deforestation continues to exceed restoration in Africa (Fagan et al., 2020; FAO, 2020). Over the last decade, Africa has contributed the highest rate of net forest loss globally (FAO, 2020). This underpins why large scale restoration methods and practices are being advocated for and deployed. The potential of large scale tree planting to achieve restoration has been critically examined (Holl and Brancalion, 2020) and often considered costly and labor intensive, with low survival rates common where environmental constraints such as moisture and temperature are coupled with uncontrolled livestock grazing that damage young, unprotected seedlings. Restoration techniques based on natural regeneration are less costly than tree planting making them a viable alternative for restoring degraded lands although success is likely to depend on the extent of soil degradation and the presence of forest vegetation in the vicinity (Chazdon and Guariguata, 2016; Catterall, 2020).

In sub-Saharan Africa, smallholder agriculture is a key driver of deforestation (FAO, 2020). Farmers continue to expand agricultural land and are increasingly cropping marginal areas to increase their production. They are also abandoning traditional practices (particularly fallowing and exclosure) that formerly allowed farmland to rejuvenate (Crossland et al., 2018). Recent estimates indicate 132 M ha of degraded cropland in Africa (Cai et al., 2011). There is evidence that natural regeneration on agricultural and pastoral land has great potential to restore biomass (Poorter et al., 2016), soil organic carbon (Bayala et al., 2019), biodiversity (Rozendaal et al., 2019) as well as other essential ecosystem functions (Lohbeck et al., 2015). However, most knowledge about natural regeneration comes from successional studies where agricultural lands are abandoned, or regeneration is happening in natural forests or expanding forest buffer zones (Chazdon and Guariguata, 2016; Chazdon et al., 2020). Regeneration on agricultural land that is still being farmed requires farmers to actively manage the regeneration process, a practice known as Farmer Managed Natural Regeneration (FMNR).

FMNR (or *Régénération naturelle assistée*—RNA- in French) has been variously defined as farmers protecting and managing regrowth of trees in their fields (Larwanou et al., 2006; Haglund et al., 2011) or used more specifically to refer to management practices involved in pruning the shoots growing from tree stumps (Francis et al., 2015). Since FMNR is a practice that integrates trees on agricultural land it is a form of agroforestry (Sinclair, 1999). For the purposes of this review FMNR is defined as an agroforestry practice that involves the deliberate protection and management of naturally regenerating woody vegetation by farmers on agricultural land. Agricultural land may be used for growing crops or livestock grazing or both, as often occurs in agropastoral landscapes where livestock roam across crop fields in the off-season. Management principally includes selecting, protecting and pruning regenerating plants arising from re-sprouting rootstock or from seeds. It does not include exclosures, where agriculture is excluded from an area of land to allow regeneration (Mekuria et al., 2017). As a practice, although it has often been conflated with community-managed natural regeneration, assisted natural regeneration and enrichment planting (Reij and Garrity, 2016), it can be usefully distinguished from them, albeit that combinations of these different practices are often integrated alongside one-another across landscapes (**Table 1**). Individual farmers' adapt FMNR to their own needs (Rinaudo, 2012) so that the autonomy of the farmer has been indentified as both a condition for success and an important outcome from adoption (Francis et al., 2015), resulting in highly variable manifestations of the practice.

FMNR has been widely cited as a key practice within "evergreen agriculture" defined as the integration of trees into annual food crop systems (Garrity et al., 2010, p. 198), which is a form of agroforestry. It has also often been considered synonymous with the Sahelian agroforestry parklands that comprise traditionally established farming systems with scattered mature trees selected by farmers over tens to hundreds, and sometimes thousands of years (Boffa, 1999).

The Sahel constitutes a transition zone between the Sahara Desert in the north and the Sudanian Savanna to the south (Gonzalez et al., 2012). The region is characterized by a semi-arid climate, high levels of poverty, recurrent droughts, food insecurity and armed conflicts between different groups (Sinare and Gordon, 2015). The management of woody vegetation on homesteads and in the surrounding agricultural landscape has been a livelihood strategy for thousands of years in the region (Larwanou and Saadou, 2011). Since the 1970s FMNR has been widely promoted by non-profit organizations in Sahelian countries on the basis that trees on farms play an increasingly important role in supporting different aspects of farmers' well-being, including income (Binam et al., 2015), carbon sequestration and climate resilience (Bayala et al., 2014, 2019; Mbow et al., 2014), food, fodder and agricultural productivity (Bayala et al., 2012, 2015), human nutrition (Arnold et al., 2011), preventing soil erosion, fixing nitrogen, and providing a wide range of other ecosystem services (Belsky et al., 1989; Boffa, 1999; Dawson et al., 2013). FMNR has led to restoration of approximately 5–6 M ha, particularly in Maradi and Zinder regions in Niger, while donor resources expended on extensive tree planting activities have typically resulted in low tree survival rates of only around 20% (Tougiani et al., 2009). This has led to FMNR being scaled up in the Sahel to other regions of

TABLE 1 | Definitions of related terms associated with establishment of woody vegetation as a restoration strategy as used in the present review.

Term (abbreviation)	Definition	Management	Notes
Farmer managed natural regeneration (FMNR)*	An agroforestry practice that involves the deliberate protection and management of regenerating woody vegetation by farmers on agricultural land. It is mainly practiced on individual farmer's fields.	Principally includes selecting, pruning, thinning, coppicing and protecting the regenerating trees arising from re-sprouting rootstock or from seeds.	Often combined with EP. Agricultural land may be used for cropping, livestock grazing or both at different times of the year.
Assisted natural regeneration (ANR)*	Deliberate human protection and preservation of naturally regenerating woody vegetation on forest land or abandoned agricultural land or exclosures.	Tree seedlings are principally protected from undergrowth and fire (extremely flammable plants) and management of livestock. It does not involve intensive management of trees.	Sometimes combined with EP.
Enrichment planting (EP)	Deliberate planting of trees in areas were natural regeneration is also occurring or in forests, including secondary and selectively logged forest. This can be through seedlings that are first grown in tree nurseries, saplings or direct sowing of seeds in the field or forest.	Planting of seeds or seedlings and their subsequent protection and management.	Often combined with FMNR or ANR.

**In French, the term Régénération Naturelle Assistée (RNA) is used to refer to both FMNR (on farms) as well as ANR (on abandoned agricultural lands, communal grazing lands and forests).*

Niger, Burkina Faso, and other countries (Reij et al., 2005; Carey, 2020) including spontaneous adoption when farmers witnessed the visible agricultural and economic benefits on neighboring farms (Weston et al., 2015). A synthesis of evidence about FMNR focused on benefits derived from the practice (Francis et al., 2015) called for development of a co-ordinated research strategy to build an evidence base for FMNR.

FMNR is now widely promoted beyond the Sahel to other parts of Africa, heralded as a panacea for restoring degraded lands on the basis that it is inexpensive, replicable, achieves rapid results in terms of vegetation cover while avoiding the risk of low survival rates common in tree planting; and builds on skills that farmers already possess (Reij et al., 2009; Reij and Garrity, 2016; Carey, 2020). Yet, despite these claims and stated benefits, widespread adoption beyond project localities is yet to be evidenced. Projects promoting FMNR are often characterized by intense long-term external intervention funded by donors, involving training farmers and incentive structures such as cash-for-food programs or improved marketing of tree products (Rinaudo, 2007; Larwanou and Saadou, 2011). This makes the hypothesis that FMNR is actually simple to replicate, well-known by farmers and easy to scale up without external intervention questionable. In this review, we examine the scientific evidence on the context, composition and consequences of FMNR, discuss its potential as a strategy for land restoration in Africa, and identify knowledge gaps.

ANALYTICAL FRAMEWORK

A three-stage *a priori* analytical framework was developed to structure the review based on the literature cited in the introduction (**Figure 1**). By applying this framework, we reviewed the scientific literature on FMNR structured around three aspects: (1) **context**, i.e., the social, economic and ecological conditions under which FMNR is practiced; 2) **composition**, i.e., the characterization of what woody vegetation arises from FMNR in terms of density, species diversity and functional properties; and (3) **consequences,** i.e., the benefits that are derived from FMNR. We use the term composition broadly, to refer to what the FMNR is composed of in terms of woody species diversity, density and the functional properties that together influence the consequences of the FMNR in terms of livelihood and environmental benefits, rather than a narrower concept of botanical composition referring only to which species are present or their relative abundance (Billheimer et al., 2001). Composition of FMNR is affected by the environment and what farmers select from what naturally regenerates in their fields, both of which are affected by governance issues that influence fire occurrence, livestock grazing pressure and the surrounding tree cover (Lohbeck et al., 2020). Such structured assessment of the literature is urgently needed to identify what evidence exists and where there are gaps required to develop evidence-based recommendations for (i) where FMNR is a suitable practice for land restoration, (ii) how the practice of FMNR may change the composition of the fields, and (iii) for what specific restoration targets FMNR may be a suitable strategy. This will also contribute to further improving and refining the practice of FMNR, enhance our understanding of its limitations and identification of knowledge gaps in the evidence base to target further research.

Illustrations of FMNR are shown in **Figure 2**.

ASSEMBLING AND CHARACTERIZING THE EVIDENCE BASE

Evidence about FMNR was collected from published journal articles starting from year 2005 to March 2020. We carried out a literature search using the terms "Farmer Managed Natural Regeneration" in English and "régénération naturelle assistée" in French in abstract, title, and keywords in web of knowledge and in Google scholar. This generated a total of 30 relevant articles after those on assisted natural regeneration had been excluded, 24 in English and 6 in French, that represent the core evidence base. We classified these papers based on whether they involved

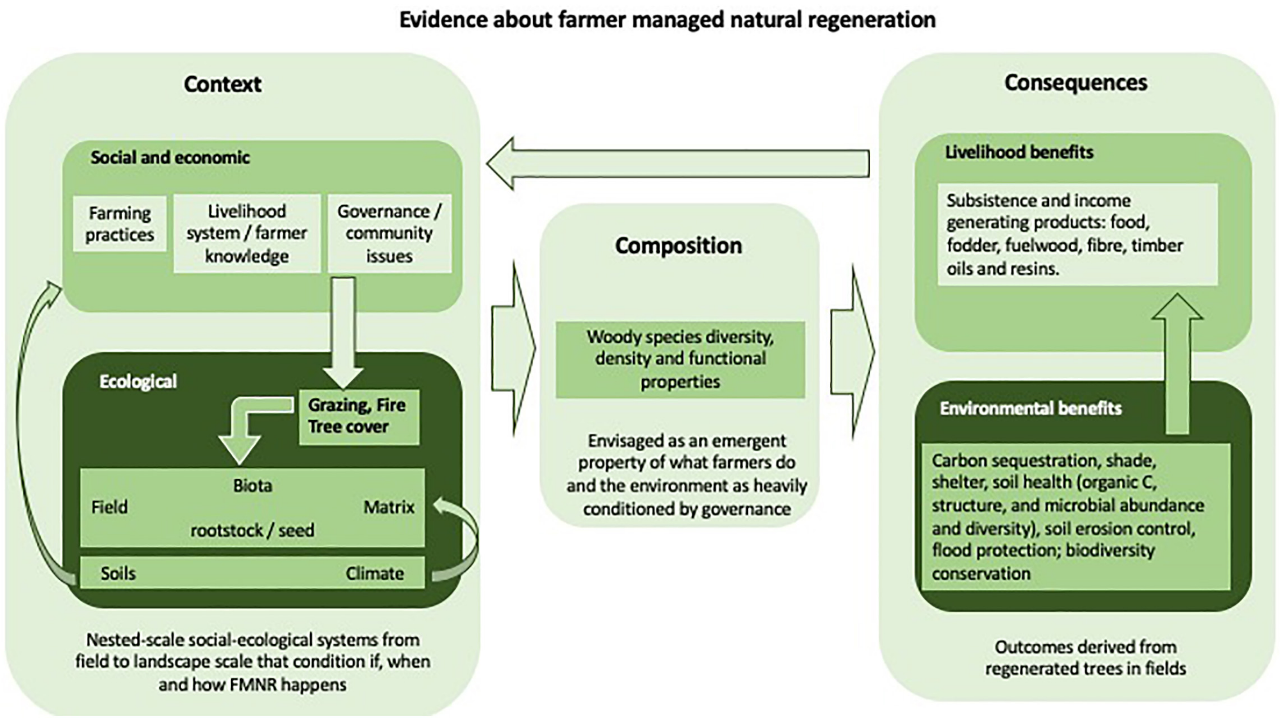

FIGURE 1 | Analytical framework for the assessment of evidence on FMNR.

original data, represented perspectives based on case studies or ideas, or were a literature review (**Table 2**). For papers based on original data, we identified the sites and countries where data were collected.

The majority of articles (22) were based on original data with a steady accumulation since 2005 and a marked acceleration since 2015 (**Figure 3**). A highly cited paper combining elements of data, perspective and review in a systems analysis (Sendzimir et al., 2011), complements five perspective papers that were published since 2009 and two reviews on specific aspects of climate-smartness and carbon stocks that appeared in 2018 and 2019, respectively.

The original data papers cover 12 countries ranging from West to East Africa but with a marked concentration in Niger and to a lesser extent Senegal, Mali and Burkina Faso (**Figure 4**). These four countries are also the only ones covered by perspective papers with four out of the five, including Niger.

THE CONTEXTS IN WHICH FMNR IS PRACTICED

Ecological Conditions

FMNR is largely being practiced in arid and semi-arid areas, also referred to as dry and sub-humid areas in sub-Saharan Africa. Rainfall is unevenly distributed and ranges between 100 and 950 mm per year (Haglund et al., 2011; Sendzimir et al., 2011; Gonzalez et al., 2012; Binam et al., 2015). This includes areas in the Sudano-Sahelian belt including countries such as Mali, Niger, Northern Nigeria, Burkina Faso, Northern Ghana, Senegal and Chad and also arid and semi-arid areas of countries in East and Southern Africa such as Kenya, Ethiopia, Tanzania, Zambia, Malawi, Sudan, and Somalia (Garrity et al., 2010; Ndegwa et al., 2017). In these regions, low moisture, high temperature, prolonged dry periods, and recurrent droughts are key factors limiting tree survival with tree planting campaigns typically having survival rates of 20% or less (Rinaudo, 2007; Tougiani et al., 2009). In contrast, in more favorable climates that allow intensive cultivation, and where tree survival is not so restricted, there is little evidence of widespread adoption of FMNR and tree planting is often favored over managing natural regeneration if farmers have sufficient assets to invest in trees (Iiyama et al., 2017).

The main soil types at the sites referred to in the literature reviewed include: arenosols (Sendzimir et al., 2011; Diallo et al., 2019) that are sandy textured soils with excessive permeability, poor structural stability and low soil fertility, prone to nutrient leaching; and ferruginous oxisols/lithosols (Yelemou et al., 2007; Badji et al., 2015; Camara et al., 2017) that are old soils characterized by alternating moist and dry soil conditions combined with nutrient leaching. Oxisols are formed through weathering, humification and pedoturbation by animals while lithosols are thin soils consisting mainly of partially weathered rocks. Sida et al. (2018) also characterize the soils under FMNR in central rift valley of Ethiopia as andosols, which are highly porous dark-colored soils of volcanic origin. This indicates that FMNR is mainly practiced in areas with low soil fertility which are sandy textured with a partially formed surface horizon,

FIGURE 2 | Pictures from the field illustrating the practice of Farmer Managed Natural Regeneration. **(A)** Shows young regeneration of Ziziphus Mauritania integrated with crops in Niger to boost soil fertility and improve crop production (photo by Patrice Savadogo). **(B)** Livestock grazing on an FMNR plot with acacia spp. in Kenya (photo by May Muthuri). **(C)** Female farmers thinning and pruning *Combretum* spp. to enhance growth of fewer but stronger stems in Ghana (photo by May Muthuri).

high permeability and low top-soil organic carbon and other nutrient contents (Larwanou et al., 2010; Haglund et al., 2011; Sendzimir et al., 2011; Moustapha et al., 2014). Agricultural use of these soils requires careful management (FAO, 2001). The soils are inherently low in fertility, very sensitive to animal pedoturbation and vulnerable to erosion, nutrient leaching and hence land degradation mainly because of their low structural stability aggravated by continuous cultivation with low organic matter inputs (Bayala et al., 2019).

Social and Economic Conditions

FMNR is predominantly practiced in agropastoral areas characterized by the cohabitation of two agrarian cultures: crop-farmers and pastoralists. Farming systems are largely subsistence oriented, predominantly based on millet and sorghum and a range of secondary crops including dual-purpose legumes such as cowpea and ground nut; or cash crops such as sesame, cotton and sorrel (Yelemou et al., 2007; Yayé and Berti, 2008; Larwanou et al., 2010; Binam et al., 2015). As trees are integrated with seasonal and annual crops, FMNR requires not only understanding of the ecological and economic function of trees in integrated land use systems, but also factors that potentially inhibit or encourage its adoption by farmers. Binam et al. (2017) note there is an optimal number of trees that can be effectively integrated with crops to optimize economic benefits before tree-crop competition results in negative impacts. Adoption of FMNR is driven by decision-making and choice of farmers, where farmers select which trees to remove and which ones to retain to suit their needs, often based on pre-existing traditional knowledge about tree management in areas where FMNR is well known and culturally accepted (Rinaudo, 2012; Francis et al., 2015).

Governance aspects have been important for the adoption of FMNR and the regreening of the Sahel more broadly and heavily influence agroecological management practices that require collective action such as control of grazing animals and fire management as well as the extent and configuration of landscape scale tree cover (Sendzimir et al., 2011). While there is evidence about governance impact on tree cover and grazing, there was no evidence relating to fire. Land and tree tenure are contentious issues in the Sahel where national policies and laws often do not allow farmers to own or use trees on their farms without authorization by state agencies (Binam et al., 2017). In arid and semi-arid areas, pastoralists often engage in seasonal migration which previously allowed FMNR to be sustained for centuries (Binam et al., 2017) but is now complicated by recent changes in governance that include land subdivision, and individual as opposed to collective land tenure, leading to collapse of traditional pastoral systems, conflicts and land degradation (Sendzimir et al., 2011).

Managing conflicts amongst crop farmers and livestock keepers is crucial for FMNR as young trees are easily destroyed by livestock. For example, crop farmers and herders in Niger cooperate and agree on grazing corridors and local institutions that enhance social cohesion through collective management of integrated landscapes (Sendzimir et al., 2011). Inclusive participatory processes that involve different user groups in formulating local by-laws and sanctions are needed to manage relations between farmers and pastoralists (Weston et al., 2015). Mapping of land uses can assist planning of rotational grazing that allows enough time for pasture and trees to regenerate (Weston et al., 2015; Reij and Garrity, 2016). Multiple actors, institutions and processes are needed at a local level to create feedback loops that reinforce each other for

TABLE 2 | Articles about Farmer Managed Natural Regeneration (FMNR) retrieved from the literature search and used as the core evidence base for this review.

#	Citation	Type	Topic	Method	Further details	Countries
1	Herrmann et al., 2005	Original data	Temporal and spatial patterns of vegetation	Remote sensing	Satellite imagery for NDVI and rainfall.	Senegal, Mauritania, Mali, Burkina Faso, Niger, Nigeria, Chad, Sudan, Eritrea, Ethiopia
2	Yelemou et al., 2007	Original data	Farmers' perceptions and adoption	Semi-structured interviews, field observations	Semi-structured interviews of 91 household heads (86 men and 5 women) were conducted to gain understanding on adoption of specific tree species coupled with ethnobotanical assessment of commonly promoted species in FMNR	Burkina Faso
3	Kindt et al., 2008	Original data	Tree species diversity and size	Inventory	Tree diversity data from 300 quadrants, randomly sampled from main land uses.	Burkina Faso, Mali, Niger, Senegal
4	Yayé and Berti, 2008	Original data	Creation of a rural wood market	Inventory	Trees on farm inventory coupled with economic valuation of fuelwood potential	Niger
5	Tougiani et al., 2009	Perspective	Effects on community livelihoods			Niger
6	Garrity et al., 2010	Perspective	Evergreen agriculture			Burkina Faso, Niger
7	Larwanou et al., 2010	Original data	Silvicultural practices in agroforestry parklands	Survey, inventory	Surveys with farmers coupled with sylvicultural data collection and species uses	Niger
8	Haglund et al., 2011	Original data	Drivers of adoption	Household survey	410 structured household surveys across 41 villages. Stratified random sampling for village selection.	Niger
9	Larwanou and Saadou, 2011	Original data	Environmental rehabilitation	Inventory	Vegetation inventories using radial transects from 4 control and 11 intervention villages.	Niger
10	Sendzimir et al., 2011	Other	Systems analysis	Field experience and perspective	Some original data from field experience but largely perspective and review within a systems analysis.	Niger
11	Hansen et al., 2012	Original data	Local use and management of trees	Survey, interview, inventory	Interviews, participatory discussions and 40 questionnaire surveys. Woody vegetation survey of 32 plots.	Ghana
12	Baggnian et al., 2013	Original data	Impact on ecosystem resilience	Focus group discussions, inventory	Focus groups and tree measurements along transects.	Niger
13	Moustapha et al., 2014	Original data	Infiltration	Interview, soil sample, inventory, infiltration	Participatory farmer meetings and soil mapping, field visit, vegetation inventory, infiltration tests and composite soil analysis.	Niger
14	Badji et al., 2015	Original data	Assessing contribution to regreening	Participatory village resource mapping, inventory	Participatory farmer meetings and on farm trees inventory	Senegal

(Continued)

TABLE 2 | Continued

#	Citation	Type	Topic	Method	Further details	Countries
15	Binam et al., 2015	Original data	Effects on income and livelihoods	Household survey	1080 household surveys collecting socio-economic, farm plot FMNR data and markets.	Mali, Niger, Burkina Faso, Senegal
16	Weston et al., 2015	Original data	Livelihood outcomes	Focus group discussions, interview, household survey	12 focus group discussions, key informant interviews and 400 household surveys.	Ghana
17	Reij and Garrity, 2016	Perspective	Scaling up			Niger, Mali, Senegal
18	Binam et al., 2017	Original data	Effect of formal and informal institutions	Household survey, focus group discussions	1080 household surveys and focus group discussion.	Burkina Faso, Mali, Niger, Senegal
19	Camara et al., 2017	Original data	Impact on millet yield	Experimental plot for yield assessment; survey	Assessment of spatial variability of millet yield associated with tree stem density and farmers' Perception analysis	Senegal
20	Chirwa et al., 2017	Perspective	Relation between forests and people			not specified
21	Iiyama et al., 2017	Original data	Understanding patterns of tree adoption	Household survey	Socio-economic survey of 687 households.	Ethiopia
22	Ndegwa et al., 2017	Original data	Socio-economic factors influencing tree management	Household survey	189 structured household surveys.	Kenya
23	Partey et al., 2018	Review	Climate-smart agriculture promotion			Ghana, Mali, Niger, Senegal, Burkina Faso
24	Sida et al., 2018	Original data	Recruitment limitation of *Faidherbia albida*	Experimental, permanent plots	Experimental plots, and 100 permanent plots.	Ethiopia
25	Ado et al., 2019	Original data	Farmers' perceptions of climate risks and adaptation	Interview, field observations, household survey	Group interviews, field visits and 160 household head semi-structured surveys.	Niger
26	Bayala et al., 2019	Original data	Soil organic carbon	Inventory, soil sample	Soil and vegetative samples under 8 randomly selected trees in concentric zones and a control plot 40 m from the tree crown.	Burkina Faso, Mali, Niger, Senegal
27	Diallo et al., 2019	Original data	Effects of trees on soil nutrients	Soil sample	Soil samples taken from 12 randomly selected trees of four species and two treeless controls at least 15 m away from crown.	Niger
28	Ouédraogo et al., 2019	Original data	Adoption of climate smart agricultural technologies	Household survey	300 household head structured interviews.	Mali
29	Van Haren et al., 2019	Review	Land cover, land productivity and carbon stocks			Not specified
30	Carey, 2020	Perspective	Natural regeneration			Niger

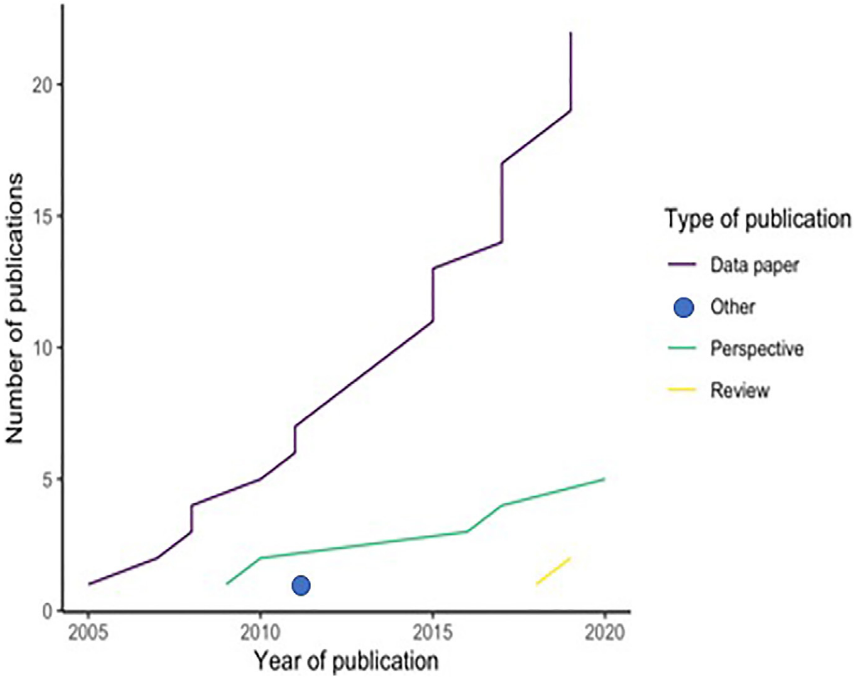

FIGURE 3 | Accumulated number of publications on Farmer Managed Natural Regeneration (FMNR) classified by type (Table 1) forming the core evidence base for this review (n = 30).

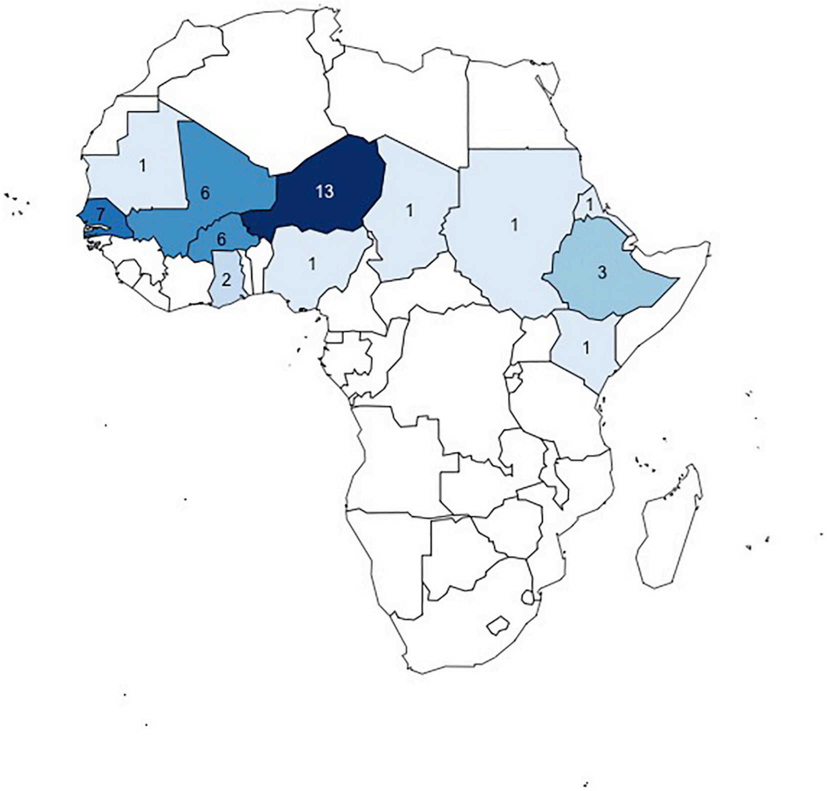

FIGURE 4 | Map showing the number of original data articles (indicated by color and number) for different African countries.

successful restoration using FMNR (Sendzimir et al., 2011). Both formal and informal institutions affect FMNR practices. Binam et al. (2017, p. 1) indicate "*in areas with well-structured formal and informal institutions, communities seem to have adopted a better collaboration attitude with the local government by developing plans for a good management and protection of natural resources including FMNR practices*."

Under current restrictive policy environments, rights to local resources may require negotiation with state agencies, and this requires collective action through farmers cooperatives, user groups or FMNR committees (Reij et al., 2009; Brown et al., 2011; Baggnian et al., 2013). Regions where FMNR is practiced have often seen shifts in formal and informal policies that have affected peoples rights and access to local resources (Binam et al., 2017). For example, in Niger, reduced oversight and interference by forestry officials and changes in land and tree tenure policy gave farmers a sense of ownership of trees and, therefore, encouraged FMNR (Larwanou et al., 2006; Reij et al., 2009; Rinaudo, 2012; Reij and Garrity, 2016) while in Ethiopia, official government recognition of user rights of communities as a group rather than as individuals, and the formulation of by-laws which defined management practices (when, how and by whom), led to regeneration of trees on farms and communal areas (Brown et al., 2011). There is also a strong effect of external agencies on the adoption and scaling of FMNR, where NGOs focusing on reversing deforestation have played a key role in catalyzing FMNR through providing training and incentives to farmers including through cash-for-work programs or in-kind contributions of farm inputs such as improved seeds and fertilizers in both Sahelian countries and parts of Ethiopia (Larwanou and Saadou, 2011; Rinaudo, 2012).

COMPOSITION OF REGENERATED VEGETATION

It is not clear in most of the articles reviewed, whether trees were established primarily through natural regeneration, or through a combination of planting (which could include use of seedlings or direct sowing of seeds) and natural regeneration (Binam et al., 2015; Ndegwa et al., 2017). As such, there is little evidence about the specific effects that FMNR may have on the abundance and diversity of trees. Of the 30 papers reviewed, eight studies reported densities of natural regeneration. These ranged widely from 19 to 360 trees ha^{-1} (Larwanou and Saadou, 2011; Badji et al., 2015; Reij and Garrity, 2016). The quantitative information of naturally regenerated tree densities from Niger were more consistent—between 100 and 151 trees ha^{-1} were reported (Yayé and Berti, 2008; Baggnian et al., 2013). Reij and Garrity (2016) estimated there are over 100 *Faidherbia albida* trees ha^{-1} in cropland in Zinder. Tree densities on FMNR fields in Niger were higher by 12–16 trees ha^{-1} compared to areas where FMNR was not practiced (Haglund et al., 2011). Programs actively promoting FMNR at scale in Niger have recommended a target of 40 mature trees ha^{-1} (Tougiani et al., 2009; Rinaudo, 2012).

Eleven out of the 30 papers reported the species that regenerate and are managed under FMNR. A total of 49 species from 15 families were reported with 21 in the Leguminosae and eight in Combretaceae (see **Supplementary Appendix 1**). Species were identified through tree inventories (Yayé and Berti, 2008; Larwanou et al., 2010; Bayala et al., 2019) while other studies used farmer recall or expert knowledge and were inexhaustive in their listing. For that reason, the number of species reported is likely to be an underestimation of the total that actually regenerate through FMNR in the regions covered. Kindt et al. (2008) reported 105 species regenerated naturally across systematically inventoried plots in Burkina Faso, Mali, Niger and Senegal. These species were not included in our tabulation because the inventories included plots in forest reserves and fallows or abandoned lands and it is not possible to distinguish which species occurred in actively managed farmers' fields. Nevertheless, the 105 species reported show that parkland landscapes in the Sahelian countries where FMNR is practiced are species-rich and that 95% of species encountered are able to regenerate naturally. This is what farmers can select from when they practice FMNR.

The majority of species mentioned in the reviewed articles (46 out of 49 or 93%) were native while the remainder were exotic to the African continent. The fact that exotics also regenerate through FMNR contradicts assertions that farmers use FMNR to regenerate indigenous tree species only, while exotics are established through tree planting (Ndegwa et al., 2017). Kindt et al. (2008) also found that of the small proportion of exotics found across farming landscapes 90% were also able to regenerate naturally. This demonstrates how exotic species can become naturalized in certain contexts and are then actively managed by farmers under FMNR. Ten out of the 30 articles mentioned the source of regeneration, all of which mention rootstock as important while five of these same articles also mention seed stock and the other 20 articles do not specify the source.

CONSEQUENCES OF FMNR

The consequences in terms of livelihood and environmental benefits that arise from FMNR are determined by the composition of what regenerates (**Figure 1**). The articles in the core evidence base focus on benefits, consistent with FMNR being a deliberate practice that farmers engage in on the expectation that benefits will accrue. Evidence is, therefore, available about benefits but there may also be other largely undocumented consequences and publication bias, since positive outcomes may be more likely to be reported than cases where FMNR does not work out (Coe et al., 2014).

Environmental Benefits

Increasing tree density, associated with FMNR, is reported to enhance various soil properties (Garrity et al., 2010; Sendzimir et al., 2011; Diallo et al., 2019). Tree species that commonly occur under FMNR, such as *Faidherbia albida* and *Piliostigma reticulatum,* are reported from comparing soil under and away from tree crowns within FMNR fields, to have a strong positive effect on different soil nutrients in studies conducted in Niger (Diallo et al., 2019) and Burkina Faso (Yelemou et al., 2007).

Faidherbia albida is promoted by FMNR proponents for its N_2-fixing ability, and for its unique characteristic of reverse phenology. This refers to *F. albida* shedding its leaves at the start of the wet cropping season (unlike most other deciduous species), thereby releasing nutrients to crops when they most need it, and being leafless over the cropping season thereby reducing competition for light and water (Garrity et al., 2010). FMNR has lead to 25–46% increases in soil organic carbon (SOC) especially in sandy soils in parkland systems across the Sahel (Bayala et al., 2007, 2019), with SOC being an important indicator of soil health. Bayala et al. (2019) reported an increase in total SOC in the top 0–10 cm soil, with SOC being more under trees than away from the tree and larger effects in sandy soils. Trees have also been reported to have a positive effect on infiltration due to the formation of root channels as well as macro and micro pores (Moustapha et al., 2014). Increase in SOC is caused by accumulated biomass from leaf litter and root turnover and the cooler and moister microclimate under shade, that reduces CO_2 efflux, so that the difference between under and away from trees is associated with the balance between inputs of organic matter and outputs as soil respiration (Bayala et al., 2019).

Some authors suggest FMNR as a mitigation strategy for climate-change by sequestering large amounts of carbon in tree biomass and the soil (Binam et al., 2015; Weston et al., 2015; Reij and Garrity, 2016), but none of the studies reviewed here quantified the actual amounts of carbon sequestered as a result of the practice. Partey et al. (2018) suggest for the Sahel that sequestration rates could be expected to be analogous to those for parkland systems as reported in Luedeling and Neufeldt (2012). Sahelian parklands are reported from a range of measurements to have a mean stock of 33.4 Mg C ha^{-1} with a range of 5.7–70.8 and a mean annual sequestration rate of 0.5 Mg C ha^{-1} yr^{-1} with a range of 0.2–0.8 (Mbow et al., 2014; Sinclair et al., 2019). Ado et al. (2019) found 85% of sampled households in Maradi region of Niger reported that they used FMNR as a climate change adaptation strategy, because their perception was that it prevents soil erosion and reduces the risks associated with increased wind speed and temperatures.

A range of other environmental benefits that were reported included reduced wind speed, higher soil moisture, shade, microclimate creation and micro-scale water effects which can buffer crops from heat stress (Garrity et al., 2010; Sendzimir et al., 2011; Reij and Garrity, 2016; Camara et al., 2017). The attributes of trees under FMNR that provide these benefits are rarely quantified, which may be because of the challenges of making the measurements and of making systematic comparisons with non-FMNR sites leading authors to often infer benefits under FMNR from literature addressing agroforestry more broadly.

Livelihood Benefits

FMNR promotes woody vegetation in crop fields. A hypothesized positive effect of FMNR on food security is explained through FMNR enhancing farm productivity, nutrition and farm income. A link between FMNR and increased crop yields was reported in a number of publications from the Sahel (Binam et al., 2017; Camara et al., 2017; Ouédraogo et al., 2019), but was only quantified in the case of millet in Senegal where a 41% improvement was recorded in two year study (Camara et al., 2017). In Mali, improved crop productivity was the reason farmers gave for practicing FMNR (Ouédraogo et al., 2019). Across four Sahelian countries, Binam et al. (2017) found a positive impact of FMNR on crop yields when the tree density was between 15 and 40 trees ha^{-1}. Beyond this density, a decrease in crop yields was observed. Overall there were variances in the reported relationships between FMNR and crop productivity. Reij and Garrity (2016) proposed that mature fertilizer trees contributed to 15–30% of cereal yields across three Sahelian countries while Haglund et al. (2011) found no significant relationship between FMNR and grain yield of cereal crops in Niger although FMNR was associated with higher overall value of crop production, attributed to higher intercrop yields of crops such as cowpea and groundnut.

FMNR has been shown to provide a range of tree products that are consumed locally and sold, thereby contributing to the amount and diversification of household income and wellbeing. These include home consumption or sale of fuelwood (firewood and charcoal) and non-timber forest products (NTFPs) including wild leafy vegetables, fodder, nuts, fruits, pharmacopeia, honey, and edible seeds (Yelemou et al., 2007; Tougiani et al., 2009; Larwanou et al., 2010; Larwanou and Saadou, 2011; Hansen et al., 2012; Reij and Garrity, 2016; Ouédraogo et al., 2019). These benefits were rarely quantified but Reij and Garrity (2016) suggested an annual value of 127–154 USD per household in Niger from the firewood from FMNR, with tree-based revenue reported as a modest contribution of around 10% of the household revenue. Quoting a non-peer reviewed study by Yamba and Sambo (2012), Reij and Garrity (2016) reported that one *Adansonia digitata* (baobab) could generate an annual income of 34–75 USD. In the Sahel, commercialization of non-timber tree products from indigenous tree species under FMNR such as shea (*Vitellaria paradoxa*), baobab (*A. digitata*), *Parkia biglobosa, and Tamarindus indica* provide cash income for households (Binam et al., 2015).

Haglund et al. (2011) estimated that FMNR adoption in Maradi region of Niger increased gross annual household income by 46–56 USD (or 18–24%) per capita, mostly arising from increases in the value of crop and wood production. Binam et al. (2015) found a 72 USD per household increase in four countries in the Sahel and an increase in value of products for those practicing FMNR by 34–38%. Stands comprising over 100 trees ha^{-1} of mainly *Combretum glutinosum* and *Piliostigma reticulatum* in the early 2000's in Niger could produce fuelwood and timber valued at 1 million CFA (approximately 1,400 USD) but there was local demand for only a third of the production from local purchasers at that time (Yayé and Berti, 2008). Weston et al. (2015) calculated that an FMNR project in Talensi Ghana generated a value of 887 USD per year for each of the 180 lead farmer households, including the social, health, environmental, community cohesion and economic benefits accrued. In Kenya, regenerated species were valued for subsistence products and environmental services such as charcoal and fodder while planted trees were valued for nutrition and medicinal products, these values were not quantified (Ndegwa et al., 2017). In Burkina

Faso, *P. reticulatum* was used for improved nutrition by 97% of surveyed farmers (Yelemou et al., 2007). Binam et al. (2015) reported that FMNR leads to a significant increase of dietary diversity by about 12–14% against control households. A gradual increase in food consumption score was reported where tree density was above 20 trees ha^{-1} across four Sahelian countries (Binam et al., 2017).

A study of 400 households from Ghana in the Upper East Region found that FMNR adoption led to indirect economic benefits such as increased consumption of wild resources, health improvements and psycho-social benefits, as well as asset creation which were of higher value than income and agricultural benefits (Weston et al., 2015). Adoption of FMNR has been linked to community empowerment as committees to manage tree protection are formed across social groups and networks of communities (Reij and Garrity, 2016). Higher migration rates in households adopting FMNR were explained through income gains from FMNR being used to finance migration for employment opportunities elsewhere (Haglund et al., 2011). The opposite was reported by Sendzimir et al. (2011) who suggest that increased production was likely to result in reduced need for migration in search of work. It remains unclear under what conditions increased production or income will promote or deter migration.

DISCUSSION

The evidence underpinning promotion of FMNR as a restoration practice in Africa was reviewed in the previous sections covering the ecological and socio-economic context under which it is practiced, the composition of the resulting regenerated vegetation and the environmental and socio-economic benefits derived from it. The lack of paired data from FMNR and non-FMNR sites limits the possibility of making systematic comparisons of FMNR outcomes. Evidence of adoption of FMNR in Africa is confined to specific agroecological contexts characterized by arid to sub-humid climate, with a wide range of mean annual rainfall of between 100 and 950 mm yr^{-1} and low fertility soils vulnerable to degradation. There is an indication that soil improvement, indicated by increased SOC content is greater on sandier soils (Bayala et al., 2019). There is need for further research to establish how suitable FMNR could be outside these conditions, given the interest in promoting the practice in other regions in Africa that may benefit from FMNR but fall outside these climatic and edaphic contexts. This can be achieved through embedding planned comparisons within the scaling up initiatives of development projects to foster co-learning about how context conditions FMNR outcomes (Sinclair and Coe, 2019).

Widespread adoption of FMNR is heavily influenced by the social context, especially governance factors commonly known to play a role in adoption and scaling up of technologies. These include farmer's choices and their decisions about tree selection and management, land and tree tenure, policy and institutions such as by-laws relating to grazing and conflict management, especially between crop farmers and pastoralists (Binam et al., 2017). NGOs often create incentives and build capacity to facilitate adoption, especially for farmers with limited previous knowledge of FMNR, through training and various other forms of support (Larwanou and Saadou, 2011; Rinaudo, 2012). This is consistent with five categories of factors that have been posited as determinants of technology adoption more broadly: (i) household preferences; (ii) resource endowments; (iii) market incentives; (iv) biophysical factors; and (v) risk and uncertainty (Pattanayak et al., 2003).

Insecure land and tree tenure remain key bottlenecks for adoption of FMNR. Complexities in tree and land tenure security can be traced back to the colonial era which set forest codes and management regimes characterized by asymmetrical power vested in the hands of forest officials that persist to date in many African countries (Chomba et al., 2016; Binam et al., 2017). Relationships between security of land and tree tenure and the adoption of agroforestry technologies by smallholder farmers is well documented (Franzel et al., 2001). Tenure rights determine the types and amounts of benefits that farmers can obtain from tree resources (Zhang and Owiredu, 2007; Chomba et al., 2016). Secure forms of tenure provide stronger rights and benefits for their holders and are more likely to stimulate tree conservation than short-term or less secure forms of tenure. There is little incentive to engage in FMNR, or other long-term investments in land, if tenure is insecure. Where trees remain property of the state, there are often perverse incentives to cut them down in order to secure access to land without state interference. Incentives provided to farmers such as, extension services, information, technical assistance, and guaranteed markets for wood and non-timber forest products (NTFPs) can increase farmers' willingness to conserve trees on-farm through FMNR (Binam et al., 2017).

Literature in ecology shows that ecosystem recovery through natural regeneration is dependent on climatic conditions (Poorter et al., 2016), soils (Becknell and Powers, 2014), landscape characteristics (Arroyo-Rodríguez et al., 2017), and land management (Jakovac et al., 2015). For the success of FMNR as a practice, but also for predicting specific restoration benefits that may be achieved, characterizing which tree species will regenerate in an area, and which ones get selected by farmers is important. Currently, there is insufficient systematic characterization of the species composition of regenerating vegetation in different circumstances. Consequently, the extent to which regeneration is facilitated by farmers (Binam et al., 2015) and the trees occurring in fields are derived from planted seedlings, direct sowing of seeds or through natural regeneration remains uncertain (Ndegwa et al., 2017).

Some general patterns that characterize regeneration through FMNR can be elicited from the review. First, that species diversity can be promoted through FMNR in stark contrast to the experience of most tree planting campaigns that rely on few species amenable to rapid multiplication in nurseries (Derero et al., 2020). Second, and linked to the first, FMNR encourages the regeneration of mainly indigenous species. In this review, only three out of 49 species reported in vegetation regenerating under FMNR were exotic, consistent with the literature on natural regeneration more generally (Kindt et al., 2008; Ndegwa et al., 2017). A positive aspect about FMNR is that the indigenous species found are likely to be in their native ecological niche. This is in contrast to plantations, where native species may exhibit different traits than when observed where they grow naturally because their interactions with other species have a critical influence. Third, tree densities differ widely under FMNR ranging from 18 trees ha^{-1} observed in some areas (Hansen et al., 2012), through 40 trees ha^{-1} promoted by projects and experts (Tougiani et al., 2009; Rinaudo, 2012) to 360 trees ha^{-1} observed in other areas (Baggnian et al., 2013). We found little justification for these numbers except where Binam et al. (2017) found that the positive impact of trees on crop yields becomes negative beyond 40 mature trees ha^{-1} for particular species. We would caution against prescriptive tree densities because optimal tree cover is highly context-dependent. Tree cover is often measured as projected crown area to take account of tree size, although sometimes, stem basal area is used as a proxy even though relationships between stem basal area and projected crown area may not hold where trees have been pruned (Shimano, 1997). Optimal tree cover is influenced by many aspects including climatic and edaphic conditions (Ilstedt et al., 2016), what crops the regenerating trees are growing with, and the characteristics of the woody vegetation promoted in terms of their canopy, size, ontogenetic stages and functional traits as well as the prevailing farm management practices such as degree of mechanization (Lohbeck et al., 2018; Sauvadet et al., 2020).

Different ecosystem functions are associated with particular tree species (Lohbeck et al., 2018). Water regulation, for example, is influenced by the balance between tree transpiration, evaporation (influenced by shading) and infiltration, crucial in arid and semi-arid areas where FMNR is predominantly practiced (Ilstedt et al., 2016). Tree species with high Leaf Area Density (LAD) tend to be competitive with crops for moisture, a phenomenon that farmers are acutely aware of Cerdan et al. (2012). Farmers often have detailed local knowledge about how a range of tree attributes influence tree-crop competition (Smith Dumont et al., 2018). Despite this, the aspects of functionality of the system being targeted for restoration through FMNR are rarely explicitly addressed through selecting species with appropriate attributes. Advocates of widescale promotion of FMNR underscore how it fosters tree diversity and abundance (Garrity et al., 2010) and hence household income (Haglund et al., 2011; Binam et al., 2015; Reij and Garrity, 2016). They rarely, however, present mechanistic detail about how tree diversity and abundance contribute to better functioning agroecosystems, and how, and by how much, this generates livelihood benefits. It is evident that a better understanding of how the composition of regenerating vegetation relate to its functioning and the provision of ecosystem services would be valuable for more targeted restoration planning. To achieve this, we can draw from the field of functional ecology that links functional characteristics of vegetation to specific local conditions and consequences for ecosystem functions, and has proven useful in the context of restoration generally (Laughlin, 2014), and agroforestry for restoration specifically, indicating contexts where enrichment planting may be required to complement FMNR to meet restoration targets (Lohbeck et al., 2018, 2020). Adopting such an approach goes beyond an emphasis on simply increasing tree densities and species richness in fields, to consider whether functional diversity increases. This is a promising avenue for further research, that also has the potential to incorporate understanding of the consequences of the composition of regenerating vegetation for system resilience (Laliberté and Legendre, 2010).

With respect to scaling FMNR, most cases in the reviewed literature involve long-term presence of donor-funded projects and interventions as opposed to a spontaneous process of adoption from farmer to farmer, and the costs of this are rarely included in discussion of FMNR as a low-cost alternative to tree planting. The often quoted figure that FMNR can be achieved at a cost of 20 USD ha^{-1} (Reij and Garrity, 2016) are based on expert estimates and personal communications rather than explicit economic analysis. Many studies completely ignore or undervalue farmer's labor and the opportunity cost of land that could have other uses. There are clear benefits for farmers in terms of access to food, fodder and fiber from FMNR, but these have rarely been fully quantified, not least because doing so for variable, species rich contexts is complex. Binam et al. (2015) found on average, households are likely to get an additional USD 72 per year from FMNR. The majority of other studies make claims based on perceptions, proxy values, unpublished data, internal project reports and views of a few farmers not systematically collected or analyzed, mainly derived from project officers or authors involved in promoting FMNR (Garrity et al., 2010; Haglund et al., 2011; Larwanou and Saadou, 2011; Weston et al., 2015; Reij and Garrity, 2016). Further research to quantify costs and benefits of FMNR in comparison with alternative restoration techniques is urgently needed to calculate the return on investment in promoting its adoption in different contexts.

In conclusion, it is clear that FMNR is promoted on the basis that it can restore land while enhancing rural livelihoods and environmental sustainability through a wide range of benefits, and that it is low cost, easy to replicate and hence can be easily scaled-up over large areas. This review cautions that FMNR has all the characteristics of what Coe et al. (2014) call "an iconic practice," that from limited experience in selected sites, is picked up and widely promoted without clear understanding of the mechanisms involved or the contexts to which scaling out may be appropriate. The evidence underpinning widescale promotion of FMNR is heavily biased toward a few studies in the Sahel, and particularly the widely cited successful case of restoration in the Maradi and Zinder regions of Niger. Overall, the scientific evidence for the general claims made about the suitability of FMNR in different contexts and the full range of benefits, including ecosystem functions, is sparse. There is, however, a widespread need for cost-effective restoration methods for agricultural land in Africa to meet multiple objectives of poverty alleviation, protecting biodiversity, climate change mitigation and adaptation; and where FMNR has been extensively practiced, indications are that land restoration and livelihood benefits accrue. This generates a strong case for systematic research to explore the variations of FMNR practice suitable for different contexts and to quantify and value the full range of costs and benefits that are likely to accrue from it. This can be achieved through embedding co-learning strategies within the scaling-up initiatives of development projects.

AUTHOR CONTRIBUTIONS

SC contributed to lead the ideas and the framing of the manuscript, research questions, literature review, and all sections of the manuscript including thorough editing, references, and finalization. FS contributed to theoretical framing and diagram, ideas in the manuscript, editing of content, and writing the discussions and conclusions. PS contributed to framing and content, wrote some of the introductions, and reviewed the French literature. MB contributed to ideas in the manuscript, reviewed the literature, and wrote the economic and livelihoods in the results section of the manuscript. ML contributed to the framing of the manuscript as well as the literature review, produced the map of countries and studies reviewed, and wrote the functional aspects of FMNR and other sections. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2020.571679/full#supplementary-material

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Natural Regeneration After Volcanic Eruptions: Resilience of the Non-legume Nitrogen-Fixing Tree *Parasponia rigida*

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Volcanic eruptions disturb vegetation at a time it is needed for preventing mudflows. A resilient indigenous non-legume nitrogen-fixing tree that is adapted to the ash and spreads rapidly protects areas downstream in a volcanic landscape in Indonesia. Within the volcanic ring of fire both the long-term benefits (including densely populated, fertile agricultural soils) and short-term ecological disturbance of volcanic ash deposition are clear. Mount Kelud in East Java has erupted on a 15–37-years cycle for the past centuries, most recently in 2014, causing damage to settlements, agricultural land, agroforestry, and watershed protection forests, as the ash deposits caused tree mortality, restricted infiltration, and led to ash flows. Rapid "restoration" or recovery of tree-based vegetation with planted Legume trees (such as *Calliandra* spp.) has been attempted but is not very effective. However, the non-legume nitrogen-fixing *Parasponia rigida,* symbiotic with rhizobium bacteria, contrasted to its non-symbiotic sibling *(Trema orientalis)* has been studied in laboratory conditions, but not in its native environment. We mapped and sampled *P. rigida* in various locations (upper, middle, and lower elevation positions in ridge-slope-valley toposequences) on the Kelud complex starting 1 year after the latest eruption, estimated biomass development, and quantified *P. rigida* root nodules in relation to N availability in the ash/soil mixtures in these locations. *P. rigida* was found as a pioneer tree at elevations between 600 and 1,700 m a.s.l. (above sea level) along ridges, in slope, and valley positions. At lower elevations *T. orientalis* dominated. Within 3 years of the eruption, stem diameters were 3–10 cm. Up to 93% of *P. rigida* root nodules were found to be effective, based on the hemoglobin color on cross-sections. *Rhizobium* bacteria were found in root nodule tissue at densities of two to a hundred times higher than in rhizosphere soil. Between a total soil N content from 0.01 to 0.04% the density of effective nodules decreased from 1,200 to 200 m^{-2}. *P. rigida* stands in the area, especially at ridges close to the crater deserve to be managed proactively as future seed sources, given the high frequency of eruption episodes, while recovery after eruptions on similar volcanoes can likely be facilitated by tactical assisted seed dispersal if effective seed collection and storage methods can be established.

Keywords: disaster preparedness, Indonesia, Mount Kelud, N_2-fixation, restoration, rhizobium, trema orientalis, volcanic ash

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INTRODUCTION

Indonesia has more than 100 active volcanoes, and many more that are dormant, as it is part of the global ring of fire linked to tectonic plate subduction zones. Densely populated Java and Bali reflect both the long-term soil fertility benefits of volcanic ash and a large number of people at risk during fresh eruptions, ash deposition, and lahar flows (Van Ranst et al., 2004; Achmad and Hadi, 2015). Volcanoes are regularly resetting the clock on vegetation succession and create a need for "restoration" when downstream impacts such as mudflows of unconsolidated ash is to be controlled (van Noordwijk et al., 2020). Beyond scenic beauty, volcanoes are also home to a limited, but specialized flora, contributing to the overall biodiversity of the country. The short-term damage of eruptions involves settlements, access roads, agricultural lands, agroforestry, and watershed protection forests, and calls for remedial disaster responses. Human resilience is challenged by damaged infrastructure, loss of boundaries of land ownership, destruction of forests, disturbed water catchment areas, and springs (Rahayu et al., 2014). Can a resilient local tree, adapted to volcanic ash environments be of help? Current emergency preparedness documents in Indonesia are not aware of any such tree.

Atmospheric deposits after a volcanic eruption can consist of ash, sand, gravel, or stones with the lighter materials traveling further. Ash deposits change the physical, chemical, and biological properties of the soil surface (Achmad and Hadi, 2015). Thick layers of ash can cause a dense, cement-like soil surface after rainfall (Suriadikarta et al., 2010). Emergent hydrophobicity decreases infiltration below what is expected given the substrate's porosity and leads to a dry soil environment (Rudianto et al., 2017), with low levels of organic C and N and a soil pH that can be acidic, neutral, or alkaline depending on SiO_2 levels in the volcano's substrate (McGeary et al., 2002). Regrowth of vegetation is hindered by a challenging soil environment (Sinaga et al., 2015), but also by a lack of viable seed supply, an absence of biological dispersal agents and shelter for seedlings; regrowth from stumps is possible, however, outside of the primary deposition zones. Lack of vegetation regrowth leads to the high mobility of the ash within the landscape and accumulations in the riverbeds, causing further problems downstream, but also opportunities for collecting "volcanic sands" that are a preferred resource for the building industry and allow former farmers a temporary source of income. Rapid recovery of vegetation, especially on the higher slopes is desirable to support the recovery of the village economy, however.

The Kelud eruption (East Java, also commonly spelled as Kelut) on 13 February 2014 was one in a long series of recorded eruptions and ash deposits with return times of 15–37 years (with ash deposits in intervening years as well): 1826, 1848, 1864, 1901, 1919, 1951, 1966, 1990 (Thouret et al., 1998) and a relatively minor event in 2007. These relatively short return times may be part of the local selection of species that rapidly recover. In 2014 the top of the plume reached to a height of nearly 30 km and the umbrella cloud spread radially at 17−20 km high; ash was recorded up to Bogor, West Java; due to the prevailing wind, there were large deposits on the north and northeast area of the volcano (Suzuki et al., 2014; Kristiansen et al., 2015). The 2014 eruption deposited about 50×10^6 m^3 of material on the upper slope of Kelud Volcano. A considerable part of this was washed down by rainfall in mudflows along the rivers and deposited downstream where the riverbed widened (Dibyosaputro et al., 2015). This was not the first time this happened, and part of the vegetation may be adapted to these circumstances. The German explorer Junghuhn had in 1,844 collected a tree specimen on Mt Kelud from which Miquel (1859) described the species as belonging to the genus *Parasponia*, as it closely resembled *Sponia*, now known as *Trema.* Local names confirm the close resemblance, with Trema known as "anggrung", and *Parasponia* as its greener sibling "anggrung hijau". Clason (1935) exploring the vegetation of the mountain slopes and valleys after the Mount Kelud eruption of 1919, reported *Parasponia* especially from the volcanic ash and lahar valley, while *Trema* grew more frequently in places where the original soil, "although probably more or less sterilized" had persisted after the eruption. Clason (1935) mentioned in passing that "*Parasponia* possesses root nodules, nitrogenous food being possibly obtained in this way so that *Parasponia* is thus adapted as a pioneer type to virgin soil." However, it took another 40 years before this observation was noticed, although Smiet (1992) described *Parasponia* as a common part of Java's mountain flora. Trinick (1973), Akkermans et al. (1978), Trinick (1979), and Becking (1979) established the exception to the rule that only the *Leguminosa*e can associate with rhizobium bacteria. The genus *Parasponia* (in the *Cannabaceae* family, formerly seen as part of the *Ulmacea*e) that is known from volcanic ash environments in Indonesia and the Philippines can form effective nodules with rhizobium bacteria (*Bradyrhizobium* species according to Trinick and Hadobas, 1989). Due to its more open canopy, *Parasponia* stands allow the development of a dense layer of the grass *Saccharum*, which in turns prevents other late-successional trees to establish. "It would seem that the *Parasponia*-socion has already attained its greatest development and that it does not hold its own; in any case, I saw very few young trees and on the other hand several old trees which had died off. It seems as if *Parasponia* became established before the edaphic conditions allowed the development of the *Saccharum*-socion." This description suggests that *Parasponia* occupies the "regeneration niche" (Grubb, 1977; Pickett and White, 2013), being able to establish itself rapidly in the extreme conditions that prevail after a recent ash deposition event (given the short return period of eruptions), but by enriching the ash deposits with nitrogen, paves the way for grasses to take over, which in turn delay succession to other woody vegetation. A deeper understanding of these ecological relations in the field and aspects of the "regeneration niche" is warranted, as the unique volcanic ash environment in which *Parasponia* is evolving may account for its unique properties.

A productive line of research has explored the molecular biology of *Parasponia*-rhizobium interactions and the evolutionary interpretation of such interactions as either independently (re)discovered in multiple plant families or lost from a large number of plant families that are otherwise related to both rhizobium hosts (Geurts et al., 2012; van Velzen et al., 2018). While many Leguminosae are not only able to initiate

N_2-fixation by rhizobium but also down-regulate it when there is sufficient nitrogen in its internal circulation system, there still is debate about the ability of *Parasponia* to do the same in laboratory test conditions (Vassey et al., 2005; Op den Camp et al., 2012; Yulia, 2013). Dupin et al. (2020) recently showed that in lab conditions exogenous fixed-nitrogen inhibits nodulation on *P. andersonii*. Much less is known on the ecology of the species in its native environment. From the existing evidence and literature, it appears that *Parasponia* evolved in the specific "regeneration niche" of volcanic ash where access to a nitrogen source is essential for early establishment but may pave the way, by enriching the soil, for more competitive non-nodulating sibling (or unrelated) species.

The specific research questions for our exploration of vegetation on Mount Kelud after the 2014 eruption were:

1) Has the most recent eruption had different effects on the populations of *Trema* and *Parasponia*? We quantified the composition of the recovering vegetation across the slope, with specific attention to the relative share of the two sibling species.
2) Which aspects of landscape position were related to biomass recovery? We compared seedling, sapling, pole, tree populations and biomass estimates with soil properties in toposequences at three elevation zones
3) Is (effective) nodulation of *P. rigida* in the regrowth stage related to soil nitrogen levels? We tested the hypothesis that down-regulation of N_2 fixation is absent in this early stage of an evolving symbiosis with *Rhizobium*, leading to soil enrichment.

In relation to options for enhancing natural regeneration to restore landscapes, we will discuss the opportunities *Parasponia* provides to existing disaster preparedness plans for the area (and similar volcanoes elsewhere in Indonesia) to embrace a more pro-active vegetation management protecting seed sources in the highest zone.

MATERIALS AND METHODS

Study Area

The research focused on the northeast side of Mount Kelud (**Figure 1**), where most of the ash of the 2014 eruption was deposited. The satellite imagery for the area (**Figure 1**) compares the land cover before the eruption (peaking 14 Feb 2014, BNPB, 2014) that covered an area at 5–10 km from the crater with ash. Vegetation at a larger distance from the crater recovered, despite some tree mortality, while regrowth closer to the crater had to start from either seeds or stumps.

The main access to the mountain slopes we used was via the Kutut Pandansari village (7°54'35.74"S, 112°22'0189"E) in the area downstream of the Selorejo reservoir in Ngantang district (Malang Regency). A path toward the crater passes through three elevation zones: lower (700–800 m a.s.l.), middle (900–1,000 m a.s.l.), and upper (>1,000 m a.s.l.) (**Figure 1**). The steeper slopes of Mount Kelud are classified as "watershed protection" forest, with lower parts classified as production forest, both managed by the State Forest Company (Perum Perhutani).

The research activity was carried out in 2 stages: Phase 1 focused on vegetation analysis 1 year after the eruption (July—December 2015), and Phase 2 on *Parasponia* nodulation was carried out 2 years after the eruption (July—November 2017), with some follow-up observations at later dates.

Data Collection

Observation Plots for Vegetation Analysis

Observation plots were selected for exploring the distribution of pioneer plant vegetation in various landscape positions on the slopes of Mount Kelud starting from Mahogany plantations in the lower zone (700–800 m a.s.l.), mixed vegetation at the middle (900–1,000 m a.s.l.), and upper zones (>1,000 m a.s.l.) using a survey scheme of plants on the slopes of Kelud mountain (Smiet, 1992). In each toposequence an East-West transect was sampled, with ridge (8–15% slope), mid-slope (40–60% slope), and valley (0–3% slope) positions. Stand density was determined within patches of vegetation, not randomly sampling the landscape.

Starting 2 years after the eruption, stem diameter and tree biomass were measured for *P. rigida* in various landscape positions: zones (upper, middle, and lower) and for a toposequence of ridge, slope, and valley, as before.

Soil Analysis

In phase 1, soil samples were collected from each observation plot from soil depths of 0–10, 10–20, and 20–30 cm, respectively; soil samples per layer were composited from five points per plot. Dried soil samples were used for the analysis of total organic carbon (C_{org}) using the Walkley and Black (1934) method, total nitrogen (N_{tot}) with a Kjeldahl procedure (Bremner, 1960), pH(H_2O), and soil texture as standard t the Chemical Laboratory, Soil Science Department, Faculty of Agriculture, Brawijaya University, Malang. Separate samples were taken for the determination of the soil bulk density (Hairiah et al., 2011).

In phase 2, soil samples were taken at 50 cm distance from the main stem of *P. rigida* at a depth of 0–10, 10–20, and 20–30 cm were taken and analyzed for C_{org}, N_{tot} (Kjeldahl), and mineral NH_4 and NO_3 concentrations in extracted soil solution using a colorimetric flow-injection autoanalyzer.

Vegetation

Observation of vegetation was carried out on all types of vegetation in various growth stages (seedlings, saplings, poles, and trees). Sample observation plots were nested within a 100 × 20 m main plot (Kusmana, 1997), with five plots of 20 × 20 m used to measure trees ($D > 10$ cm; D = diameter at 1.3 m above the ground, also known as diameter at breast height) (trees), subplots of 10 m × 10 m used for poles ($5 < D < 10$ cm), sub-sub plots of 5 × 5 m for saplings ($D < 5$ cm, $H > 2$ m), and sub-sub-sub plots of 2 × 2 m for seedlings ($H < 2$ m).

Assessment of the Effectiveness of Root Nodules

Root nodules were sampled by sorting through all soil in a 50 × 50 × 10 cm depth sample adjacent to 10 trees that were considered representative of the stand (avoiding the largest and smallest 20% of the distribution as found in the stand). All root nodules were separated from the roots, counted, and

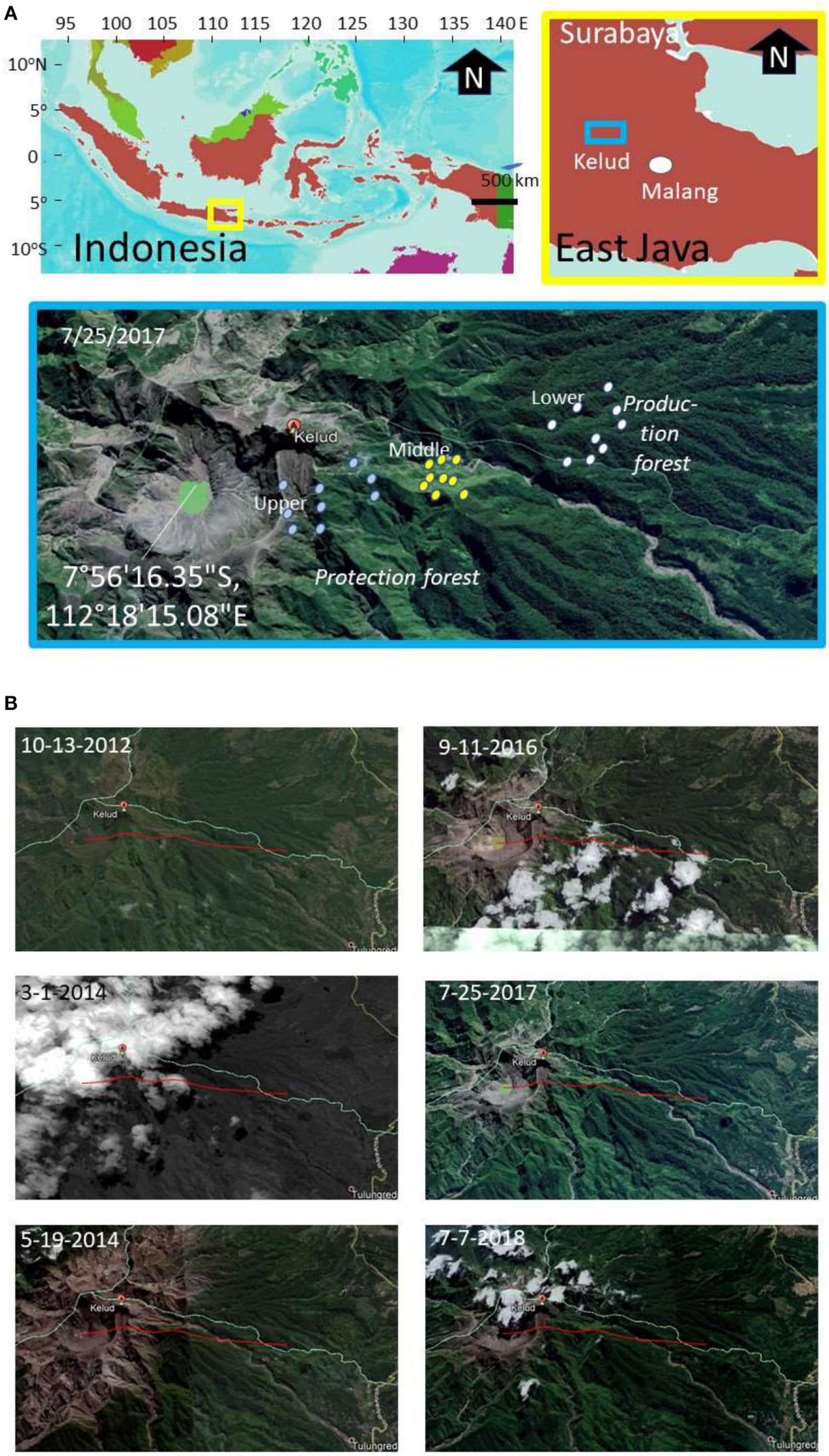

FIGURE 1 | (A) Location of Mount Kelud (East Java, Indonesia), **(B)** with satellite imagery before (2012), directly after (March 2014), and in recovery phase from the 2014 eruption and the position of sampling points in lower, middle and upper elevational zone; the red line indicates a 5 km transect.

stored in 70% alcohol. All nodules were observed under a dissecting microscope for hemoglobin color on a cross-section. Red hemoglobin was taken as an indicator of effectiveness, white nodules were classified as non-effective (Sarasawati, 2007).

Additional fresh nodule samples and rhizosphere soil adherent to roots was also collected for quantification of rhizobium density, via a dilution series and plating on petri dishes kept at room temperature (around 20°C) for 7 days to estimate the number of Colony Forming Units (CFU). Details of the method are described by Sarasawati (2007). The (autoclaved at 250°C) growth medium consisted of Potato Dextrose Agar (7.8 g), Mannitol (2 g), Yeast extract (0.2 g), K_2HPO_4 (0.1 g), $MgSO_4$ (0.04 g), NaCl (0,1 g) in 200 ml distilled water, with Congo Red (0.25 g) added as indicator. The highest dilution that still showed bacterial colony formation was taken as an indicator of the rhizobium concentration in the original sample, with calculations specified in Sarasawati (2007).

Parasponia's Taxonomic Position

The GlobalTreeSearch (Beech et al., 2017) mentions only one *Parasponia* species for Indonesia *P. rigida* Merr. & Perry (Hassler, 2019). In the Kew Garden plant list, all species in the genus *Parasponia* are indicated as "unresolved." Part of the literature on Indonesia [including Ishaq et al. (2020) refers to *P. andersonii* Planch. which has been confirmed for islands in the Pacific. Part of recent taxonomic interpretation places the species into the genus *Trema* (which has *Sponia*, to which *Parasponia* refers, as a synonym), as *T. rigida* (Merr. & L.M. Perry) Byng & Christenh. Pending this taxonomic debate, we will here use *P. rigida* as the botanically correct name for the tree species found on Mount Kelud.

Data Analyses

Pedotransfer as Reference Values for Soil Parameters

A reference value C_{ref} for the C_{org} concentration expected under long-term forest conditions for a soil of the same texture and pH at the same elevation (with additional factors for Andisol and Wetland conditions) was used, based on van Noordwijk et al. (1998) and Hairiah et al. (2020), including a depth correction for a soil layer from Z_H to Z_L cm depth:

$$\begin{aligned} C_{ref} &= 0.9 * (Z_L^{0.705} - Z_H^{0.705})/(0.705 * (Z_L - Z_H)) * \mathrm{EXP}(1.333 \\ &+ 0.00994 * \mathrm{Clay\%} + 0.00699 * \mathrm{Silt\%} - 0.156 * \mathrm{pH(KCl)} \\ &+ 0.000427 * \mathrm{Elevation} + 0.834 * \mathrm{Andisol?} + 0.363 * \mathrm{Wetland?}) \end{aligned}$$

with elevation expressed in m a.s.l. and "Andisol?" and "Wetland?" are zero unless the specific soil condition (with higher C_{org}) applies and the value is 1.

Vegetation Analysis

The diversity of vegetation was characterized by identifying all woody plants in the observation plots and calculating several indices from the results: density (number of individuals per unit area), frequency (fraction of plots in which a species was found), dominance (relative abundance) and the INP or Index of Importance Values (Soerianegara and Indrawan, 1978).

$$\mathrm{Density\ (PD)} = \frac{\textit{number of individuals of a type}}{\textit{sample plot area}}$$

$$\mathrm{RelativeDensity\ (RD)} = \frac{\textit{density of a type}}{\textit{density of all types}} x100\%$$

$$\mathrm{Frequency\ (F_i)} = \frac{\textit{the number of sample plots containing type}(i)}{\textit{total number of sample plots}}$$

$$\mathrm{RelativeFrequency\ (FR)} = \frac{\textit{frequency of a type}}{\textit{frequency of all types}} x100\%$$

$$\mathrm{Dominance\ (DM)} = \frac{\textit{total basal area of a type}}{\textit{sample plot area}}$$

with basal area (BA) derived as $\Sigma\ \pi\ \mathrm{DBH}^2/4$ from measurements of DBH or stem diameter at breast height (1.3 m).

$$\mathrm{RelativeDominance\ (DR)} = \frac{\textit{Dominance of a type}}{\textit{Dominance of all types}} x100\%$$

$$\mathrm{Importance\ (INP)} = \mathrm{FR} + \mathrm{RD} + \mathrm{DM}.$$

Diversity Index (Shannon and Wiener, 1949):

$$\mathrm{H}' = -\sum\nolimits_{n-1}^{n} \left(\frac{ni}{N}\right) \ln \left(\frac{ni}{N}\right)$$

where H' = Diversity index, N = Total number of individuals sampled, n_i = Number of species *i*.

Evenness index (with values between 0 and 1):

$$SEI = -\sum (\mathrm{P}_i^* \ln\ (\mathrm{P}_i))/\ln(\mathrm{m})$$

where P_i are the frequencies of the m species observed.

Tree Biomass

Measured stem diameters of poles and trees (for $D > 5$ cm) were converted to aboveground biomass (AGB) estimates using allometric equations for wet tropics (average rainfall 1,500–4,000 mm y^{-1}) from Chave et al. (2005):

$$\begin{aligned} (\mathrm{AGB})_{est} &= \rho\, ^*\exp(-1.499 + 2.148\ln(\mathrm{D}) \\ &+ 0.207(\ln(\mathrm{D}))^2 - 0.0281(\ln(\mathrm{D}))^3\ ) \end{aligned}$$

Where ρ = wood density (g cm^{-3}), derived from http://db.worldagroforestry.org/wd. A locally developed (Alfian, 2017) species-specific allometric equation was used: $AGB = 0.4992\ D^{1.0012}$.

Statistical Analysis

The results of observations and measurements of biophysical data were analyzed by Analysis of Variance using Genstat (18th edition) software to test possible rejection of a null-hypothesis of no effects of toposequence and landscape positions as main factors, along with a simple interaction term. Where statistically significant differences ($p < 0.05$) were noted, a Duncan test was used to compare means at the combination of the two factors. Correlation and linear regression analysis (in the MS-Excel software) were used to describe relationships between response (Y) and explanatory (X) parameters, as $Y = b\ Y_m + (a\ Y_m / X_m)\ X$, after normalizing or rescaling data sets relative to their means, Y_m and X_m, respectively.

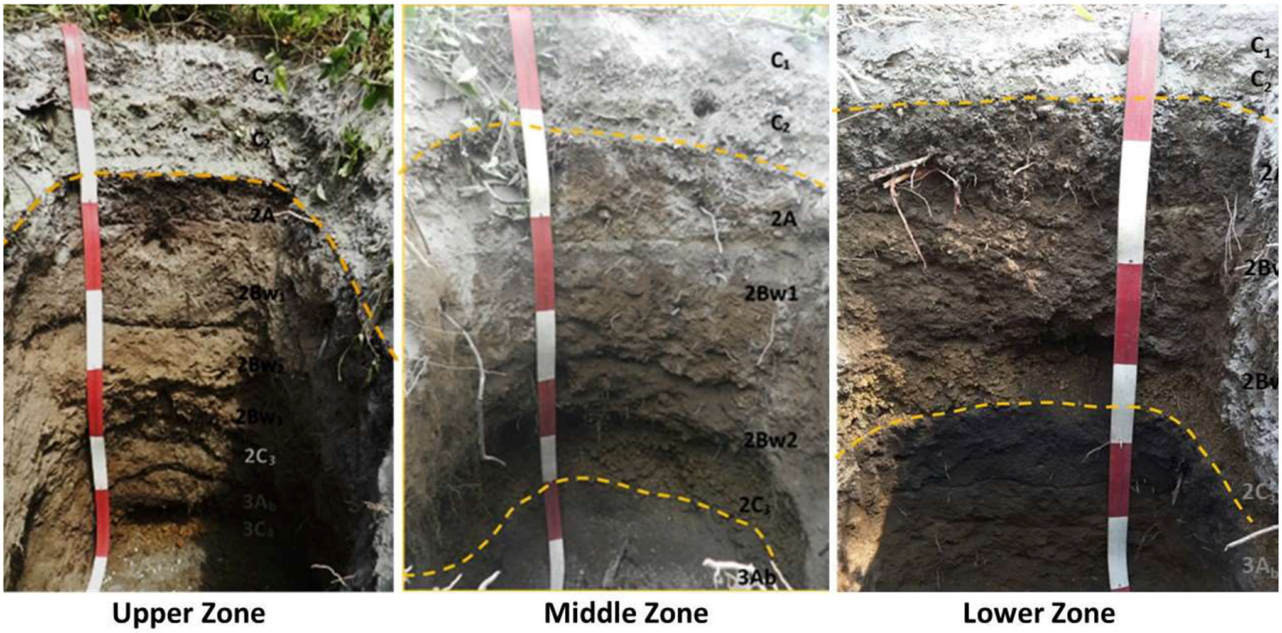

FIGURE 2 | Soil profile on the ridge position at three elevations, with soil layers as identified in the field indicated by dashed lines and topsoil recent ash deposits of close to 20, 12, and 7 cm, respectively; the measuring tape indicates depth increments of 10 cm (Photo courtesy from Nugraha, 2015).

TABLE 1 | Soil properties for three soil layers in various landscape positions (BD, bulk density; C_{ref}, reference Corg concentration based on pedotransfer function; averages for three replicate plots).

Landscape position	Depth	BD	pH	C_{org}	C_{ref}	C_{org}/C_{ref}	Texture*, %		
	cm	g cm^{-3}	H_2O	%	%		Sand	Silt	Clay
Upper (Shrub)	0–10	1.12	4.62	1.11	2.60	0.427	80	16	4
	10–20	0.90	4.78	0.18	1.43	0.126	95	2	3
	20–30	0.96	4.97	1.40	1.43	0.978	69	24	6
Middle (Shrub)	0–10	1.03	4.70	0.13	2.36	0.055	80	19	2
	10–20	0.88	4.80	0.57	1.41	0.404	84	14	2
	20–30	0.80	5.04	2.53	1.37	1.85	64	27	9
Lower	0–10	1.14	4.70	0.09	2.15	0.042	75	20	5
(Production forest)	10–20	1.14	4.88	0.74	1.33	0.555	72	26	2
	20–30	0.98	5.06	1.83	1.17	1.56	66	28	6
Lower (Annual plants)	0–10	1.07	4.69	0.31	2.20	0.141	67	25	8
	10–20	1.00	4.75	0.26	1.42	0.183	64	25	11
	20–30	0.96	4.97	0.45	1.22	0.369	59	28	13

**Data from Yunita (2016).*

RESULTS

Vegetation and Soil Properties

Soil profiles in the area showed evidence of multiple ash deposition events, with topsoils buried by the 14 February 2014 and earlier Kelud eruptions at various depths (**Figure 2**). Soil analysis (**Table 1**) showed buried topsoil (with relatively high C_{org}) in the 20–30 cm depth layer, and slightly higher pH values. Lower elevations had higher silt content, but the sand fraction dominated in all samples.

Most of *P. rigida* plants were found in clusters on sites with a slope of 30–80%, spread over an altitude of 600–1,700 m a.s.l. at the lower, middle, and upper landscape positions, with sandy and relatively wet soil conditions. Usually, *P. rigida* was found in open shrubland, but it also developed well in the lava flow deposits (layers of sand and gravel) in the riverbeds (**Figure 3D**).

Basal area, biomass, and necromass of trees differed significantly between landscape positions (**Table 2**). Necromass was 34 and 26% of biomass at upper and middle landscape positions, indicative of eruption-related tree mortality, but no necromass was observed in the lower zone, while biomass there was highest. In the middle and upper zones, several trees had survived, as indicated by the biomass of trees above 30 cm diameter. Please note that the vegetation sampling referred to existing stands, not to their frequency within the wider landscape. The absence of necromass at lower elevation can be an indication of firewood collection by the neighboring village.

Tree population data (**Table 3**) matched the basal area (**Table 2**) data, with the high biomass but low tree diversity (and near-absence of internal regeneration) in the Mahogany stands in the lower zone). Tree diversity in the middle zone was significantly ($p < 0.01$) higher than that in the upper zone for trees ($D > 10$ cm) and poles ($5 < D < 10$ cm) but was not distinguishable between these two zones for the sapling and seedling stages. In the latter two categories, however, sapling and seedling diversity reflected that in poles and trees at the high landscape position.

For further analysis of the differences between the zones, the Importance Value Index combines relative density, relative frequency, and relative domination for the commonest species. In the middle zone the seedling and sapling stage was dominated

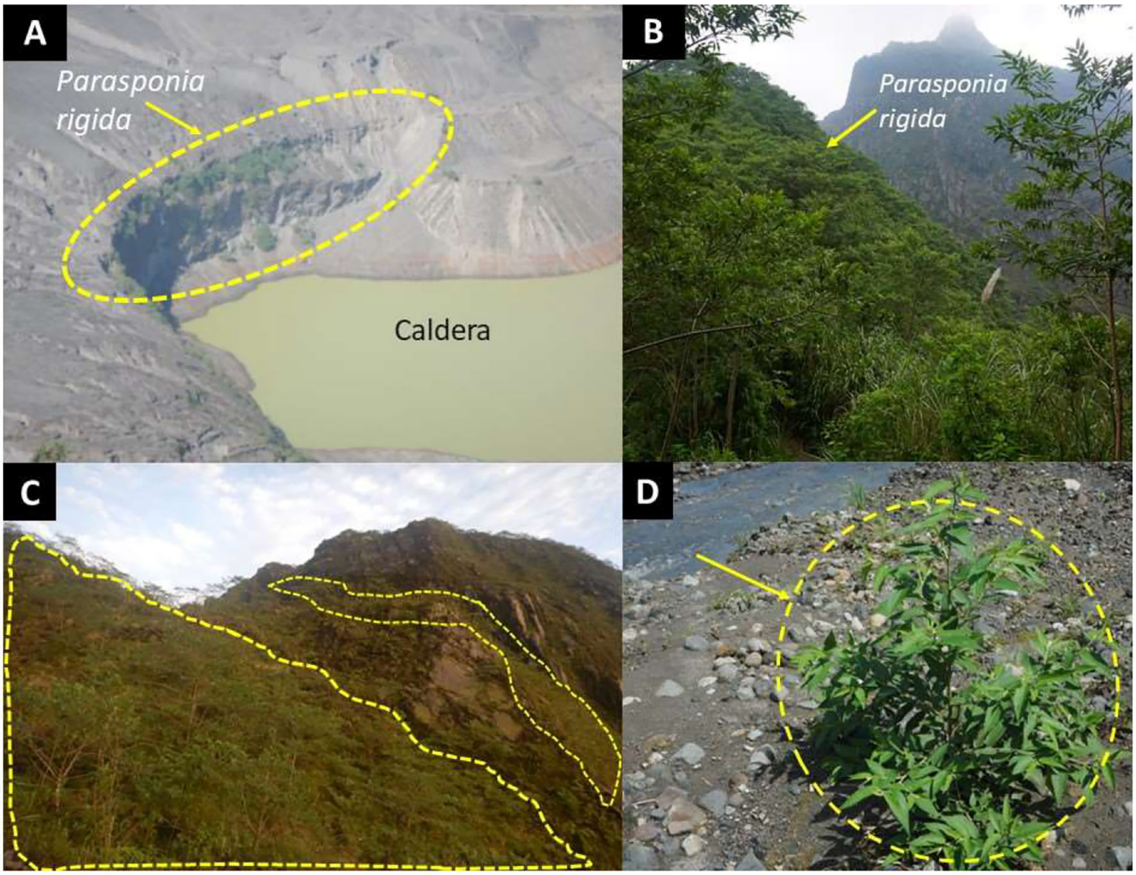

FIGURE 3 | *P. rigida* (dashed yellow lines) stands at various landscape locations: **(A)** Caldera, **(B,C)** high ridges, **(D)** Ash deposits in a river valley (Photo credits: first author).

TABLE 2 | Tree biomass and necromass differentiated by stem diameter in stands in three landscape positions (based on three replicates in each of three elevational zones).

Landscape position	Basal area	Tree biomass (Mg ha^{-1})		Tree necromass (Mg ha^{-1})	
	(m^2 ha^{-1})	5<D<30 cm	D >30 cm	5<D<30 cm	D >30 cm
Upper	8.93 a	13.41 c	60.77 a	13.49 a	12.04 b
Middle	8.21 a	7.74 b	58.71 a	13.44 a	3.56 ab
Lower	37.03 b	0 a	381 b	0 a	0 a
s.e.d	3.40**	1.76**	35.2**	9.02^{NS}	0.95**

*Values followed by the same letter within a column were not statistically distinguishable; s.e.d, standard error difference, *significant difference (P < 0.05), **highly significant difference (P < 0.01), NS no significant difference.*

by *Ageratum conyzoides* (babadotan, locally called "Tropos") with INP = 177% and INP = 116%, respectively, and the pole stage by *T. orientalis* (INP = 61%). In the upper zone seedling and sapling, stages were dominated by *Begonia multangular* ("Mencok") with INP = 100% and INP = 63%, respectively, while the pole stage was dominated *P. rigida* and *T. orientalis*, both?? with INP = 226%.

Biomass Production and Root Nodule Density of *P. rigida*

Results for the second survey showed that for each of the three elevational zones, the *P. rigida* population density, as well as average stem diameter, varied with position along the local toposequence (**Figure 4**). While population density was highest (80–200 trees/ha) in the valley positions in the upper and middle elevational zone, respectively. Tree diameter was highest in the ridge. Please note that in this second survey the lower zone toposequence did not include the Mahogany plantation, but *P. rigida* numbers were relatively low while other vegetation dominated.

Plot-level biomass estimates (**Figure 5A**) show by far the highest *P. rigida* biomass (164 kg plot^{-1}) on the ridges in the upper zone. The relative share of *P. rigida* and *T. orientalis* in their combined tree population showed that *T. orientalis* was absent at the highest elevation and dominated at the middle elevation (**Figure 5B**).

Soil samples of the rhizosphere soil in existing *P. rigida* stands (**Table 4**) showed domination by the sand-sized fraction (fresh ash), with silt and clay at slope and ridge positions in the middle

TABLE 3 | Tree populations in various growth stages and biodiversity indices in three landscape positions (based on three replicates in each of three elevational zones).

Landscape position	Population	Diversity Index (H')				Evenness Index (E)			
	(Indiv.ha^{-1})	Seedling	Sapling	Pole	Tree	Seedling	SapLing	Pole	Tree
Upper	114 a	0.68 a	1.18 b	0.87 b	1.30 b	0.67 a	0.63 b	0.60 b	0.66 ab
Middle	119 a	0.97 a	1.58 b	1.64 c	2.36 c	0.65 a	0.72 b	0.80 c	0.95 b
Lower	394 b	0 a	0 a	0 a	0.19 a	0 a	0 a	0 a	0.27 a
s.e.d	39.6**	0.44^{NS}	0.45*	0.17**	0.39*	0.28^{NS}	0.19*	0.07**	0.22*

*Seedling: $H < 2$ m, Sapling: $H > 2$m, $D < 5$ cm, Pole: $5 < D < 10$ cm, Tree: $D > 10$ cm, with D = stem diameter and H = height; values followed by the same letter within a column were not statistically distinguishable; s.e.d, standard error difference, *significant difference ($P < 0.05$), **highly significant difference ($P < 0.01$), NS, no significant difference.*

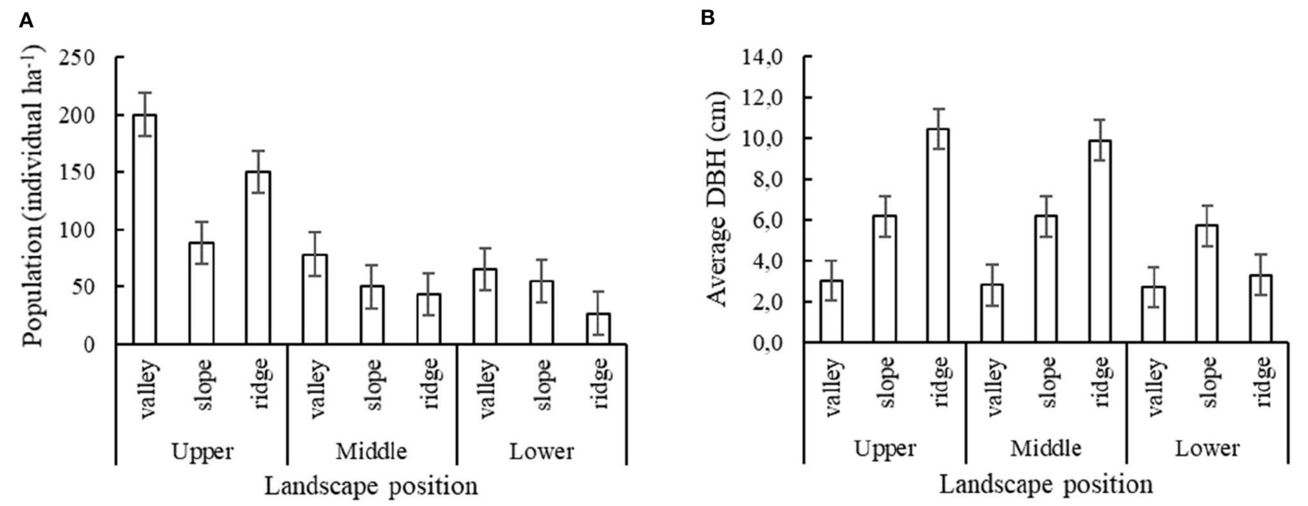

FIGURE 4 | *P. rigida* performance in various toposequence and elevational positions on the slopes of Mount Kelud (three sample plots per elevation * landscape position). **(A)** Total population of *P. rigida* with standard error of differences, **(B)** Average stem diameter (DBH).

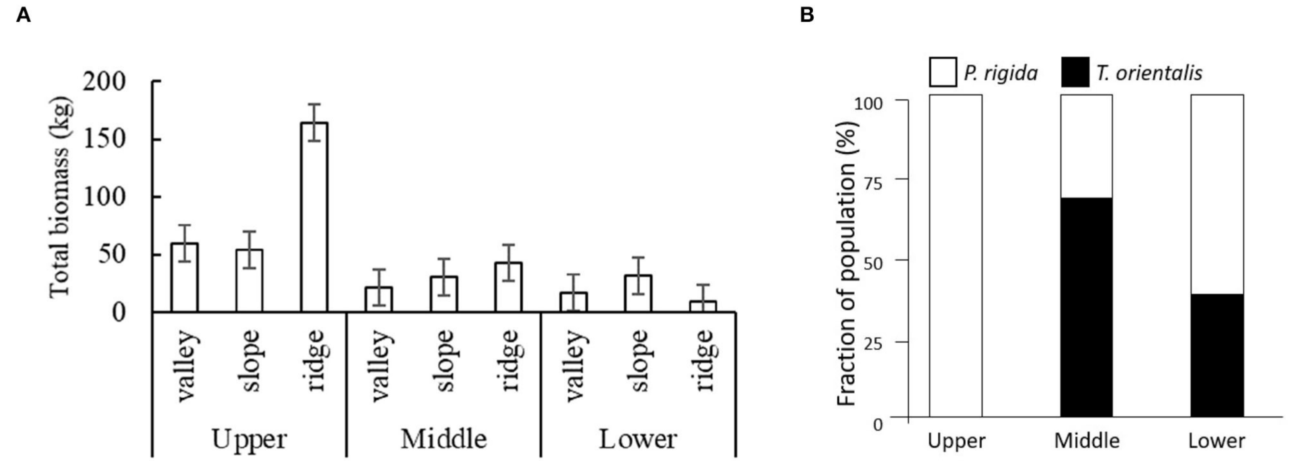

FIGURE 5 | (A) Total biomass production of *P. rigida* (per 20 × 20 m^2 plot) in the various landscape positions and elevation zones, with standard error of differences; **(B)** relative share of *P. rigida* and *T. orientalis* in their combined tree population.

and lower zone. Bulk density was high (1.2 g cm^{-3} to 1.6 g cm^{-3}, N_{tot} (0.012–0.040%), and C_{org} (0.13 to 0.26%) concentrations very low in all stands.

Based on the hemoglobin color assessment 79–93% of nodules were classified as "effective," while nodule densities per m^2 of soil surface were highest in the valley positions at low and

TABLE 4 | Characteristics of soil physico-chemical properties in the *P. rigida* rhizosphere (three replicates).

Elevation	Position	Bulk density	pH H_2O	Texture			N-Tot	C-Org	C/N
		g cm^{-3}		%Sand	%Silt	%Clay	———%———		
Upper	Valley	1.6	5.1	95	5	0	0.029	0.15	5
	Slope	1.28	5.6	93	6	1	0.023	0.18	8
	Ridge	1.32	5.1	94	4	2	0.021	0.13	6
Middle	Valley	1.55	5.2	93	5	2	0.018	0.14	8
	Slope	1.41	5.4	87	10	3	0.023	0.21	9
	Ridge	1.45	5.1	75	20	5	0.030	0.25	8
Lower	Valley	1.32	5.0	90	10	0	0.012	0.16	13
	Slope	1.2	5.3	85	10	5	0.027	0.19	7
	Ridge	1.35	5.2	65	25	10	0.040	0.23	6

TABLE 5 | Root nodules of *P. rigida* in various locations, distinguished by effectiveness (hemoglobin color) (averages for three replicates).

Elevation	Position	Root nodules, m^{-2}			Effectiveness
		Effective	Non-effective	Total	%
Upper	Ridge	472 d	61 e	533 e	89
	Slope	348 c	50 d	398 d	87
	Valley	127 a	34 bc	161 b	79
Middle	Ridge	348 c	48 d	396 d	88
	Slope	364 c	32 ab	396 d	92
	Valley	526 e	62 e	588 f	89
Lower	Ridge	112 a	22 a	134 a	84
	Slope	314 b	44 cd	358 c	88
	Valley	610 f	44 cd	654 g	93
s.e.d.		8.71**	4.72*	8.93**	-

*Values followed by the same letter within a column were not statistically distinguishable; s.e.d., standard error difference, *significant difference ($P < 0.05$), **highly significant difference ($P < 0.01$).*

middle zone, and in the ridge position in the upper zone (**Table 5**).

Regression analysis of nodules on the three indicators of soil nitrogen supply in *P. rigida* stands, N_{tot}, mineral NO_3^- and NH_4^+, was based on normalized parameters to allow direct comparison between these indicators. The regression of the density of effective nodules on soil nitrogen indicators accounted for at least 85% of the observed variation (**Figure 6**). Nodulation was most abundant and effective on the poorest sites.

DISCUSSION

We found *P. rigida* populations over a considerable elevational range, from 600 to 1,700 m a.s.l., on around Mount Kelud after the recent eruption. A comparison of satellite imagery before (2013) and after (2014) the eruption (Nuzulah, 2016) indicated a decrease in vegetation density up to a radius of 10 km from the caldera, with a vegetation density index decreasing from 0.64 to 0.34 in 2013 to 0.52–0.01 in 2014; despite a partial recovery in 2016, vegetation was affected until a radius of 5 km. The observations of dominance by *P. rigida* in the highest zone (>1,000 m a.s.l.) demonstrate the remarkable adaptation of this species to the extreme environment of frequently erupting volcanoes and abundant ash deposition. Similar observations in 2018 in about 2 km from the active crater of Mount Merapi (Central Java) after an eruption in 2010 showed low levels of plant diversity, but *P. rigida* was observed in dense monospecific stands with some patches of *Acacia decurrens* (Dr. Subekti Rahayu, *pers. comm.* 2020). According to local informants on Mount Merapi *P. rigida* only occurred on the ridge and along riverbanks before the recent eruption, but it spread out throughout the landscape after the eruption. The literature on the vegetation of Mount Kelud in the past and the high frequency of eruptions match an interpretation that the species combines the effective colonization of *T. orientalis* (Mangopang, 2016) a pantropical pioneer species with the ability to thrive on soils of very low nitrogen content. The distribution of *P. rigida* observed suggests that its seeds may be carried by overland and river flows from trees on higher ridges, including the slopes of the caldera itself. *P. rigida* appeared to develop well in nutrient-poor and open soil conditions where the plants produce root nodules and the fresh green of leaves (**Figure 3**).

Our observations suggest that the stands on ridges in the highest zone (with populations of around 150 trees ha^{-1}) had the highest biomass and were the likely seed source for abundant regeneration in the valley positions at the middle and lower elevation. Seeds can be produced within 1 year of a regrowing stand. The trees also contribute to soil formation, with a half-life time of litter of around 20 weeks (Ishaq et al., 2020). The sibling species *T. orientalis* and *P. rigida* co-occurred at lower and middle elevation, while only *P. rigida* was found in the highest zone. These findings suggest that the selective advantage of the nodulated *P. rigida* over its non-nodulated sibling species *T. orientalis* is most pronounced in the most extreme and N-poor parts of the landscape. In the lusher vegetation at lower elevations, *T. orientalis* can maintain a presence among grasses and other trees, *P. rigida* is abundant as a pioneer on the ash deposits in the valley but appears to lose out from other vegetation later in the succession. From the absence, at this stage of the recovery after the most recent eruption, of *T. orientalis* in the highest zone we cannot distinguish between lack of seed sources or lack of ability to grow as direct explanation, while *P. rigida* clearly meets both requirements for restoration success. Successful seed sources that can reach the rest of the landscape, however, do depend on the ability of pioneer plants to grow in the relatively harsh and nitrogen-poor soil conditions. The reduced role of *P. rigida* beyond the pioneer zone may suggest that the ability of *Parasponia* species to nodulate has had negative consequences, relative to their *Trema* siblings, for competitiveness under less extreme soil conditions. From these observations, it appears that explanations of the distributions of P. rigida and T. on the slopes of Mount Kelud will consist of the position of seed sources that survive the eruption, supported by the successful colonization of N-poor substrates by *P. rigida*. In more sheltered and N-rich landscape positions, *T. orientalis*

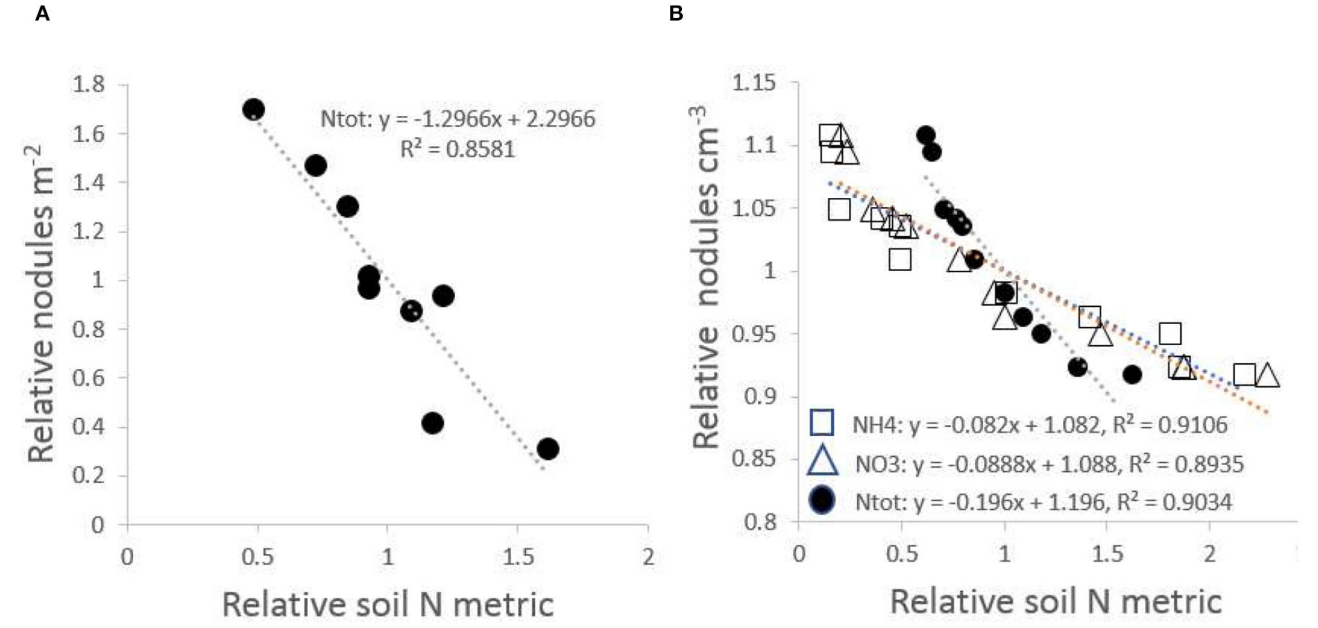

FIGURE 6 | Relationship of effective root nodules with total N-content of the soil, with both X and Y variates normalized and expressed relative to the mean; **(A)** nodules per unit soil area vs. N_{tot}; **(B)** nodules per unit soil volume vs. N_{tot}, nitrate and ammonium levels in soil solution.

appears to have an edge in growth rates—but a direct test of competitive ability across levels of soil N availability has yet to be performed. Styger et al. (2009) reported from secondary forest regeneration sites in Madagascar that 3-years old *T. orientalis* had a biomass of 8.5 Mg ha^{-1} and 5-years old stands 24.7 Mg ha^{-1}. These biomass data, in a less extreme environment, are higher than what *T. orientalis* and *P. rigida* achieved on Mt Kelud, but effective soil cover was achieved and ash deposits along the riverbed were stabilized by *P. rigida* seedlings.

Our findings of a negative response of nodule formation to external nitrogen supply in the field match the laboratory results reported recently by Dupin et al. (2020). The density of effective nodules per unit soil surface area was associated with below-average soil nitrogen indicators, with rhizobium populations in the nodules (153×10^4 to 112×10^6 CFU g^{-1}) up to a 100-fold increase above their concentrations in rhizosphere soil (average 82×10^4 CFU g^{-1}). For comparison, Widawati (2015) reported a rhizobium density in the legume kaliandra (*Calliandra tetragona)* nodules of 2.2×10^6 CFU g^{-1}.

Current emergency management plans for active volcanoes like Mount Kelud rely on nursery-produced legume trees as planting material to stabilize ash and reduce downstream mudflow risks. Three years after the eruption of Mount Kelud other surveys in the restoration area (Tanjungsari et al., 2018) found the introduced legume tree *Calliandra* [both the red (*C. tetragona calothyrsus*) and white (*C. tetragona*) species to have been planted, along with naturally dispersed mahang (*Macaranga hispida*), and anggrung (*T. orientalis*)]. Relative to such plans and practice, our findings of a key role for *P. rigida* stands on the ridges at high elevation are highly relevant. These trees can recover rapidly after an eruption and probably are the main seed source for successful natural regeneration of tree-based vegetation in the post-eruption landscape. *P. rigida* is not only a very interesting biological object of study, suggesting the conditions under which association between higher plants and rhizobium bacteria can evolve, it also deserves a key role in emergency preparedness plans for the area. Some investment in securing local *P. rigida* seed sources for assisted seed rains could likely speed up the recovery process in next steps of the eruption cycle.

CONCLUSIONS

1. *P. rigida* populations survived the recent eruption of Mount Kelud at an elevation of 600–1,700 m a.s.l. The sibling species *T. orientalis* and *P. rigida* (differing in their ability to nodulate) co-occurred at lower and middle elevation, while only *P. rigida* was found in the highest zone.
2. The rate of biomass recovery was related to landscape position: Stands on ridges in the highest zone (around 150 trees ha^{-1}) had the highest biomass and were the likely seed source for abundant regeneration in the valley positions at middle and lower elevation.
3. The density of effective nodules per unit soil surface area was associated with below-average soil nitrogen indicators.
4. A practical implication of these findings is that existing *P. rigida* stands on the ridges at high elevation are key to the successful natural regeneration of tree-based vegetation in the

post-eruption landscape and deserve protection and a key role in emergency preparedness plans for the area.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

The field and laboratory research was carried out by RM and IA as part of their Master of Science program at Brawijaya University, under direct supervision of KH. RM and IA collected and analyzed the data. RM, KH, and MN designed the research and drafted the manuscript, for which all authors agree to be accountable for the content of the work. All authors contributed to the article and approved the submitted version.

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Biophysical and Socioeconomic Factors Associated to Deforestation and Forest Recovery in Brazilian Tropical Dry Forests

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The determination of land cover changes (LCCs) and their association to biophysical and socioeconomic factors is vital to support government policies toward the sustainable use of natural resources. The present study aimed to quantify deforestation, forest recovery and net cover change in tropical dry forests (TDFs) in Brazil from 2007 to 2016, and investigate how they are associated to biophysical and socioeconomic factors. We also assessed the effects of LCC variables in human welfare indicators. For this purpose, we used MODIS imagery to calculate TDF gross loss (deforestation), gross gain (forest recovery) and net cover change (the balance between deforestation and forest recovery) for 294 counties in three Brazilian states (Minas Gerais, Bahia, and Piauí). We obtained seven factors potentially associated to LCC at the county level: total county area, road density, humidity index, slope, elevation, and % change in human population and in cattle density. From 2007 to 2016, TDF cover increased from 76,693 to 80,964 km^2 (+5.6%). This positive net change resulted from a remarkable forest recovery of 19,018 km^2 (24.8%), offsetting a large deforested area (14,748 km^2; 19.2%). Practically all these cover changes were a consequence of transitions from TDF to pastures and vice-versa, highlighting the importance of developing sustainable policies for cattle raising in TDF regions. Each LCC variable was associated to different set of factors, but two biophysical variables were significantly associated both to TDF area gained and lost per county: county area (positively) and slope (negatively), indicating that large and flat counties have very dynamic LCCs. The TDF net area change was only associated (negatively) to the humidity index, reflecting an increase in TDF cover in more arid counties. The net increase in Brazilian TDF area is likely a result from an interplay of biophysical and socioeconomic factors that reduced deforestation and caused pasture abandonment. Although the ecological integrity and permanence of secondary TDFs need further investigation, the recovery of this semi-arid ecosystem must be valued and accounted for in the national forest restoration programs, as it would significantly help achieving the goals established in the Bonn agreement and the Atlantic Rain Forest pact.

Keywords: restoration, conservation strategies, land use and cover changes, human welfare, natural regeneration

INTRODUCTION

The detection of land cover change (LCC) and its causes is fundamental to the formulation of public policies aiming at reducing the loss of biodiversity and ecosystem services, especially in highly threatened tropical regions. The typical land use cycle in the tropics starts with deforestation of mature or secondary forests, frequently with the use of fire, to the establishment of pastures or croplands (Thomaz, 2013; Mesquita et al., 2015; Barlow et al., 2020; Schmidt and Eloy, 2020). Indeed, livestock raising and agriculture are the most important drivers of land cover change in Latin America (Armenteras et al., 2017; Curtis et al., 2018; Bonilla-Moheno and Aide, 2020). The extent and consequences of such process are well-illustrated by the recent and drastic increase in fires and deforestation in Brazil, especially in the Amazon (Barlow et al., 2020; Escobar, 2020).

Usually, tropical agricultural lands are managed using fertilizers, pesticides, and fire [Barona et al., 2010; Organization for Economic Co-operation Development (OECD), 2018], frequently causing soil exhaustion (Sousa et al., 2012; Rocha-Júnior et al., 2017) followed by land abandonment (Lawrence et al., 2010; Thomaz, 2013; Mesquita et al., 2015). Very degraded soils in tropical regions are generally less suitable to plant recolonization (Jakovac et al., 2016; Rezende and Vieira, 2019), which can cause desertification especially in semi-arid regions (Sousa et al., 2012; Marengo and Bernasconi, 2015; Queiroz et al., 2020). However, natural regeneration is somewhat frequent, but its speed and pathways depend on several factors, such as landscape configuration (e.g., distance to forested areas, amount of forest cover) that affect the sources of plant colonizers (Jakovac et al., 2015; Rozendaal et al., 2019), and previous land use practices that determine soil biotic and abiotic conditions for seed germination and plant growth (Jakovac et al., 2015, 2016; Rezende and Vieira, 2019).

In recent years, the importance of forest recovery and secondary forests to biodiversity conservation has received increased attention (Wright and Muller-Landau, 2006; Lugo, 2009; Poorter et al., 2016). Usually, forest recovery through natural regeneration is more cost-effective than active restoration through tree planting, especially at the regional and national scales (Catterall and Harrison, 2006; Nunes et al., 2017; Crouzeilles et al., 2020). A recent global meta-analysis also indicated that, in tropical regions, natural regeneration is more successful to restore biodiversity and vegetation structure than active restoration when abiotic and biotic factors are controlled (Crouzeilles et al., 2017). However, the effectiveness of natural regeneration can be hindered in isolated, dry and/or highly degraded regions, where active restoration is considered more adequate (Holl and Aide, 2011; Crouzeilles et al., 2017)

In order to develop policies to stimulate large-scale restoration initiatives, it is necessary to determine the spatial occurrence of both deforestation and forest recovery, as well as their association to biophysical and socioeconomic factors. It is also important to assess the effects of LCC on human welfare, because agricultural sectors in tropical countries claim that deforestation is necessary for increasing employment and income (frequently based on Kuznets environmental curves) (Bhattarai and Hammig, 2004; Espírito-Santo et al., 2016; Santiago and Couto, 2020). On the other hand, environmental agencies and researchers indicate that decreasing natural vegetation cover inevitably erode ecosystems services that support human well-being (IPBES, 2019). In many cases, forest recovery occurs after land abandonment in private properties for economic reasons, including decreasing demand for commodities (e.g., beef, soybean, palm oil), change in technology, urbanization and rural exodus, among others (Rey-Benayas et al., 2007; Lambin and Meyfroidt, 2010; Espírito-Santo et al., 2016; Stan and Sanchez-Azofeifa, 2019). However, the frequency of land abandonment is influenced by biophysical characteristics that affect productivity, such as terrain slope, soil fertility, and climate (Díaz et al., 2011; Aide et al., 2013; Xie et al., 2020). Local and regional socioeconomic factors are also important, including access to bank loans, government subsidies, distance to consuming markets and transport infrastructure, among others (Laue and Arima, 2016; Trigueiro et al., 2020).

High deforestation and degradation rates were observed for TDFs in the Americas (Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010; Grinand et al., 2013; Rudel, 2017; Dupin et al., 2018), a situation that is worsened in Brazil by the neglection of these ecosystems in terms of research and conservation efforts, especially when compared to tropical wet forests (Sánchez-Azofeifa et al., 2005; Santos et al., 2011; Blackie et al., 2014). The present study aimed to estimate the extent of LCC (with focus on forest recovery, deforestation and net forest cover change) in Brazilian TDFs during 10 years (from 2007 to 2016). Based on previous studies at different scales (Aide et al., 2013; Beuchle et al., 2015; Dupin et al., 2018), we predict that TDF recovery is extremely important to offset the huge deforestation rates observed in this ecosystem. Furthermore, we hypothesize that deforestation and forest recovery (and also the balance between them), which are motivated by distinct reasons, are associated to different biophysical and socioeconomic factors. For these purposes, we mapped an area of 917,768 km^2 in the states of Minas Gerais, Bahia and Piauí, where most TDFs are concentrated (143,813 km^2, 52.5%), using counties as analytical units. We expect that deforestation will be higher in large, flat, and humid counties with high density of roads, human population, and cattle herd. Regeneration will also be higher in large, flat, and humid counties, but negatively associated to the density of roads, human population, and cattle herd. Finally, we hypothesize that human welfare indicators are associated with LCC. In this case, we predict that counties with high deforestation from 2007 to 2016 will exhibit an increase in inequality and a decrease in gross domestic product and human development index.

MATERIALS AND METHODS

Study Region

In this study, we use the tropical dry forest definition of the Brazilian Institute for Geography and Statistics (IBGE), which is based on vegetation structure and phenology [Instituto Brasileiro de Geografia e Estatística (IBGE), 2012]. As such, TDFs are considered to have four strata (herbs, shrubs, treelets, and trees), with dominance of trees with 20–30 m in height, and are composed by deciduous plants that lose more than 50% of their leaves during the dry season. This definition is also concurrent with those of Murphy and Lugo (1986) and Sánchez-Azofeifa et al. (2005). According to this *stricto sensu* definition, Brazilian TDFs cover ca. 273,678 km^2, and do not include most of the Caatinga biome which does not have a forest structure [**Figure 1**; Instituto Brasileiro de Geografia e Estatística (IBGE), 2012].

Since 1993 TDFs are considered "associated ecosystems" to the Brazilian Atlantic Rain Forest (Federal Decree 750), due to their floristic similarity with coastal forests. In 2006, such status was ratified by the so-called Atlantic Rain Forest Law (Federal Law 11428), and a map with the distribution of legally protected TDFs (218,662 km^2) was published (Federal Decree 6660) (Espírito-Santo et al., 2011; Muylaert et al., 2018), which we used in the present study (**Figure 1**). Thus, most TDFs are fully protected under the umbrella of the Atlantic Rain Forest, with much stronger restrictions on land clearing (only permitted for early successional stages or in cases of public utility or social interest) (Dupin et al., 2018). TDFs are distributed along three Brazilian biomes that cover the study region: Atlantic Rain Forest (18.3%), composed by coastal ecosystems ranging from mangroves to evergreen, tall closed-canopy forests; Caatinga, a semi-arid woodland composed mostly of thorny and deciduous plants (39.9%); and Cerrado, a savannic ecosystem characterized by a grass layer and fire-adapted shrubs and trees (41.8%). These states are composed by 10 meso-regions encompassing 619 counties, with a total population of 18 million inhabitants [Instituto Brasileiro de Geografia e Estatística (IBGE), 2016].

Image Acquisition, Processing, and Classification

To determine the land cover changes in the study region, we obtained MODIS (Moderate Resolution Imaging Spectroradiometer, MOD13Q1) visible and infrared reflectance data at 250 m spatial resolution from January to December of 2007 and 2016. The select time frame refers to 10 years after the Atlantic Rain Forest law took effect (December 2006). Four MODIS tiles encompassing the whole study region were integrated to compose a single Raster product, a procedure that was repeated for each month for 2007 and 2016, coming to 24 mosaics (**Supplementary Table 1**). As an initial standardization process, these mosaics were reprojected from sinusoidal projection to 1984 World Geodetic System—WGS/World Mercator using the MODIS Reprojection Tool (available from http://lpdaac.usgs.gov/; Justice et al., 2002) and resampled to 250 m original spatial resolution (minimum mapping unit of 6.25 ha). In order to reduce the number of products applied in the classification scheme, monthly datasets were converted into seasonal averages. This step was fundamental for determining the periods in which the vegetation classes mainly recorded the best seasonal contrast. By such criterion, the summer (December–March) and winter (July–September) seasonal averages were employed to derive the majority of inputs used in the Decision Tree (see below).

We defined eight land cover classes: TDFs, other native vegetation types, urban areas, water, croplands, pastures/bare soil, burned areas, and ecotones (a transitional native vegetation type). Given the large extent of the study region and the fact that many of the land cover classes exhibited spatial variations in spectral responses, we decided to compartmentalize the study region into 10 control sub-regions based on spectral (red and near-infrared bands) and topographic criteria (Carvalho et al., 2006), in order to cope with the spatial-spectral variability inside the Decision Tree. For the specific purpose of region compartmentalization, we derived slope and elevation using the Digital Elevation Model—DEM from Shuttle Radar Topographic Mission—SRTM (1:250,000 scale).

We used the Decision Tree as the supervised classification method, in which a varied number of inputs can be employed to assign each pixel to the most adequate class through binary decisions (ENVI, 2004; Otukei and Blaschke, 2010). We assessed pixel changes from 2007 to 2016 to describe the large-scale patterns investigated at the county level. The red and near-infrared bands of the winter and summer mosaics were used in the classification, as well as the following derived vegetation indices: Normalized Difference Vegetation Index—NDVI (Rouse et al., 1973), Soil-Adjusted Vegetation Index—SAVI (Huete, 1988), and Normalized Difference Built-up Index—NDBI (Zha et al., 2003). The final classification was improved by visually checking confusing areas with digitized ground control points for all land cover types obtained from medium to high spatial resolution imagery (Landsat TM, OLI, and Google Earth products). Finally, we performed a ground-truth validation during March 2017 by visiting 23 different areas in the study region where classification was difficult. To assess the accuracy of our classification, we constructed an Error Matrix (Congalton and Green, 2008) comparing our validation points with our land cover map, which was used for the calculation of general (Overall Accuracy and Kappa Coefficient) and individual (User's Accuracy) validation metrics. Image processing and classification were conducted with ArcGIS 10.2.1, ENVI 5.3 and Google Earth 7.1.5.

Factors Associated With LCC

In the present study, forest recovery was considered as both unassisted and assisted natural regeneration (i.e., secondary succession) and active restoration (i.e., full planting of native species) of TDFs in areas without this land cover class in a previous period. Thus, it represents gross gains in TDF cover during the studied period, henceforth "TDF area gained." We considered deforestation as the change in land cover from the class "TDF" to all other classes, except other types of natural vegetation, including ecotones. In this sense, it indicated losses in TDF cover (henceforth "TDF area lost"). We did not consider forestry areas (plantations of exotic species such as *Eucalyptus* and *Pinus*) as forest recovery. These areas were included in the "croplands" class during the classification process, meaning that conversion of TDFs to forestry was computed as deforestation. Finally, we calculated the TDF net area change as the balance between deforestation (gross loss in area) and forest recovery (gross gain in area). Because of the large scale of the analysis and the resolution of MODIS imagery, we did not assess the ecological integrity of the mapped TDFs.

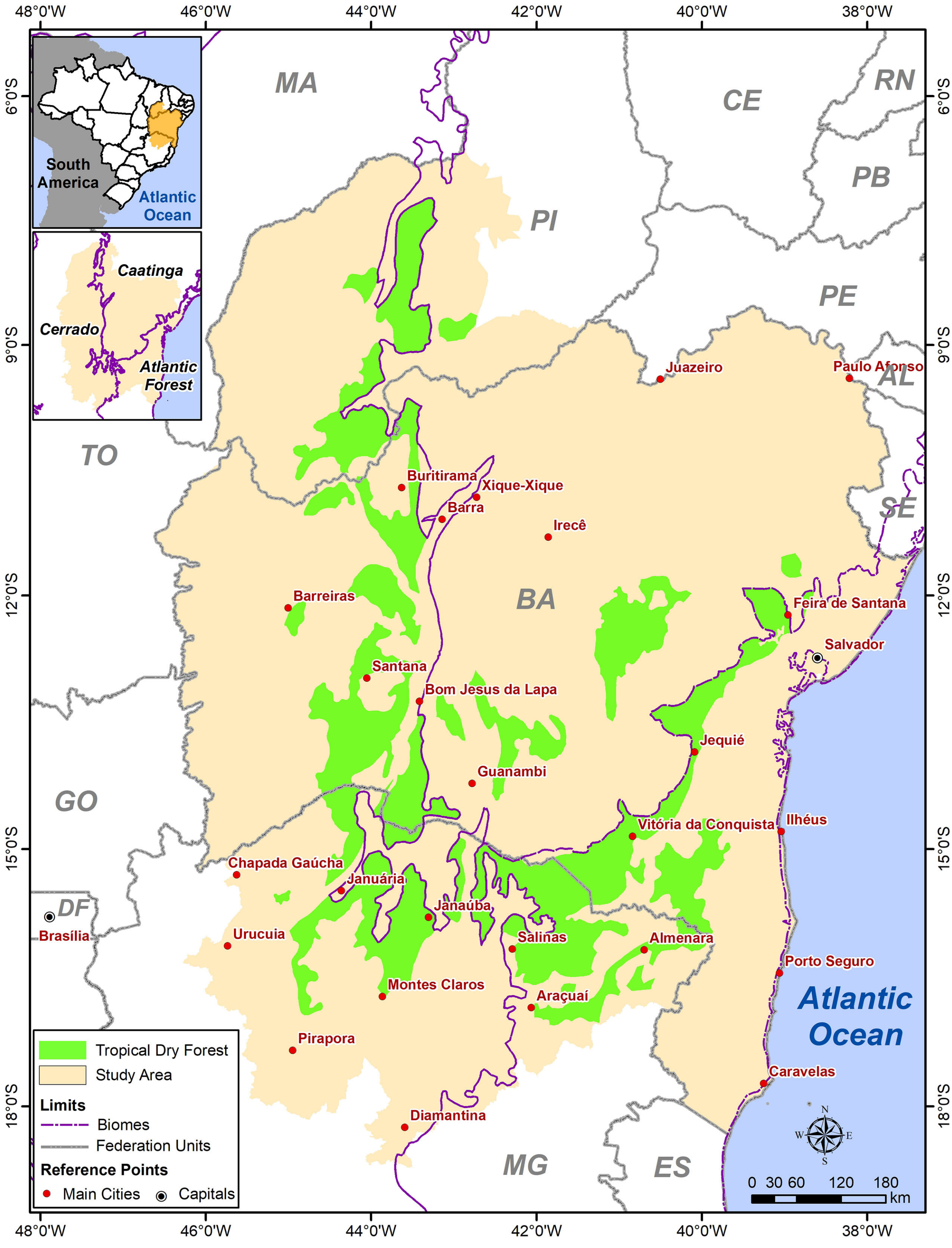

FIGURE 1 | Distribution of tropical dry forests (TDFs) in the northeastern region of Brazil, as legally defined by the Brazilian Institute of Geography and Statistics (IBGE, Federal Decree 6660/2008) to the enforcement of the Atlantic Rain Forest law (see text for further details). Lines represent state (gray) and meso-region (black) limits.

Using a map of the Brazil's administrative regions [Instituto Brasileiro de Geografia e Estatística (IBGE), 2010a] and the SRTM, we obtained the following variables per county: total area (km^2), average slope (%) and average elevation a.s.l. (m). We also calculated the road density (m/m^2) using the IBGE's transport system database [Instituto Brasileiro de Geografia e Estatística (IBGE), 2010b], and the humidity index using the IBGE's climatic map [Instituto Brasileiro de Geografia e Estatística (IBGE), 2002]. IBGE defined nine climate classes based on the number of dry months per year, ranging from semi-arid (-100) to super-humid ($+100$) (**Supplementary Table 2**). When the county area contained more than one climate class, we calculated a weighted average humidity index, considering the proportion of the county covered by each climate class. Socioeconomic parameters for each county were acquired from two different databases (demographic and agricultural) from IBGE's censuses. We used demographic censuses from 2000 and 2010 [Instituto Brasileiro de Geografia e Estatística (IBGE), 2010c] to obtain population density (individuals/km^2). Finally, we used agricultural censuses from the IBGE to obtain the cattle herd density (heads per km^2) per county in 2006 and 2016 [Instituto Brasileiro de Geografia e Estatística (IBGE), 2017b]. These variables were selected because they were considered as important drivers of LCC in previous studies that used counties as analytical units (e.g., Aide et al., 2013; Espírito-Santo et al., 2016; Dupin et al., 2018; Trigueiro et al., 2020).

Welfare Indicators

We used demographic censuses from 2000 and 2010 [Instituto Brasileiro de Geografia e Estatística (IBGE), 2010c] to obtain the Gini Inequality Index. We also generated the disaggregated version of the Human Development Index (HDI-I) that considers only income [Programa das Nações Unidas para o Desenvolvimento (PNUD), 2015], as it reflects more directly the economic gains from the conversion of the TDFs at the county level (Espírito-Santo et al., 2016). The Gross Domestic Product (GDP in Brazilian reais; standardized for the year 2010) was extracted from the IBGE databases for 2006 and 2017 [Instituto Brasileiro de Geografia e Estatística (IBGE), 2017a].

Statistical Analyses

Temporal Variations

LCC was assessed by calculating the total TDF area lost (deforestation) and gained (forest recovery), and the TDF net area change per county between 2007 and 2016 (three response variables). We included seven explanatory variables as potential factors associated with LCC: total county area, average slope, average elevation, road density, humidity index, and percentage variation in population and cattle density. To evaluate whether the LCC variables and their associated factors (except for county area, average slope, average elevation, and humidity index) differ between 2007 and 2016, paired t-tests based on permutations were used because the samples were temporally dependent. The spatial autocorrelation (SAC) was estimated using spatial filters (MEMs, Moran's eigenvector maps; Dray et al., 2006) that were selected progressively (Blanchet et al., 2008). For these analyses, we followed the R code proposed by Eisenlohr (2014). The same analyses were conducted for human welfare indicators (Gini Index, GDP, and HDI-I).

Factors Associated With LCC

We used multiple linear regressions through generalized linear models (GLMs) to test the effects of the seven factors on the three LCC response variables. We built three complete GLM models with Gaussian error distribution, and the models for TDF area gained and lost were additionally adjusted for a log-link function (Crawley, 2012). The variance inflation factor (VIF) was used as measure of multicollinearity. We verified that there was no collinearity between the predictor variables (variance inflation factor <10; Quinn and Keough, 2002), which were all maintained in the complete models. The models were adjusted for orthogonal partitioning of variance (type III sum of squares), to verify the proportion of variance attributed to each explanatory variable regardless of their sequential order in the models (Crawley, 2012). None of the variables (either response or explanatory) was scaled for these analyses.

We tested our models for SAC of the residuals through minimal adequate GLMs using correlograms, with Moran's I coefficient as an indicator of SAC (obtained by package "pgirmess" in the R software; R Development Core Team, 2020). The minimal adequate models were submitted to residual analyses to verify the adequacy of the error distribution. The significance of SAC in the residuals was detected by the sequential Bonferroni criteria (Fortin and Dale, 2005). We found SAC in all the minimal adequate GLMs. To address SAC, we obtained spatial filters (MEMs; Dray et al., 2006) using the "adespatial" and "spacemakeR" packages in the R software. We performed a forward selection of spatial filters, following the double stopping and R^2 adjusted criteria recommended by Blanchet et al. (2008). Finally, the best-fit model for each response variable was selected based on the minimum Akaike's information criterion adjusted for small sampled size (AICc) (Burnham and Anderson, 2002), using the function "dredge" in the package MuMin (R Development Core Team, 2020). We compared 2^{31} competing models for each LCC response variable, including a null model with no explanatory variables. In these analyses, the best model has a ΔAICc value of 0, but all models with ΔAICc ≤ 2 have substantial support and may be considered equally plausible when the null model has an ΔAICc >2. However, alternative models that differ from the best model by one additional parameter with unchanging maximized log-likelihood should not be considered competitive (i.e., larger models with uninformative parameters) (Burnham and Anderson, 2002; Arnold, 2010). No significant SAC was detected for these models (see **Supplementary Tables 3**, **4**; **Supplementary Figures 1–3**). The R code used for these analyses was modified from Eisenlohr (2014) and is available at https://github.com/pedroeisenlohr/variancepartition.

LCC and Human Welfare

We evaluated the potential association of LCC variables with human welfare following the same procedure previously described for the analyses of potential factors associated with LCC. For this purpose, we calculated the percentage change per

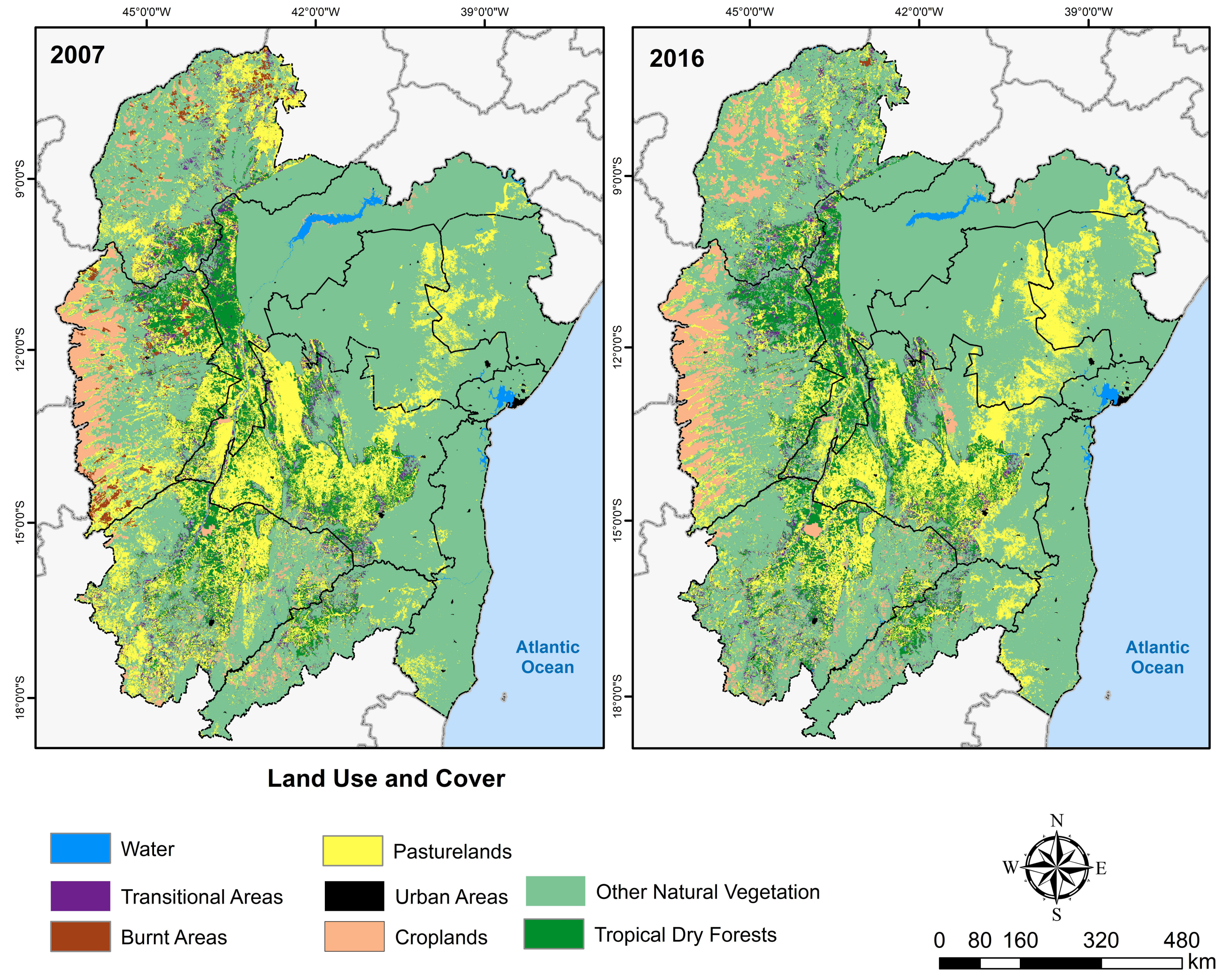

FIGURE 2 | Land cover changes in the studied region from 2007 to 2016. Forestry was included in the Cropland class. Lines represent state (gray) and meso-region (black) limits.

county in the Gini Index and HDI-I between 2000 and 2010, and in the GDP between 2006 and 2016. These parameters were inserted as response variables in separate GLMs, with three explanatory variables: TDF area gained, TDF area lost and TDF net area change per county. All three models were adjusted with a Gaussian error distribution. We tested the multicollinearity between the predictor variables and, after detecting a VIF >10, we removed TDF net area change from the complete models (Quinn and Keough, 2002). To address SAC, we obtained spatial filters (MEMs; Dray et al., 2006) using the "spatialreg" package in R, because one region has no neighbors at the 1 km threshold. This means that the general weights sum is zero for this region (see Borcard et al., 2011; Legendre and Legendre, 2012). Model selection for environmental and spatial variables and residual inspection for SAC were performed as described in the previous models, using the R code proposed by Eisenlohr (2014). No significant SAC was detected for these models (see **Supplementary Table 5**; **Supplementary Figures 4–6**).

RESULTS

Trends in Land Cover Change

The overall accuracy of the generated map was estimated to be 89.4%, with a Kappa coefficient of 86.8%. Accuracy varied among LCC classes, being 85% for tropical dry forests (**Supplementary Table 6**). We detected large changes in land cover during 10 years in the study region. From 2007 to 2016, TDF cover increased from 76,690 to 80,960 km^2 (+5.57%), which was proportionally higher than the observed for other natural vegetation types (+1.62%) (**Figure 2**; **Table 1**). This positive net change resulted from a remarkable forest recovery of 19,018 km^2 (24.8%), offsetting a large deforested area (14,748 km^2; 19.2%). Practically all these cover changes were a consequence of TDF-pasture transitions: 18,459 km^2 of pastures recovered to TDFs and 14,394 km^2 of TDFs were converted to pastures (**Table 1**). Pasturelands cover a much larger area than croplands in the region, but decreased from 200,170 to 181,580 km^2 (−9.2%)

TABLE 1 | Changes among land cover classes in the studied TDF region from 2007 to 2016.

	Land cover classes (km^2)							
2016	**2007**							
	TV	**Burned**	**Water**	**Urban**	**Croplands**	**Pastures**	**TDF**	**OVT**
TV	30,231.8	0	0	0	0	0	0	0
Burned	0	83.8	0	0	0	34.3	7.7	86.9
Water	0	0	3,895.2	32.2	1.2	159.1	18.1	320.3
Urban	0	0	11.0	1,703.8	0.4	6.3	2.03	7.9
Croplands	0	1,680.2	11.7	0.3	27,027.1	5,667.8	325.3	12,701.9
Pastures	0	2,107.5	274.4	5.7	1,908.4	113,035.1	14,393.9	49,855.3
TDF	0	468.9	36.7	2.3	48.5	14,459.2	61,942.2	2.9
OVT	0	3,763.1	1,560.0	5.3	3,966.9	62,809.3	1.8	498,939.0
Total 2007*	30,231.8	8,103.4	5,879.0	1,749.5	32,952.5	200,170.9	76,690.8	561,914.3
Total 2016**	30,231.8	212.7	4,516.0	1,731.3	47,414.2	181,580.4	80,960.6	571,045.3
Loss	0.0	−8,019.6	−1,893.8	−45.8	−5,925.4	−87,135.8	−14,748.6	−62,975.3
Gain	0.0	+128.9	+530.8	+27.5	+20,387.1	+68,545.3	+19,018.4	+72,106.3
Net change (km^2)	0.0	−7,890.7	−1,363.0	−18.3	+14,461.7	−18,590.5	+4,269.8	+9,131.0
Net change (% of 2007 area)	0	−97.3	−23.2	−1.04	+43.9	−9.23	+5.57	+1.62

**Sum of column values.*

***Sum of row values.*

TV, transitional vegetation; TDF, tropical dry forest; OVT, other vegetation types. Forestry was included in the Cropland class.

TABLE 2 | Changes in the area (km^2) of tropical dry forests per meso-region from 2007 to 2016.

Meso-region	Total area		Loss	Gain	Net change
	2007	**2016**			
Southwest of Piauí (8)	6,061.2	7,716.9	1,702.8	3,358.5	+1,655.7 (27.3%)
Far West of Bahia (3)	13,026.7	14,417	1,826.1	3,216.4	+1,390.3 (14.0%)
São Francisco Valley of Bahia (10)	15,101.3	15,737.5	2,038.5	2,674.6	+636.2 (4.2%)
Central-South of Bahia (2)	20,922.1	21,522	4,514.5	5,114.4	+599.9 (2.86%)
Jequitinhonha (4)	3,846.9	4,038.2	628.4	819.8	+191.3 (5.0%)
Central-North of Bahia (1)	252.9	277.2	29.9	54.2	+24.3 (9.6%)
North of Minas Gerais (7)	17,480	17,250.6	4,010.1	3,780.7	−229.4 (1.3%)

Meso-regions are in decreasing order of TDF area net change.

during the study period. On the other hand, croplands exhibited the greatest change from 2007 to 2016, increasing from 32,952 to 47,414 km^2 (43.9%), mostly replacing other vegetation types and pasturelands, but affecting a very limited TDF area. Although a large area of other vegetation types was converted to pasturelands (68,809 km^2; 11.2%), the relative impact of this LCC was higher for TDFs (18.9%) (**Table 1**).

TDFs were unevenly distributed across the 10 studied meso-regions. For the three coastal meso-regions (5, 6, and 9), TDF occurrence (as indicated in **Figure 1**) was very small and not detected in our mapping. TDFs were mostly concentrated in Central South and São Francisco Valley in Bahia state, and in the North of Minas Gerais state (**Figure 1**; **Table 2**). A positive TDF net area change was detected in six out of seven studied meso-regions, varying greatly from more than +1,650 km^2 (Southern Piauí state) to only +24 km^2 (Central-North Bahia state) (**Table 2**). In relative terms, the Southern Piauí state and the Center-West of Bahia exhibited the highest forest recovery, with TDF net gain of 97 and 76% higher than TDF loss. The only meso-region with net TDF loss was the north of Minas Gerais state (−229 km^2). This pattern was reflected at the state level, with Minas Gerais being the only state with a negative TDF net area change (**Supplementary Table 7**).

Factors Associated With LCC

In the whole studied region, 294 out of 619 counties presented TDFs either in 2007 or 2016. The number of counties with positive TDF net area change (196) was twice the number of counties with negative TDF net area change (98) (**Figure 3**). In average, the TDF area per county showed a slight but statistically significant increase (+0.5%) from 2007 to 2016 (**Table 3**). Temporal differences were also observed for the two potential socioeconomic factors associated with LCC: population density slightly increased and cattle density slightly decreased during the study period (**Table 3**).

Our model selection indicated 10 models with ΔAICc ≤ 2 that explain the relationship between TDF recovery (area gained) per county and its potential associated factors in the study region. Our best-fit model (i.e., with the lowest ΔAICc; **Supplementary Table 3**) showed that three biophysical factors were significantly associated to TDF recovery: county area (positively), slope (negatively), and the humidity index (negatively) (**Figure 4**). These variables reduced the AIC of the

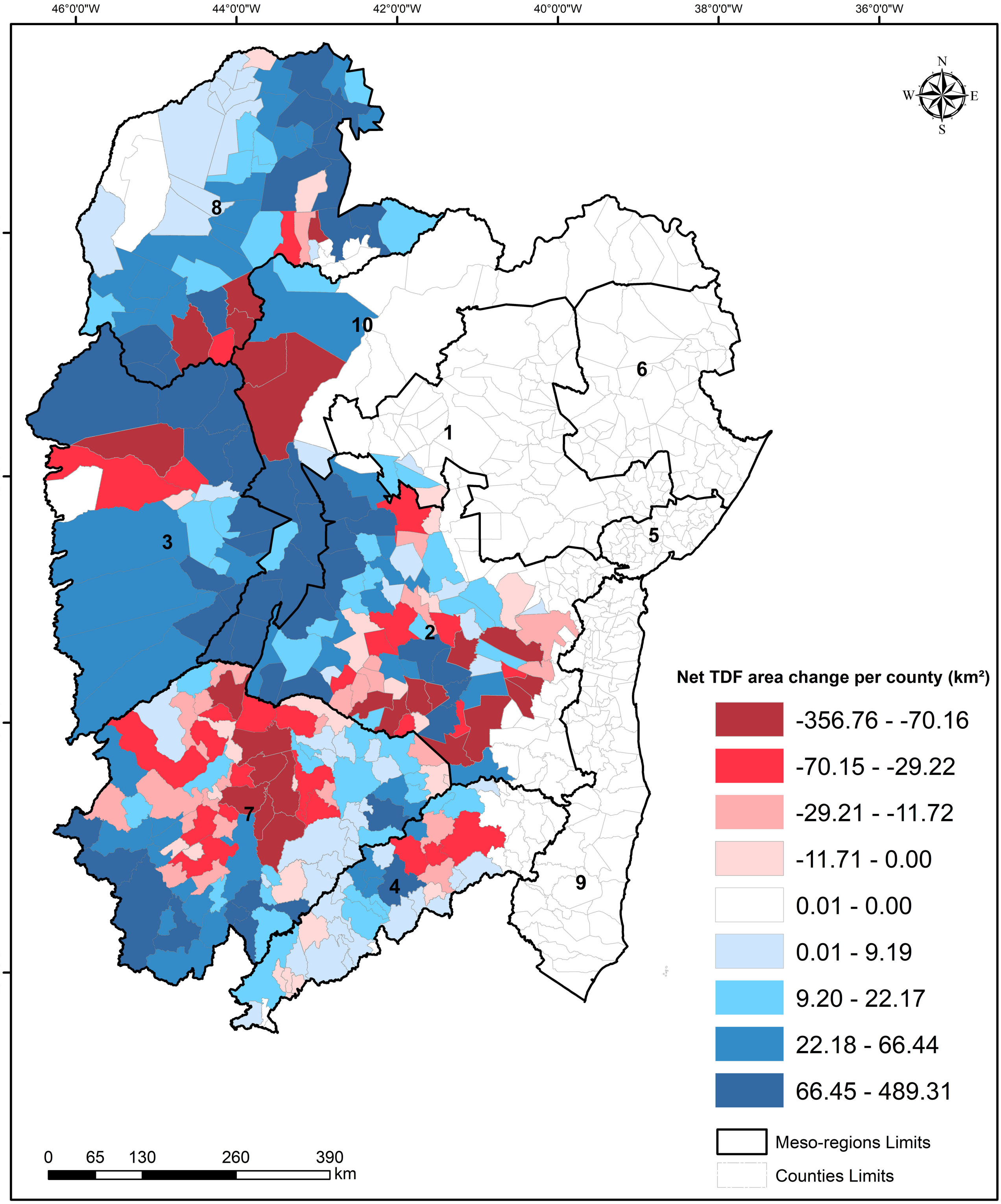

FIGURE 3 | Net change in tropical dry forest (TDF) cover along the 619 counties in each of 10 meso-regions, encompassing three Brazilian states (Minas Gerais, Bahia and Piauí). 1 = Central-North of Bahia; 2 = Central-South of Bahia; 3 = Far West of Bahia; 4 = Jequitinhonha; 5 = Metropolitan Region of Salvador; 6 = Northeast of Bahia; 7 = North of Minas Gerais; 8 = Southwest of Piauí; 9 = South of Bahia; 10 = São-Francisco Valley of Bahia. The eight classes of net change, from net deforestation in red to net regeneration in blue, were defined based on four positive and negative quartiles for the 619 counties.

TABLE 3 | Average tropical dry forest (TDF) area, factors associated with land cover change and welfare indicators for the years 2007 and 2016 per county (mean ± standard error).

Source	Year		Change (%)	Paired *T*-test	*P*
	2007	2016			
TDF area (km^2)	180.70 ± 12.95	186.72 ± 12.46	+0.5%	7.69	**<0.001**
Associated parameters					
Population density (ind/km^2)	20.94 ± 5.41	22.36 ± 6.24	+6.78%	3.13	**<0.001**
Cattle density (heads/km^2)	23.76 ± 1.82	22.19 ± 2.03	−6.61%	4.72	**<0.001**
Welfare indicators					
Gini inequality index	0.56 ± 0.01	0.51 ± 0.01	−8.92%	12.06	**<0.001**
GDP (thousands R$)	70.43 ± 5.93	168.36 ± 9.37	+139.0%	70.47	**<0.001**
IDH-I	0.51 ± 0.01	0.58 ± 0.01	+13.7%	1.17	**<0.05**

Statistically significant differences (P < 0.05) are in bold.

null model from 1116.6 to 1032.8 (**Supplementary Table 3**). The remaining models were not considered because they contained additional uninformative parameters. Thus, forest recovery was higher in flat and more arid areas. The minimal adequate model had an adjusted R^2 of 0.51, and each factor explained only a small proportion of the observed variance (**Supplementary Table 4**; **Supplementary Figure 7**). The same pattern was observed for the effects of county area and slope on deforestation (TDF area lost). In contrast, TDF loss was negatively associated to the increase in population density but not to the humidity index (**Figure 5**). In this case, only three models had ΔAICc ≤2, and the three explanatory variables of the best-fit model reduced the AIC of the null model from 1243.0 to 1205.3 (**Supplementary Table 3**). Alternative models were not considered competitive due to their lower weight. The minimal adequate model had an adjusted R^2 of 0.50 (**Supplementary Table 4**). Finally, our model selection indicated 12 models with ΔAICc ≤2 that explain TDF net area change. The best-fit model showed that this variable was associated only to the humidity index (negatively; **Figure 6**), which reduced the AIC of the null model from 3471.3 to 3462.1 (**Supplementary Table 3**). The remaining models were not considered because they contained additional uninformative parameters. The minimal adequate model had an adjusted R^2 of 0.58 (**Supplementary Table 4**).

LCC and Welfare Indicators

The human welfare indicators considered in the present study changed significantly from 2007 to 2016, reflecting improvements in socioeconomic conditions in all three states (**Table 3**; **Supplementary Table 7**). The GDP showed the greatest change (+139% in average) in 10 years, increasing in all counties but one. The HDI-I increased 13.7% (in all counties but two) and the Gini inequality index decreased 8.92% (**Table 3**). For the latter, variation per county was more pronounced:

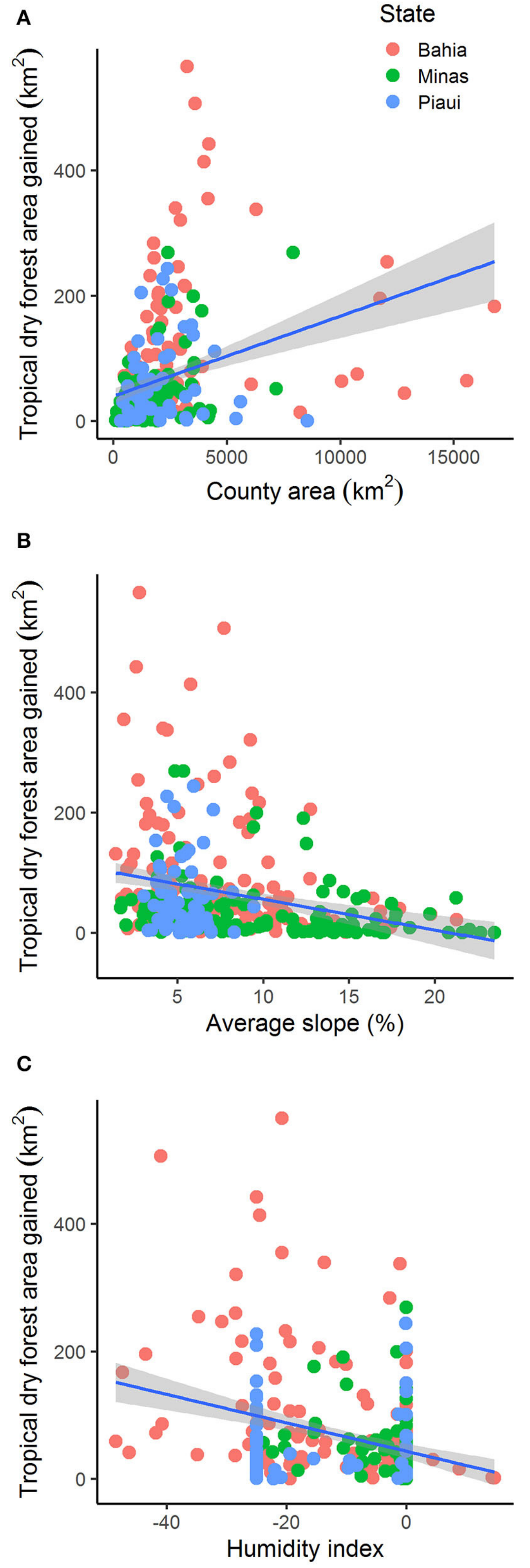

FIGURE 4 | Effects of the **(A)** county area, **(B)** average slope, and **(C)** humidity index on tropical dry forest area gained (km^2) at the county level for three Brazilian states. These explanatory variables were retained in the minimal

(Continued)

FIGURE 4 | adequate generalized linear model with a Gaussian error distribution (adjusted $R^2 = 0.51$, $p < 0.05$) after stepwise model selection ($n = 294$). Circles represent values obtained after summation of raw residuals with the predict values for each variable, assuming average values for other covariates. Partial model parameters: **(A)** Y = log(2.693 + 0.0001*area), $R^2 = 0.109$; **(B)** Y = log(3.969 – 0.081*slope), $R^2 = 0.011$; **(C)** Y = log(3.103 – 0.021*humidity), $R^2 = 0.090$. Additional parameters for complete and minimal adequate models are given in **Supplementary Table 3**.

13 counties had no change in the Gini inequality index, whereas 61 showed an increase in this indicator. Human welfare indicators were not associated with TDF area gained or lost (**Supplementary Table 5**).

DISCUSSION

Tropical dry forests in the studied region experienced very dynamic land cover changes from 2007 to 2016, with 33,766 km^2 (23.5% of the original extent considered here) under some type of transition among land cover classes. Deforestation was unexpectedly high, considering that TDFs are fully protected by the Atlantic Rain Forest law. However, such loss was offset by an impressive extent of forest recovery, although we could not assess the ecological integrity of recovered areas (e.g., if deforestation of old-growth forests was offset by the recovery of early-successional forests). Despite that, our results highlight the importance of this process to the maintenance of forest cover and associated ecosystem services (e.g., water provision, soil fertility, carbon sequestration, climate regulation and pollination, among others). We observed meso-regional differences in LCC, and the main factors associated to deforestation and forest recovery at the county level were county area, slope, humidity, and population density. Although these results are important to inform policy-makers on developing conservation strategies to Brazilian TDFs, the trends detected in the present study should be confirmed by multiple time-steps and updated frequently to reveal detailed LCC dynamics.

Trends in LCC

The vast majority of TDF recovery in the study region occurred in pastures used predominantly for cattle raising, reinforcing that this economic activity deserves special attention for the design of restoration policies (Strassburg et al., 2014; Latawiec et al., 2015; Poore, 2016; Xie et al., 2020). This observed TDF regrowth can be the result of (i) passive or active restoration to conform to the Brazilian Native Vegetation Protection Law (Federal Law 12727/2012); (ii) management practices such as pasture rotation and (iii) land abandonment for socioeconomic reasons. In the first case, the mentioned law indicates that every rural private property must preserve at least 20% of its total area as a "legal reserve" in the Atlantic Rain Forest (Brancalion et al., 2016). Although this restriction existed for decades, it was barely enforced in most regions, leading to a huge deficit in legal reserves in this biome (Soares-Filho et al., 2014; Freitas et al., 2017). Compliance to legal reserve requirements would demand the restoration of 5.17 million hectares (Soares-Filho et al., 2014)

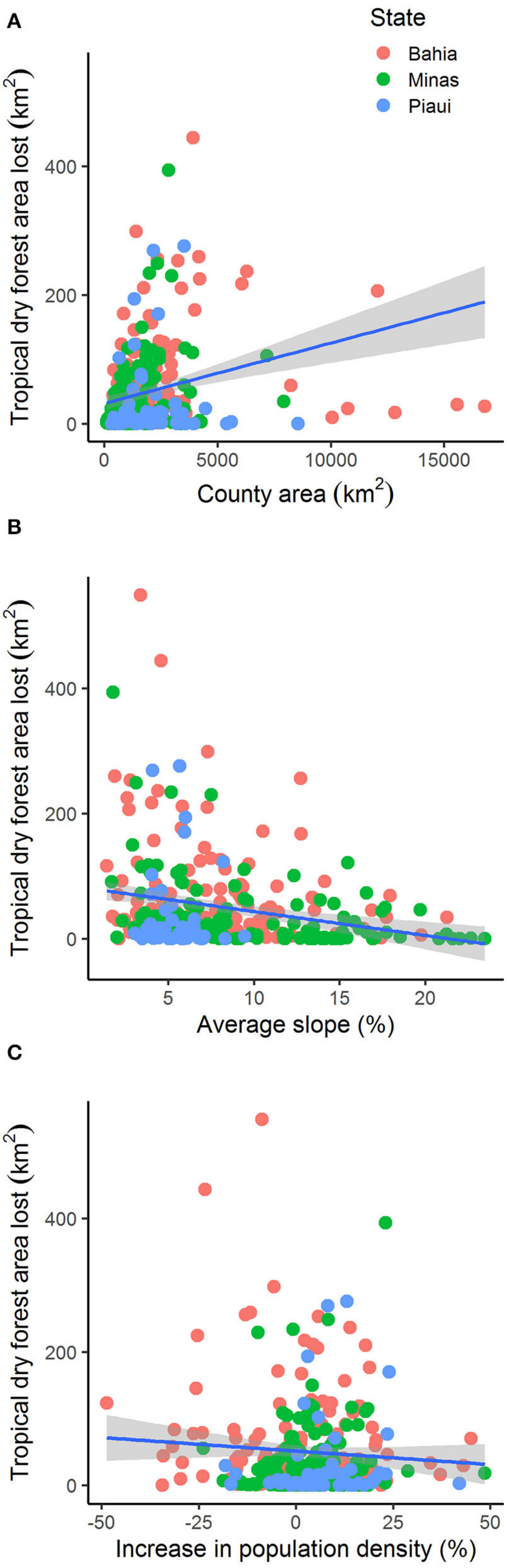

FIGURE 5 | Effects of the **(A)** county area, **(B)** average slope, and **(C)** increase in population density (%) on tropical dry forest area lost (km^2) at county level for three Brazilian states. These explanatory variables were retained in the

(Continued)

FIGURE 5 | minimal adequate generalized linear model with a Gaussian error distribution (adjusted $R^2 = 0.50$, $p < 0.05$) after stepwise model selection ($n = 294$). Circles represent values obtained after summation of raw residuals with the predict values for each variable, assuming average values for other covariates. Partial model parameters: **(A)** Y = log(2.653 + 2.22E-05*area), $R^2 = 0.060$; **(B)** Y = log(3.583 – 1.08E-01*slope), $R^2 = 0.021$; **(C)** Y = log(2.753 – 1.65E-02*populational density), $R^2 = 0.011$. Additional parameters for complete and minimal adequate models are given in **Supplementary Table 3**.

and, although the first steps toward this goal are ongoing (i.e., formally delimiting and registering areas to be permanently assigned as legal reserves in each property in a standardized database—the Rural Environmental Registry System—CAR in Portuguese; Brancalion et al., 2016; Oakleaf et al., 2017), actual TDF restoration initiatives are still limited. Recent reviews indicate a large knowledge gap on TDF restoration in Brazil, given that only 4–5% of the studies on this subject were conducted in this ecosystem (Gardon et al., 2020; Guerra et al., 2020).

In the second case, it is possible that some extent of short-term TDF recovery is related to pasture rotation. The Atlantic Rain Forest law prohibits the clearing of any TDF (i.e., the areas indicated in **Figure 1**) except those in early successional stages. Indeed, the Brazilian government has established technical criteria to differentiate TDF successional stages based on species composition, forest structure, plant life forms, and even the amount of litterfall [e.g., CONAMA Resolution #392 for Minas Gerais state; Ministério do Meio Ambiente (MMA), 2007]. For example, TDFs with an average diameter at breast height (DBH) higher than 8 cm can be considered as intermediate successional forests and thus become fully protected under the Atlantic Rain Forest law. As a consequence, it is likely that farmers in this region would prevent TDFs to regrow, or adopt short rotation intervals to keep the forest at a very early successional stage and avoid being prohibited to clear fallow areas to establish new pasturelands. Because our study period encompasses only 9 years (2007–2016), it is possible that regenerated areas result from a rotational system for pasture management with a short fallow period of natural regeneration. However, long-term TDF recovery is less likely in this case because of possible legal restrictions on the future use of regrowing areas. Thus, further studies are needed to evaluate the persistence of recovered TDFs in the landscape.

In this way, it is reasonable to assume that most TDF recovery in northeastern Brazil during the study period is unlikely related to active willingness to restore. Instead, TDF regrowth probably occurred after land abandonment for socioeconomic and/or biophysical reasons, and also as a consequence of management practices (i.e., pasture rotation). In the northeastern region of Brazil, which encompasses most of our study, estimates indicate that approximately 73% of the pasturelands are degraded and prone to abandonment (Dias-Filho, 2014). Indeed, our LCC analyses demonstrated that pasture area decreased 10% from 2007 to 2016 (see **Table 1**), which can reflect either land abandonment or an intensification of cattle raising (i.e., an increase in the number of animals per hectare). However, the total size of the cattle herd in the study region decreased 11.2%, from 7.2 to 6.4 million heads [Instituto Brasileiro de Geografia e Estatística (IBGE), 2017b], suggesting that economic factors are causing land abandonment thus opening space for natural regeneration. This reduction was probably intensified by the prolonged drought that occurred in the northeastern region from 2011 to 2016 (Mariano et al., 2018), causing land abandonment and/or the replacement of cattle by goats, which are more resistant to the semi-arid conditions and demand less pasture area per head (Carvalho et al., 2005; Sousa-Júnior et al., 2008).

Such changing economic scenario can create opportunities for large-scale restoration programs based on natural regeneration. According to Dias-Filho (2014), the recovery of 25% of degraded pastures in Brazil would be enough to sustain current cattle raising levels, with the remaining area being released for other purposes. If we consider that 73% of the pasture area in our study region is degraded (=132,553 km^2), we can estimate that 99,415 km^2 would be available for restoration initiatives. However, it is important to highlight that, despite the importance of forest recovery (either through natural regeneration or planting) to the potential reestablishment of biodiversity and ecosystem services (Melo et al., 2013; Crouzeilles et al., 2017), secondary forests are usually functionally different from old-growth forests (Espírito-Santo et al., 2014; Crouzeilles et al., 2017; Rozendaal et al., 2019). Indeed, the speed of natural regeneration in abandoned areas and the ecological integrity of the resulting secondary forests depends on the proportion of old-growth forests at the landscape level (Chazdon et al., 2009; Jakovac et al., 2015; Rozendaal et al., 2019). Thus, environmental policies that stimulate forest recovery should be coupled to strategies to avoid further clearing and degradation of old-growth forests.

Factors Associated With LCC

At the county level, we observed that deforestation and forest recovery are mainly associated to the county area and slope. However, deforestation was additionally associated to changes in population density, whereas forest recovery was associated to the humidity index. These results partially corroborate other studies that used the same approach at different spatial scales (Aide et al., 2013; Espírito-Santo et al., 2016; Dupin et al., 2018; Crouzeilles et al., 2020; Trigueiro et al., 2020). The positive relationship between both TDF area gained and lost with county area and slope indicates that large, flat counties have very dynamic LCC, a pattern already reported for TDFs in the north of Minas Gerais (Dupin et al., 2018). It is likely that large counties also possessed greater extent of TDFs and abandoned pastures in 2007, making them prone to further deforestation and forest recovery. Indeed, the previous existence of vegetation remnants (Aide et al., 2013; Trigueiro et al., 2020) and the county forest proportion (Crouzeilles et al., 2020) are important drivers of forest recovery, which is strongly influenced by the distance to forest edges (Jakovac et al., 2015; Rozendaal et al., 2019). The negative relationship observed between deforestation and slope is common, indicating that flat areas are preferred for cattle raising because mechanization is facilitated (Jasinski et al., 2005; Aide et al., 2013; Espírito-Santo et al., 2016; Dupin et al., 2018;

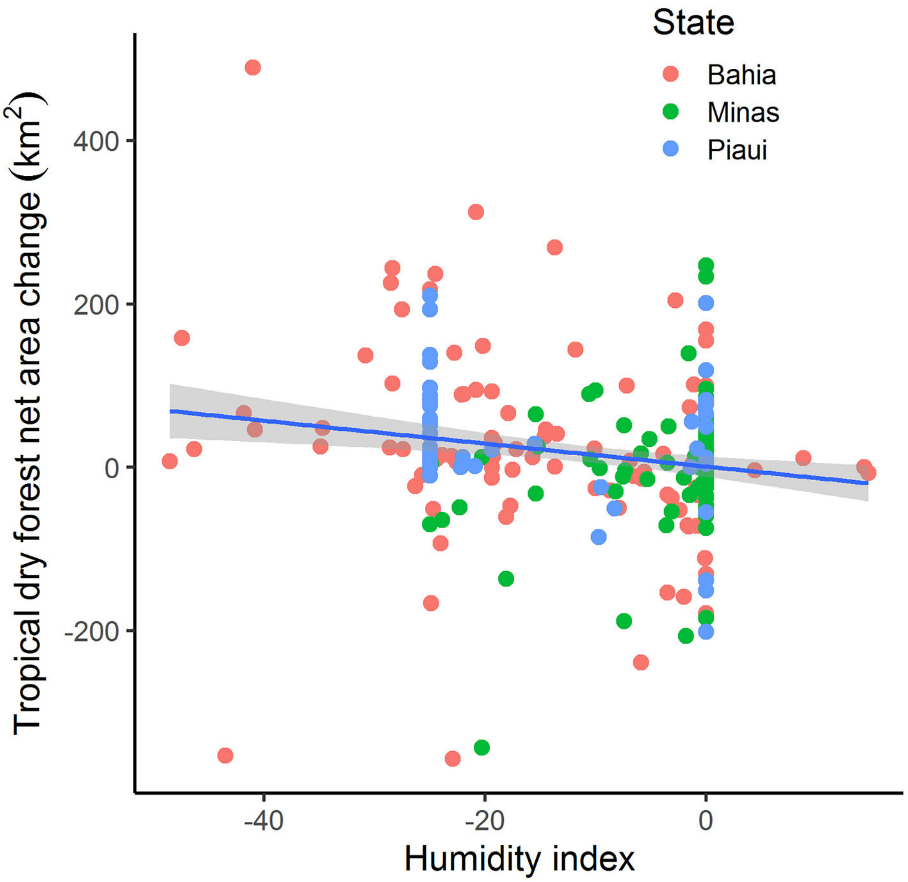

FIGURE 6 | Effects of the humidity index on the net change in tropical dry forest (TDF) area for three Brazilian states. This was the only explanatory variable retained in the minimal adequate generalized linear model with a Gaussian error distribution (adjusted $R^2 = 0.50$, $p < 0.05$) after stepwise model selection ($n = 294$). Positive values indicate net area gain (natural regeneration) whereas negative values indicate net area loss (deforestation) at county level between 2007 and 2016. Circles represent values obtained after summation of raw residuals with the predict values for each variable, assuming average values for other covariates. Partial model parameters: Y = 3.468 – 1.146*humidity, $R^2 = 0.027$). Additional parameters for complete and minimal adequate models are given in **Supplementary Table 3**.

Trigueiro et al., 2020). Thus, it is likely that flat counties also have larger areas of abandoned pastures prone to forest recovery.

TDF area lost was slightly higher in counties with a decrease in population density during the studied period, but no relationship was observed with TDF area gained or net area change. The effects of demographic variables on LCC reported in studies using counties as analytical unit have been inconsistent. Although no influence of population density was described for the Brazilian Cerrado (Espírito-Santo et al., 2016; Trigueiro et al., 2020) and the Atlantic Rain Forest (Crouzeilles et al., 2020), a negative effect of population increase on forest recovery was detected for TDFs in the north of Minas Gerais state (Dupin et al., 2018). In their study for all Latin America and the Caribbean, Aide et al. (2013) found a negative effect of population density on forest recovery, but only for counties with more than 50% of forest cover in the beginning of the study period. These authors also found that low population counties, which were in the beginning of the colonization process, had higher rates of deforestation, whereas densely populated counties had already been deforested, exhibiting high forest recovery rates.

The humidity index was negatively associated to both TDF area gained and net area change, indicating that arid counties had higher forest recovery. This is an important finding because some studies on the definition of priority areas for restoration programs suggested that active restoration may be more appropriated in regions with low precipitation levels (Crouzeilles et al., 2017, 2019a, but see Holl and Aide, 2011), where natural regeneration is too slow or not very successful (Chazdon and Guariguata, 2016; Poorter et al., 2016). It is possible that, in more arid counties, the frequency of land abandonment is higher, a pattern already reported in other studies in northeastern Brazil (Redo et al., 2013; Sampaio et al., 2017). Nevertheless, the remote sensing techniques used here only indicate structural vegetation recovery, and other parameters related to biodiversity and ecosystem functioning are necessary to determine the potential of forest recovery in low humidity TDF areas. Studies using high resolution images (García-Millán et al., 2014; Almeida et al., 2020) to discriminate between TDF successional stages are also important, as the causes of deforestation may differ from early to old-growth forests.

It important to highlight that, in general, our models explained 50–60% of the total variance in LCC variables, suggesting that other biophysical and socioeconomic factors need further investigation. Alternatively, it is possible that the limited predictive power of the models was caused by the observed spatial variation on the effects of each factor. We found that most factors were differently associated to TDF area gained, lost and net area change in Minas Gerais, Bahia and Piauí (**Supplementary Figures 8–10**). Indeed, such spatially structured effect of factors associated to LCC have already been reported in large scales studies encompassing several contrasting regions (e.g., Aide et al., 2013; Trigueiro et al., 2020). These findings reinforce the importance of analyzing causes of LCC, preferably using high-resolution imagery and multiple time-steps, to develop environmental and development policies finely adjusted to different counties and regions in Brazil.

LCC and Welfare Indicators

The temporal variation in welfare indicators was not associated with LCC at the county level in the study region, suggesting that the relationship between deforestation and socioeconomic development is complex and deserves further investigation. The developmentalist association between deforestation and well-being is usually based on the Kuznets environmental curve, which illustrate an increasing environmental degradation in the first stages of development, when per capita income also increases until a turning point is reached (Bhattarai and Hammig, 2004). After that, usually the dependence on the primary sector (e.g., agriculture, mining) decreases with industrialization (as predicted by the forest transition theory), and human welfare would continue to improve with decreasing degradation and even regeneration of natural ecosystems (Barbier et al., 2017). Although the study region experienced an improvement in all evaluated welfare indicators and an increase in TDF area, the lack of association between these variables at the county level do not support the conclusion that Brazilian TDFs are in a steady, consistent transition. Thus, the establishment of alternative development policies based on sustainable practices and social justice are still necessary.

CONCLUSIONS

Our results provide valuable basic information on the factors associated to land cover change in Brazilian TDFs, which can help supporting the design of environmental and development policies aimed at reducing deforestation and maximizing forest recovery. Further studies with fine spatial and temporal resolution need to focus on the reversibility (see Schwartz et al., 2020) and ecological integrity of regenerated areas in order to assess their potential to provide long-term ecosystem services. Such approach would also allow to more precisely determine the causal relations between biophysical and socioeconomic factors and LCC at the county level and their spatial structure at larger scales (e.g., the state level), which is important to adjust restoration strategies to different regional political scenarios. In TDF regions, large, flat and more arid counties with very dynamic LCC deserve special attention. Given that TDF-pasture transitions vastly dominate LCC in the studied region (and also other vegetation types in Brazil), environment-friendly practices are urgently needed to avoid soil exhaustion and optimize cattle raising efficiency. Such goal can be achieved in regional planning programs through sustainable intensification in high productivity areas and TDF restoration in marginal agricultural lands with low opportunity costs (Latawiec et al., 2015). Although TDFs are mostly neglected in restoration programs compared to wet forests, the net forest recovery observed in the present study was expressive (427,106 ha) and provides a significant contribution to Brazil's commitment under the Bonn agreement (3.6% of 12 million ha by 2030) and the Atlantic Rain Forest pact (42.7% of 1 million ha by 2020) (Crouzeilles et al., 2019b). Considering that the total TDF recovery in 10 years was 1,901,800 ha, most of these goals would be achieved with efficient enforcement of current environmental laws and clear policies for passive restoration.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

ME-S, GS-A, ML, and AR conceptualized the article. ML, AR, and LS obtained and processed satellite imagery. AR, ME-S, and LS organized the database. JS and ME-S analyzed the data. All authors contributed to data acquisition, data interpretation, manuscript revision, read and approved the submitted version, and wrote sections of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2020.569184/full#supplementary-material

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Rooting Forest Landscape Restoration in Consumer Markets—A Review of Existing Marketing-Based Funding Initiatives

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Forest landscape restoration (FLR) is globally important to mitigate a wide range of social and environmental problems driven by landscape degradation and deforestation. Despite widespread recognition of the urgent need to restore biodiversity and ecological functioning across many forest landscapes, there is an apparent mismatch between political commitments and direct actions on the ground. Global markets and consumption patterns remain prominent drivers of land degradation. Alternatively, market forces could be transformed to have net positive rather than negative influence on land use change, offering innovative pathways to incentivise and finance FLR. Understanding current market mechanisms that finance FLR is essential for establishing best practices and effective policy. We reviewed 40 eco-marketing initiatives to provide an overview of the types of organizations involved in funding of FLR, and how they finance and enable FLR interventions. We identified three groups of initiatives: *for-profit business*, *certified social enterprise*, and *non-profit organization*. In total, 36 out of the reviewed initiatives collaborated with enabler-organizations to implement FLR activities. All initiatives promoted active tree planting, primarily in regenerative agroforestry systems. Only six analyzed initiatives included natural regeneration as a type of FLR intervention. This suggests that eco-marketing initiatives primarily focus on funding tree planting initiatives, possibly because tree planting is the easiest message to communicate to consumers. Strong safeguards and governance of FLR projects are necessary to ensure that tree planting projects do not overshadow other FLR interventions in areas where other approaches have more significant ecological, environmental, and social benefits.

Keywords: ecological restoration, sustainable finance, social enterprise, agroforestry, tree planting, forest restoration, eco-marketing, natural regeneration

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INTRODUCTION

Every year, millions of hectares of forest are being cleared or degraded to satisfy global demand for food, land, mining, and forest products (FAO UNEP, 2020). This has led to large scale loss of ecosystem services (for example: Fugère et al., 2016; Tan-Soo et al., 2016; Celentano et al., 2017; Kasaro et al., 2019). FLR initiatives aim to not only restore ecological integrity in deforested or degraded areas and enhance ecosystem services, but also to improve forest-based livelihoods (Chazdon et al., 2015; Mansourian et al., 2017; IUCN, 2018). Governments (partly in international agreements) have set ambitious targets to restore 350 million hectares by 2030 (Convention on Biological Diversity, 2013; IUCN, 2014). However, action on the ground falls short. As of 2019, only 18% of the land pledged to be restored by 2020 had been brought under restoration (NYDF Assessment Partners, 2019). Insufficient financing has been identified as a major constraint of restoration efforts (Brancalion et al., 2019; Chapman and Lindenmayer, 2019), it has been estimated that between USD 36−49 billion are required to achieve yearly FLR targets (FAO, 2015). As the scale of restoration efforts required to achieve worldwide targets is likely to go far beyond the financial capacity of governments and NGOs, it is necessary to mobilize new streams of finance from the private sector (Löfqvist and Ghazoul, 2019).

Under the neo-liberal market system, consumption patterns have been one of the main drivers of deforestation and forest degradation (European Commission, 2013; Lawson et al., 2014), but markets could also offer pathways to finance restoration efforts (Gutierrez and Keijzer, 2015; Brancalion et al., 2017; Ceccon and Boucher, 2017; Faruqi et al., 2018). As consumer awareness around environmental impacts from the production of consumer goods has increased, especially in the Global North (Padel and Foster, 2005; Andorfer and Liebe, 2012; The Nielsen Company, 2015; Vlaeminck and Vranken, 2015; Nielsen, 2018), a range of eco-marketing mechanisms have been developed which enable consumers to directly finance FLR. Eco-marketing, also called green marketing, is a strategic business management concept, and can be defined as a branding strategy for companies aiming to create positive economic, social, and environmental impacts (Virdi and Gill, 2016). These strategies are based on the assumption that consumers not only select products and services because of attributes such as quality and price, but also consider what effects their consumption choices have on the wider society and the environment (Cusot and Falconi, 2012). Hence, with growing consumer awareness around the importance of restoration, eco-marketing mechanisms could increasingly become a lever to finance restoration initiatives.

The contribution of eco-marketing initiatives to financing global FLR targets will partly depend on how these initiatives are organized and which types of FLR initiatives they finance. FLR interventions can include both passive and active restoration practices, each with their own context-specific social, ecological, and financial benefits (Morrison and Lindell, 2010; IUCN WRI, 2014). Active restoration can include the planting of trees on degraded land to facilitate ecological restoration, and the planting of trees in agroforestry systems, for example by planting fruit trees. In this paper, we use the term "agroforestry" for regenerative agricultural systems which aim to promote diverse and multi-layered food production that restore degraded landscapes. Passive restoration (including assisted natural regeneration) does not include planting of seedlings or seeding, but assists the natural recovery of native tree species on degraded forested land through activities such as controlling livestock grazing, weed growth, or fire protection (Crouzeilles et al., 2017). Assisted natural regeneration can, in specific contexts, be a low-cost method of forest restoration in areas where secondary forest is present (Chazdon, 2014; Crouzeilles et al., 2017; Reid et al., 2018), while active restoration typically is initiated within highly deforested landscapes (Reid et al., 2018). Assisted natural regeneration can thus be an effective approach in areas where there is no high opportunity cost of land use, while active restoration such as planting of valuable tree species can offer more direct local livelihood opportunities (FAO, 2017).

The funding mechanism behind a restoration project is likely to influence the type of intervention that is promoted. This can be problematic if funders favor interventions that do not align with what is ecologically, environmentally, and socially optimal (Löfqvist and Ghazoul, 2019). Thus, it is crucial to understand what type of restoration interventions can and should be funded through eco-marketing mechanisms, and in what regions. In this review, we conceptualize how eco-marketing mechanisms contribute to financing FLR and provide an overview of which FLR intervention types are financed and enabled based on 40 reviewed eco-marketing initiatives.

CONCEPTUALIZING HOW ECO-MARKETING INITIATIVES FINANCE FLR

To identify active eco-marketing initiatives, we conducted online searches using a list of relevant keywords including "plant trees," "forest restoration," "FLR," "natural regeneration," "buy one plant one," "carbon offsetting," "travel emissions," "compensate," "buy," "company," and "finance," etc. Furthermore, a variety of initiatives were identified through the websites of the enabler organizations, and our own network of partners. This allowed us to identify a sample of 40 global initiatives. Our goal was not to provide an exhaustive overview of eco-marketing initiatives, but to provide a representative review of different types of organizations which are involved in FLR eco-marketing strategies. Selection criteria for the initiatives were that they (1) are private sector initiatives funding FLR activities in developing countries, (2) communicate their restoration activities directly to the consumers, either through the packaging of the products or marketing of a service and consequent impact, or through wider outreach campaigns, and (3) provide specific information on their FLR interventions on their websites.

We categorized three different organizational types of FLR eco-marketing initiatives; *for-profit businesses*, *certified social enterprises*, and *non-profit organizations* (**Figure 1**). We selected certified B-corporations for social enterprises, as these certified businesses are legally required to meet rigorous standards of social and environmental performance, accountability, and transparency (Harjoto et al., 2018). Whereas, these businesses fund restoration alongside their normal profit-driven activities (which do not have to be related to forests or FLR), initiatives from non-profit businesses have restoration at the core of what

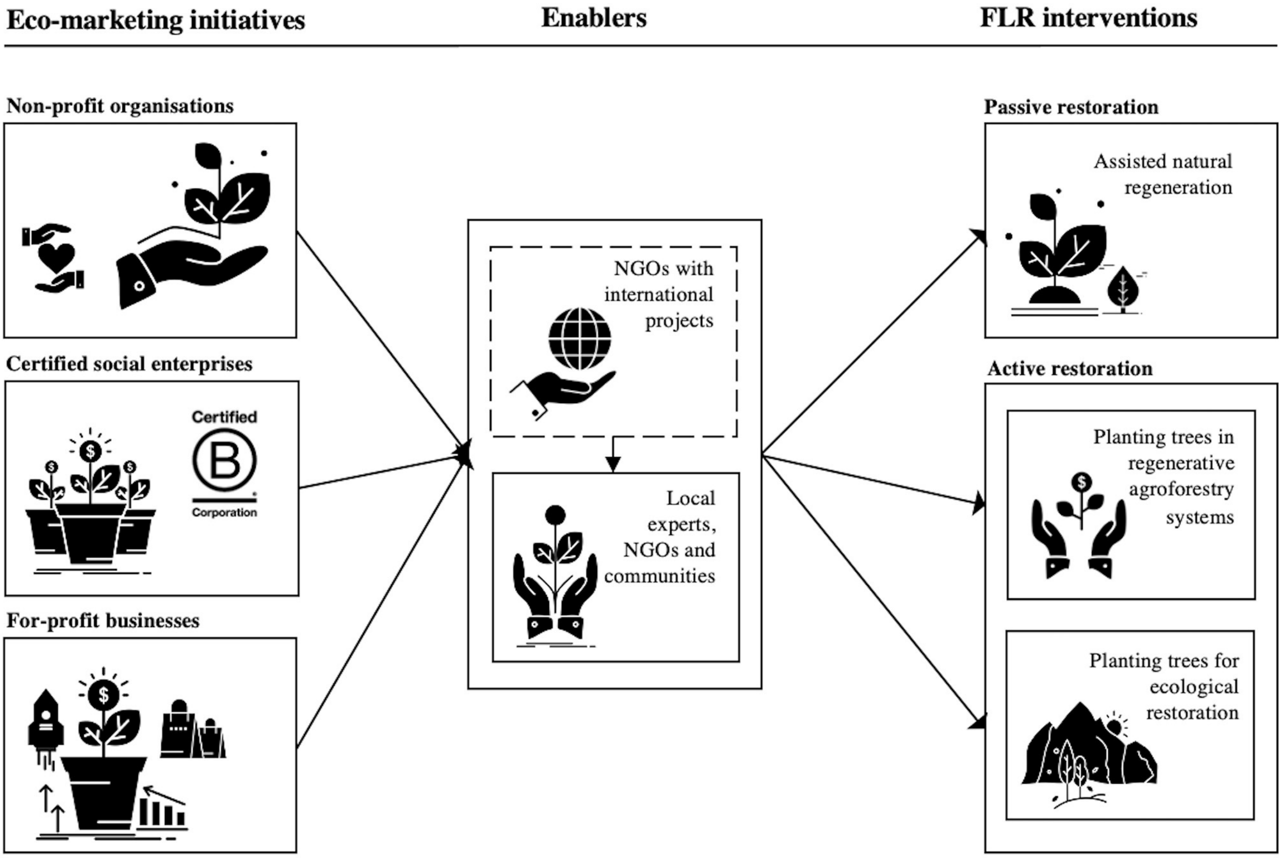

FIGURE 1 | Conceptual overview of how the reviewed eco-marketing initiatives finance FLR. All three identified types of eco-marketing initiatives **(left)** collaborate with enablers **(center)**, i.e., international NGOs, and/or local experts and communities, which realize different FLR intervention types **(right)**.The dashed line around "NGOs with international projects" indicates that this type of enablers were not involved in all initiatives, whereas "local experts, NGOs, and communities" were always involved directly or indirectly.

they work toward and have established products and services around this goal to finance restoration activities.

Most eco-marketing initiatives were not actively involved in restoration efforts on the ground and did not own the land on which the FLR interventions are conducted. Instead, they collaborated with so-called enablers, which can either be third party non-profits or NGOs who have international projects, or local experts and communities that conduct FLR activities (**Figure 1**).

UNPACKING ECO-MARKETING MECHANISMS FOR FINANCING FLR

Out of the 40 reviewed eco-marketing initiatives, 32 were for-profit businesses, six were certified social enterprises (B-corporations), and only two were non-profit eco-marketing initiatives with an FLR focus (**Figure 2**). Three of the for-profit businesses (Fly-eco, 8 Billion Trees and flyBARBARA) included carbon offsetting. The most frequently applied financing schemes across the reviewed initiatives were a "one for one" method (where one or more trees are planted for every product sold or service provided), and a donation of a percentage of the profits from each sale to tree planting. In total, 36 out of the reviewed initiatives collaborated with enabler-organizations to implement FLR activities. We identified 22 enabler organizations which executed the FLR interventions, out of which Trees for the Future was employed most often, with 17 of the identified initiatives using them as an enabler (**Figure 2**). Eden Reforestation Projects and WeForest were employed by seven initiatives each. Only six initiatives did not mention collaboration with any of the identified enabler organizations, but instead stated that they collaborate directly with local NGOs, experts, and/or communities (**Figure 2**).

All reviewed initiatives focused primarily on active restoration, out of which 12 financed projects which pursue more than one FLR intervention type, and most of the reviewed FLR interventions aimed toward creating socio-economic as well as ecological benefits. Ecosia and Plant-for-the-planet were the only two initiatives that fund all three identified

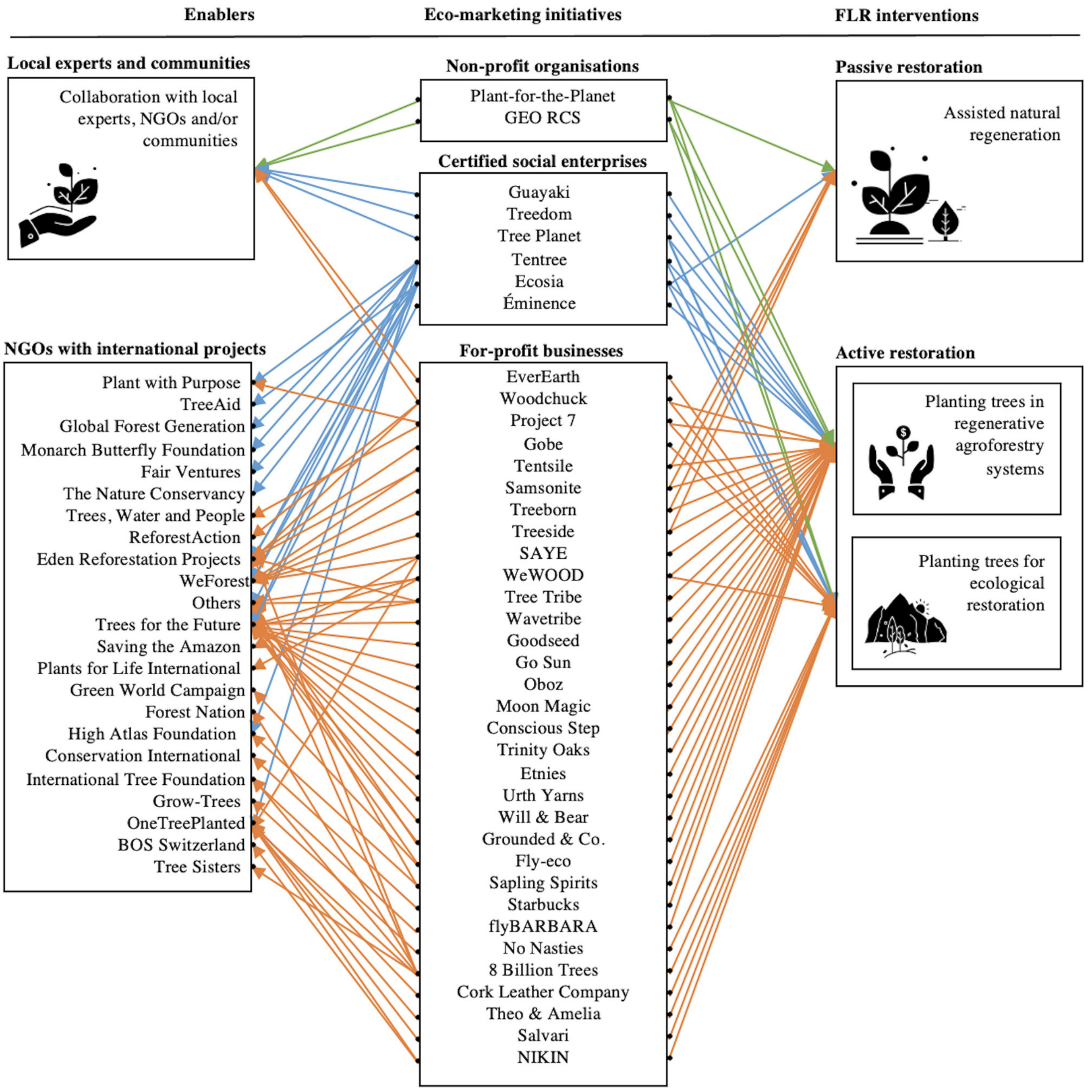

FIGURE 2 | Overview of which FLR intervention types were financed and which enabler organizations were employed by the reviewed eco-marketing initiatives. The color of the arrows corresponds to the identified eco-marketing groups (non-profit organization = green; for-profit social enterprise= blue; for-profit business = orange). As some of the initiatives worked with a large number of enablers, the provided list of enablers is not exhaustive which is why the option "others" is included.

FLR intervention types. In total, 32 of the initiatives finance the planting of trees in agroforestry systems, and 30 of these specifically stated on their website that this concerns regenerative agroforestry. Furthermore, 16 initiatives finance tree planting for ecological restoration, and 14 of these specified that this is achieved through the planting of native species in diverse systems. We conclude from this that none of these initiatives finance the establishment of exotic monoculture plantations. Only six out of the 40 initiatives mentioned assisted natural regeneration as an FLR intervention that they support.

DISCUSSION

Our review of existing eco-marketing initiatives suggests that for-profit businesses are the most common type of organizations to use eco-marketing to fund FLR. Enabler organizations, especially the international NGOs discussed, are playing a crucial role in realizing FLR interventions funded through these channels. Our review also suggests that planting trees in regenerative agroforestry systems is the most frequent FLR activity funded by market-based mechanisms. Possibly, many eco-marketing initiatives aim to not only support ecological restoration, but also to increase resilience in supply chains and enhance the livelihoods and food security of rural communities (Jansen et al., 2020). By incorporating regenerative agroforestry in FLR interventions, local communities, and farmers are often more directly involved into the restoration activities, which plays a crucial role in making FLR efforts successful in the long term (Uprety et al., 2012; IUCN WRI, 2014).

Only a few of the reviewed eco-marketing initiatives included assisted natural regeneration, and no initiative focused solely on this intervention. A possible explanation for the strong focus on tree planting rather than assisted natural regeneration might be that tree planting is a more straightforward narrative to communicate to consumers. It might also be that there is an imperative to support community activities and incomes, which is harder to do with natural regeneration. However, it might be that some of the identified initiatives who apparently only finance tree planting, also support other FLR approaches but chose to not specifically mention this on their website to simplify communication. The disproportionate focus on tree planting in eco-marketing initiatives may be problematic in situations where other FLR interventions have higher potential to lead to ecological, and/or socially beneficial outcomes (Brancalion and Holl, 2020). Especially in ecosystems where trees are already present, assisted natural regeneration can be a more effective strategy from both a financial and biodiversity perspective (FAO, 2015; Brancalion et al., 2016; Chazdon and Guariguata, 2016; Crouzeilles et al., 2017). Furthermore, the information provided by the eco-marketing initiatives did not always disclose if trees are planted in monoculture plantations or not. If trees are planted in (exotic) monocultures, the establishment of tree plantations might replace native forests or cultural lands where forests might have naturally regenerated, and lead to overall negative environmental impacts (Lewis et al., 2019; Brancalion and Holl, 2020; Heilmayr et al., 2020). This issue is enhanced by the way our global targets are designed, namely in numbers of trees planted (e.g., the Trillion Trees Campaign) or hectares restored (e.g., the Bonn Challenge). With these types of targets, countries, companies, and eco-marketing initiatives can, in theory, realize their FLR commitments through massive monocultures, which could be environmentally and socially detrimental. Further, if socio-economic contexts are not accounted for, there is the risk that local communities are marginalized as a result of ill-designed restoration interventions.

The funding of FLR through eco-marketing initiatives could potentially make a very significant contribution to reaching global landscape restoration targets. For example, in 2019 alone, Ecosia financed the planting of 35.9 million trees (Ecosia, 2019). This momentum can be leveraged in a way that could have strong positive impact on ecosystems, our climate, and livelihoods, but it is important to emphasize the potential risks that come with large financial flows being channeled to tree planting specifically. For this reason it is necessary that strong safeguards are in place to promote tree planting in places where it is socially, environmentally, and ecologically beneficial, and to make sure on-the-ground context is understood before a restoration project is executed (Brancalion and Holl, 2020). In addition, for successful restoration, it is essential that not only the tree planting itself, but also follow-up maintenance (e.g., tending and irrigation) is facilitated to prevent high mortality rates in the first years after planting (Kettle, 2009).

Using eco-marketing initiatives for FLR funding might be dangerous if it promotes increased consumption that offsets part of the environmental benefits created through the tree planting activities. Eco-marketing may leads to the belief by consumers that the products and services marketed have low environmental impacts, but simply planting trees for every commodity sold does not imply that the wider supply chain is sustainable. To safeguard against such "greenwashing," certification of products or corporations which facilitate FLR could be used, such as the B-corporation certification presented in our review. Simultaneously it is also important to increase consumer awareness around the merits of natural regeneration and different types of FLR interventions. With increased awareness, other types of FLR interventions will be easier to communicate, which can leverage more funding from eco-marketing initiatives.

CONCLUSION

Eco-marketing initiatives provide new funding pathways for FLR, which can support the implementation of global FLR targets. Our review of 40 eco-marketing initiatives highlights that tree planting is a key restoration focused activity of eco-marketing initiatives, likely because this a straightforward and convincing message to communicate to consumers. As these funding streams are leveraged, it is important that safeguards are in place to decrease the risk that tree planting is executed in places where it has negative social, environmental, and/or ecological consequences. Should consumer awareness around the benefits of other types of restoration increase, market-based mechanisms such as eco-marketing could potentially be a lever for funding for a wider variety of restoration interventions. Some of our reviewed initiatives use restoration as a branding strategy to promote consumption, and it is important that these type of funding streams do lead to "green washing" that encourages unnecessary over consumption, which is a key issue in keeping society within a safe and just space (Raworth, 2017). It is important to acknowledge that though market-based mechanisms can be one stream of funding for FLR, the wider solution to environmental degradation and climate change lies in societal shifts toward an economic system that acts within planetary boundaries.

AUTHOR CONTRIBUTIONS

EB conducted the online research and wrote the first draft of the manuscript. All the authors contributed critically to manuscript revisions and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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ORIGINAL RESEARCH
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Canopy Leaf Traits, Basal Area, and Age Predict Functional Patterns of Regenerating Communities in Secondary Subtropical Forests

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Secondary forests originate from natural regeneration after fallow (succession) or restoration. Species assembly in these communities, which can affect ecosystem functions and successional trajectories, is very unpredictable. Trait-based trajectories can shed light on the recovery of ecosystem functions and enable predictions of how the regenerating communities will change with forest age. Regeneration communities are affected by initial conditions and also by canopy structure and functional traits that alter dispersers' attractiveness and coexistence mechanisms. Here we evaluated how community functional traits change over time and tested if functional diversity and composition of the established canopy, as well as the structure of the canopy and forest age, influence the functional structure of regenerating tree communities when compared to their reference forests. For this, we calculated dissimilarity in trait composition (community-weighted means) and in functional diversity of regenerating communities of each succession/restoration stand, using the tree stratum of nearby mature forests as baseline values. Functional trait information comprises leaf, wood density, and reproductive traits from tree species. Our community data contain information from natural successional forests and restoration sites, in the South-Brazilian Atlantic Forest. Predictor variables of functional dissimilarities were forest age, canopy structural variables, canopy functional composition, and functional diversity. Results showed leaf traits (leaf dry matter content, leaf nitrogen content, leaf nitrogen-phosphorus ratio) and seed mass varying with forest age. Canopy functional composition based on leaf traits and total basal area significantly predicted multiple trait functional dissimilarity between the regeneration component of secondary forests and their reference community values. Dissimilarity increased when the canopy was composed of species with more acquisitive traits. Difference in functional diversity was only influenced by forest age. Mid-stage secondary forests showed lower functional diversity than early-stage forests. Our results indicated the importance of canopy traits on the natural regeneration of secondary subtropical forests.

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If functional similarity with reference forests is a desired objective in order to recover ecosystem functions through natural regeneration, leaf functional traits of canopy trees that establish or are planted in degraded areas must be considered in the successional processes.

Keywords: community-weighted means, functional diversity, succession, restoration, Atlantic Forest, South Brazil

INTRODUCTION

Secondary forests are important for biodiversity conservation and ecosystem services, such as biomass stocks and water cycling, given the widespread deforestation and forest degradation processes in the tropics and subtropics (Chazdon et al., 2009). These forests are originated from natural regeneration processes after the abandonment of anthropogenic land-use types (succession) or after intentional actions to assist the recovery of ecosystems (restoration). Regeneration trajectories from both succession or restoration processes and the recovery of functioning and composition of these forests depend on ecosystem resilience, land-use history and landscape context, including many local and regional features (Holl and Aide, 2011; Crouzeilles et al., 2017; Holl et al., 2018). Even though many abiotic and biotic variables, as well as socio-economic context, are key drivers associated with the success of restoration strategies and regeneration trajectories (Pichancourt et al., 2014; Meli et al., 2017), biodiversity-based ecosystem services should be considered in restoration planning and monitoring to optimize forest restoration targets (Kollmann et al., 2016; Reij and Garrity, 2016; Rosenfield and Müller, 2020a). Ecosystem functioning and services are key goals in restoration projects, therefore biodiversity and trait-based researches have a high potential in informing the success of restoration efforts, embracing species parameters, interactions, and ecosystem functioning (Montoya et al., 2012; Rosenfield and Müller, 2019).

Successful regeneration of secondary forests should consider multifaceted parameters, including biodiversity, species composition, ecosystem functioning and services, to achieve a more holistic restoration. However, predicting secondary forest regeneration under natural conditions or even after active restoration actions is a big challenge. Even when considering the effect of distinct factors, studies from successional and restoration forests have shown that time is mandatory for tropical forest recovery (Holl et al., 2018), indicating that forest structure, species richness, and biomass are highly resilient in forests under natural regeneration processes (Martin et al., 2013; Zanini et al., 2014; Poorter et al., 2016; Meli et al., 2017; Rozendaal et al., 2019). Species composition, however, when compared to structural parameters or species richness, is the most unpredictable factor along succession, taking centuries to recover or even not recovering to similar pre-disturbances patterns at all (Chazdon, 2008; Liebsch et al., 2008; Rozendaal et al., 2019). Considering this and the importance of species characteristics and assemblies to ecosystem functions (Diaz et al., 2007), understanding and predicting the recovery of plant functional traits along the successional process of secondary forests is of most importance. A central question in recovering these forests is if secondary forests can achieve similar ecosystem functionality regardless of reaching similar values of former species composition. This is especially important in tropical and subtropical forests, where the number of rare species (with potential distinct and unique traits) is high when compared to the amount of common, abundant species.

Species establishment is a well-known barrier in early regeneration stages and, in forest restoration projects, planting seedlings is widely applied as a restoration tool (Holl and Brancalion, 2020). The choice of species to be used in these plantings can be a challenge, as they have distinct chances to survive and might further influence regeneration trajectories by altering the conditions for secondary species establishment or by determining coexistence mechanisms (Muscarella et al., 2017; Fernandes Neto et al., 2019; Charles, 2020). In areas of natural succession, earlier stages of forest under moist and wet conditions often have species that present a higher investment in leaf traits with high potential for acquiring resources, such as light and soil nutrients (e.g., high specific leaf area and leaf nitrogen content), and consequently grow faster (e.g., low wood density), quickly occupying the available space (Lohbeck et al., 2013; Boukili and Chazdon, 2017). However, under dry conditions, forests in earlier stages of succession, which are under more severe environmental conditions, are often dominated by species with conservative characteristics, showing denser wood stems and thicker leaves (Lohbeck et al., 2013; Poorter et al., 2019). Even though these general patterns are predictable to one extent, successional trajectories in the long-term might follow stochastic patterns or converge toward the functional composition of reference forests (Norden et al., 2015), which depends on the trait or function being analyzed (Boukili and Chazdon, 2017). Convergent trajectories regarding functional trait composition during forest development seem to prevail, but there are only few studies and less information about functional diversity trajectories along the successional time (Teixeira et al., 2020).

In addition to time and site conditions that influence community recovery trajectories, plant traits associated with the initial colonizers might influence the ongoing process (Mesquita et al., 2001), potentially causing priority effects (Fukami, 2015). Under natural regeneration, initial colonizers are influenced by land-use legacy and drive successional trajectories: colonizers of intensively used sites (e.g., pasture) arrest succession and trajectories might be unpredictable when compared to regeneration trajectories on sites that were clear-cut and abandoned without any type of soil-use (Mesquita et al., 2015; Fernandes Neto et al., 2019). Besides purely structural features of the canopy (e.g., height and cover), which affect microclimatic conditions associated with light and soil (Chazdon, 2008), morphological, physiological, and phenological traits of initial colonizers might influence the ongoing regeneration community, altering dispersal attractiveness (Viani et al., 2015) and coexistence mechanisms associated to growth and survival. Under the lens of priority effects, these mechanisms are associated with niche preemption and niche modification (Fukami, 2015). Some initial colonizers have traits that determine their own success in establishing and becoming dominant across time, also slowing down the colonization by other species with different traits (Jakovac et al., 2014; Fernandes Neto et al., 2019). This may result in stable states that retard the successional process toward reference conditions, whereas other traits can lead to community attributes that improve colonization by later species or ecosystem functions, thus speeding the successional process (Weidlich et al., 2018; Fernandes Neto et al., 2019). Forest regeneration success (trajectory and speed) might thus be associated with characteristics of first colonizers along the successional process (e.g., Werden et al., 2018), besides the already known influence of structural features, landscape, and abiotic conditions. Beyond the potential priority effects from first colonizers of community reassembly, the established forest canopy and their characteristics might continuously affect the regeneration mechanisms within forest dynamics (Muscarella et al., 2017).

By understanding the influence of some key traits of initial colonizers on forest regeneration patterns, relevant restoration actions can be employed. For example, by choosing tree species for planting through traits that may best influence subsequent regeneration trajectories, one could enhance the chance of restoring ecosystem functioning in a similar way as found in pre-disturbance communities, i.e., the target forest communities (Laughlin, 2014; Laughlin et al., 2018). Here we aim to assess if functional trait composition and diversity of regenerating tree communities in successional forests increase their similarity in relation to reference forests over time, also considering the characteristics of the established canopy as potential drivers of observed trajectories. More specifically, we are interested in evaluating (i) how community functional traits change with the age of secondary forests; and whether (ii) the functional diversity and composition of the established canopy, the structure of the canopy, or the time since forest abandonment influence the similarity of regenerating tree communities in relation to the functional structure of reference forests. This similarity was evaluated considering trait composition and functional diversity differences between each successional forest and their nearby reference forest. We are interested in possibly making predictions of trait-based trajectories of regenerating tree communities based on the leaf, reproductive, and wood characteristics of initial colonizers or planted trees (which are the main components of the established canopy), in order to recover reference baseline values of ecosystem functioning.

MATERIALS AND METHODS

Study Region

The study was conducted in the southern Brazilian Atlantic Forest domain. The most dominant climate in the region is classified as Cfa temperate humid climate, lacking a marked dry season, with hot summers above 22°C (Peel et al., 2007). In the eastern highlands, the climate type is Cfb, with the average temperature of the warmest month not exceeding 22°C, and the annual isotherm below 18°C. The southern Atlantic Forest encompasses different forest types such as the Atlantic moist forest, Araucaria forest (a mixed subtropical forest type located in the highlands), and seasonal forests, with high levels of beta diversity (Bergamin et al., 2017).

We included seven study sites from which we collected data on the regeneration tree communities in secondary forests and on reference tree communities (one for each site) in nearby mature forests. Secondary forests of four of our study sites consist of stands under natural succession after land abandonment (Zanini et al., 2014; Vicente-Silva et al., 2016), whereas the remaining three are sites undergoing ecological restoration after planting interventions of tree seedlings (Rosenfield and Müller, 2019) (**Table 1**). Planting of seedlings was conducted under legal requirement, using native species with distinct number of species and density (see Rosenfield and Müller, 2019). Forest stand age of restoration sites was determined by considering the regeneration time after the end of interventions, whereas for the stands under natural succession, the information was gathered through interviews and crosschecked with satellite images (Zanini et al., 2014; Vicente-Silva et al., 2016). Land-use history of the studied secondary forests was not intensive in terms of mechanization: Maquiné areas were used for slash-and-burn small subsistence agriculture; Pró-Mata areas were used for subsistence agriculture and pasture, and the restoration areas were formerly used for cattle grazing (Cachoeirinha), *Eucalyptus* plantation (Canela), and grape production (Santa Tereza). The age range of secondary forests, with the respective forest type and other relevant information of the study areas, are shown in **Table 1**. For each study site, we identified and surveyed a nearby reference site (old-growth or mature forest) to be used as baseline values of a desired tree functional structure (trait composition and functional diversity). For the reference forests, we set an approximated age since the interruption of human interventions.

Data Sampling

In each study site, we surveyed tree and treelet species in both successional/restoration and reference forests. Reference forests were described by the *tree stratum*, including information of trees with diameter at breast height (DBH) ≥ 5 cm, in order to represent adult tree communities of mature forests. Secondary forests (successional/restoration stands) were described by the *canopy* (trees of the upper stratum, including all individuals with DBH ≥ 10 cm) and the *regeneration component*. The upper stratum of trees in secondary forests was defined as *canopy*, although we recognize that in very initial successional forests the crown of such individuals might not yet form a

TABLE 1 | General information for each study site in terms of site name, forest type, number of secondary forest stands evaluated, and stand age.

Site	Central coordinates	Forest type	Number of secondary forest stands and the reference	Age (years of regeneration)	#100 m^2-plots per stand
Maquiné—Vale do Forqueta 1	29°32′27.6″ S	Atlantic moist forest	Reference	> 150 years	12
	50°11′24″ W		9 Succession stands	6, 9, 12, 24, 26, 40 years	3 (for each stand)
Maquiné—Vale do Forqueta 2	29°33′0″ S	Atlantic moist forest	Reference	> 150 years	12
	50°10′48″ W		4 Succession stands	10, 18, 22, 28 years	3 (for each stand)
Maquiné—Vale da Encantada	29°36′43.2″ S	Atlantic moist forest	Reference	> 150 years	12
	50°11′16.8″ W		7 Succession stands	7, 15, 24, 45 years	3 (for each stand)
São Francisco de Paula (Pró-Mata)	29°28′51″ S	Araucaria forest	Reference	> 150 years	12
	50°10′42″ W		4 Succession stands	∼ 20 years	3 (for each stand)
Cachoeirinha	29°52′41″ S	Seasonal forest	Reference	> 75 years	15
	51°05′48″ W		2 Restoration stands	12 years	7; 4
Canela	29°22′43″ S	Seasonal forest	Reference	> 100 years	15
	50°43′50″ W		3 Restoration stands	8 years	6; 5; 3
Santa Tereza (StTereza)	29°09′27″ S	Seasonal forest	Reference	> 100 years	15
	51°41′45″ W		1 Restoration stand	10 years	13

Each site comprises one reference forest and a set of secondary forest stands (restoration or successional forests that compose the study sampling units). Functional composition and diversity were standardized within each site, by comparing secondary forest values with baseline values of their respective site reference. Forest stands comprise a distinct number of plots (100 m^2) for the tree stratum in reference forests and for the canopy of secondary forests; in each secondary forest plot, subplots were used for sampling the regeneration component (see Methods for details).

closed canopy. Structural characteristics of this stratum were also evaluated, including tree height, abundance and total basal area. By describing these features we intend to explicitly analyze the potential effect of these canopy trees (overstory) on the understory regeneration. The *regeneration component* was considered to be saplings from tree and treelet species with height $\geq$ 1.50 m and DBH $<$ 5 cm.

Sampling design differed between study sites, so there is a variation in the number of stands and plots depending on the study site (**Table 1**). For the tree stratum in reference areas and the canopy of secondary forests, plots were 100 m^2 in size, but the number of plots per stand varied depending on site characteristics. For the regeneration component, the sampling within each 100 m^2 plot varied from 12 to 40 m^2: in areas where restoration interventions were conducted (Cachoeirinha, Canela, and Santa Tereza), sampling consisted of three subplots of 4 m^2 (i.e., 12 m^2 per plot), while in the successional areas (Maquiné and São Francisco de Paula), sampling consisted of four subplots of 10 m^2 in size (i.e., 40 m^2 per plot). For our analysis, sampling units consisted of each secondary forest stand with a distinct age in each study site (i.e., six sampling units in restoration sites and 25 in successional sites; **Table 1**). Data from reference forests were only considered as baseline values, being used to calculate the dissimilarity in functional composition and diversity with the secondary forest stands within each study site (see Statistical analysis for more details). Data on species composition was averaged for number of individuals per 100 m^2 per forest stand.

Functional Traits

We selected traits related to resource acquisition, structure, establishment, and reproduction. Resource acquisition traits are represented by leaf traits—leaf area (LA, cm^2), specific leaf area (SLA, cm^2/g), leaf dry-matter content (LDMC, mg/g), leaf nitrogen and phosphorus content (LNC and LPC, respectively, %), and the ratio of leaf nitrogen and leaf phosphorus content (LNC: LPC). These traits are related to photosynthetic assimilation, leaf stem structures, and nutrient concentration (Wright et al., 2004; Poorter et al., 2008). Wood density (WD, g/cm^3) is related to stem structures, hydraulic conductance, and competitive ability (Poorter et al., 2008; Chave et al., 2014). Plant height is another key trait used to explore species competitive ability, however, in the present study, we did not include it as a trait because we used field-measured canopy height directly as a predictor variable in the models. Finally, reproductive traits are represented by seed mass (SM, g) and fruit size (FS, small: up to 5 mm of a mean size, medium: between 5.1 and 14 mm, large: larger than 14.1 mm (Githiru et al., 2002), which are related to seed dispersal and establishment (Pérez-Harguindeguy et al., 2013).

Leaf trait information was obtained from our Plant Ecology Lab at the Federal University of Rio Grande do Sul (LEVEG-UFRGS), which has a functional trait database based on field samples collected from individuals of the regional tree species pool that had been collected since 2009. Thus, for the present study, we consider trees measured within the region to calculate trait means per species. Collection and measurement protocols follow Pérez-Harguindeguy et al. (2013). Currently, all data is available under request from the TRY database (Kattge et al., 2020). Wood density was mostly obtained from the literature (Chave et al., 2014; Zimermann Oliveira et al., 2019), as well as tree reproductive traits (e.g., Sobral et al., 2006; Galetti et al., 2011; Seger et al., 2013). The list of species per study site and their mean trait values can be seen in **Supplementary Table 6**.

Statistical Analysis

The community-weighted mean of traits (CWM) was used as a functional composition measure (Garnier et al., 2004), while community functional diversity was represented by Rao's entropy index (Botta-Dukát, 2005). Before CWM and RaoQ calculation, we tested the correlation between functional traits. We excluded LPC due to its high correlation with LNC ($r = 0.60$) and retained the remaining traits in the analyses: LA, SLA, LDMC, LNC, LNC:LPC, WD, SM, and FS.

For objective (i), we calculated CWM values for each trait, based on a matrix of species abundances, and RaoQ for each sampling unit of secondary forests (regeneration component) and reference sites (tree stratum). We then tested the association between forest age and CWM values for each trait using simple linear regressions, standardizing trait values within each study site before fitting the models. The age of forest was log-scaled prior to the analysis.

For objective (ii), we first log-transformed values of LA, SLA, LNC, LNC:LPC, and SM, and standardized all traits to zero mean and unit variance [using the "decostand" function in the *vegan* package (Oksanen et al., 2019)]. Following this procedure, with the matrices of species abundance per stand and species by traits, we calculated CWM and RaoQ values for (1) the tree stratum of the reference forests, (2) the regeneration component of the successional/restoration stands, and (3) the canopy of the successional/restoration stands, using the *Syncsa* package in R (Debastiani, 2020).

Functional composition and diversity of the tree stratum from reference forests were used to set baseline values (target) for each site (**Table 1**), whereas the regeneration component of the successional/restoration stands was used to set the status of secondary forest regeneration. Based on this, we calculated the dissimilarity between the regeneration component and the respective reference baseline (i.e., within each site) to evaluate how distant (or similar) from the target tree regeneration of secondary forest stands were. For CWM values, we used the pairwise Euclidean distance between each regeneration community and their reference ("CWM.dist") to reflect the functional composition dissimilarity of tree regeneration communities in secondary forest stands with its target forest. For RaoQ values, we directly calculated the difference (RaoQ.diff) between the values found in each reference and regeneration stand: [$\text{RaoQ.diff} = \text{RaoQ}_{\text{reference}}\text{-}\text{RaoQ}_{\text{regeneration}}$]. This parameter thus shows if regenerating tree communities are reaching similar functional diversity values (near zero) or if they have lower (positive values) or higher (negative values) diversity than their reference forests. As the values of CWM.dist and RaoQ.diff consider comparisons within each site, we were able to control for differences associated to forest type, species pool, and regeneration process (succession or restoration), and only the differences in terms of functionality (composition and diversity) were considered as response variables in the statistical analyses. We repeated this procedure three times: with all traits analyzed together, with leaf traits only and with reproductive traits plus wood density (named "reproductive traits," hereafter). Due to high correlations ($r \geq 0.70$) between some of the variables generated by this procedure (see **Supplementary Table 1**), we selected the following response variables to be used in the models: CWM distance for leaf and reproductive traits ($\text{CWM.dist}_{\text{leaf}}$ and $\text{CWM.dist}_{\text{rep}}$), and RaoQ difference for all traits ($\text{RaoQ.diff}_{\text{all}}$).

Community data of the established canopy in successional/restoration stands was used to determine the predictor variables in our analysis, which were related to functional composition (CWM), diversity (RaoQ), and structure (total basal area, abundance, canopy mean height and variance). We conducted Principal Component Analyses (PCA) with canopy CWM traits in order to synthesize the main functional composition axes associated with this component. We performed three different PCAs: one including all traits, a second using only leaf traits, and a third with only reproductive traits. We then evaluated correlations between the first two axes of each PCA to select variables (functional composition axes) to be used in the models (see below). In order to meet model analysis requirements, we conducted log-transformation on stand age and square-root transformation on basal area and then standardized all predictors to mean zero and unit variance.

For all three response variables described above ($\text{CWM.dist}_{\text{leaf}}$, $\text{CWM.dist}_{\text{rep}}$, $\text{RaoQ.diff}_{\text{all}}$), we fitted linear mixed models in order to evaluate the effect of predictor variables from the secondary forest canopy on regeneration trait compositional and diversity differences. Site (**Table 1**) was used as a random effect to control for local conditions. We first determined four main groups of predictor variables, each with a set of operational variables (**Supplementary Table 2**): Stand age (years after fallow or from the end of restoration activities), Canopy structure (structural variables), Functional composition (PCA axes originated from CWM values), and Functional diversity (RaoQ's values). Within each group of variables, we tested for correlations between variables (**Supplementary Tables 3**, **4**) and only kept variables with $r < 0.70$. Predictor variables used in our full models were: stand age; basal area (canopy structure variables); PC1_{leaf}, PC2_{leaf}, and PC2_{rep} (canopy functional composition variables); and RaoQ_{all} (canopy functional diversity variable). We additionally used the variance inflation factor (VIF) to test for multicollinearity among these variables before running the regression models of each response variable. We found no inflation among the chosen variables. We also accounted for the presence of spatial autocorrelation between our plots by fitting each model with and without an autocorrelation structure (i.e., linear, spherical, exponential, Gaussian, and rational quadratics relations based on local X and Y coordinates), and then selecting the model with the lowest AICc. This diagnosis showed no significant spatial structure regarding our response variables. Finally, regressions were conducted using the full model for each response variable and then running a backward selection (using the "stepAIC" function). The optimal model was considered the one with the lowest AICc (Burnham and Anderson, 2002). Variables considered significant within each optimal model were analyzed based on their confidence intervals. We performed all statistical analyses in R v.3.6.1 (R Core Team, 2019).

RESULTS

The associations between forest age and functional composition or diversity showed a high range of variation in tree regeneration in secondary forests, even between forests with similar ages (**Figure 1**). Significant relationships between forest age and functional composition values were observed for leaf dry-matter content and seed mass (positive association) and leaf nitrogen content (negative association) (**Figure 1**). The ratio between nitrogen and phosphorus (LNP:LPC) also increased with stand age (with a marginally significant *p*-value of $p = 0.057$).

Principal Component Analyses indicated functional composition patterns from the canopy of secondary forests and synthesize the differences according to leaf and reproductive traits (**Figure 2**). For leaf traits, the first PCA axis (PC1_{leaf}) showed a variation from communities where trees have mostly acquisitive traits—higher LA, LNC and SLA (positive scores)—to communities with higher dominance of trees with conservative traits and small leaves, especially in restoration sites (warm colors), but also in some successional stands (**Figure 2A**). The second leaf trait axis (PC2_{leaf}) was associated with tough leaves (higher LDMC) and higher limitation of nitrogen (LNC:LPC). For reproductive traits and wood density, large fruit size, and denser wood trees separated communities along the first PCA axis (PC1_{rep}), whereas the second axis (PC2_{rep}) represented a gradient from larger seed mass values (positive scores) to smaller fruits (**Figure 2B**). Axes PC1_{leaf}, PC2_{leaf}, and PC2_{rep} constitute predictor variables used in the models that evaluated drivers of community regeneration dissimilarities with reference targets (see below).

Results from linear mixed models indicated three predictors for $\text{CWM.dist}_{\text{leaf}}$, two for $\text{CWM.dist}_{\text{rep}}$, and four for $\text{RaoQ.diff}_{\text{all}}$ in their respective optimal models (**Figure 3**, **Supplementary Table 5**). The optimal model for $\text{CWM.dist}_{\text{leaf}}$ showed a positive influence of PC1_{leaf} (which represents an acquisitive strategy gradient), and a negative effect of basal area (**Figure 4B**) on the functional distance between secondary forest stands and their reference forests (**Figure 4A**). This indicates that the regeneration component of secondary forests is functionally more similar to their reference baseline when the canopy trees are composed by species with more conservative traits (lower LA, LNC, and SLA) and under forest stands with higher total basal area of canopy trees. The selected optimal model for $\text{CWM.dist}_{\text{rep}}$ showed a negative influence of basal area on the functional composition distance (**Figure 4C**), evidencing a regeneration component functionally more similar to reference forests in communities characterized by larger trees on the upper stratum. The optimal model for functional diversity ($\text{RaoQ.diff}_{\text{all}}$) indicated a significant positive association with stand age (**Figures 3**, **4D**). Values of $\text{RaoQ.diff}_{\text{all}}$ close to zero indicate similar functional diversity between the regeneration component and their reference forest, whereas positive values indicate lower diversity in the regeneration component. Thus, regenerating tree communities of older secondary forests showed lower functional diversity than the observed in their reference forests and early secondary forests.

DISCUSSION

In this study, we show that functional leaf trait composition and total basal area of the established canopy, as well as forest age, determine the functional patterns of natural tree regeneration in the understory of secondary subtropical forests (ranging from 6 to 45 years old). Leaf attributes of the upper stratum trees in early to intermediate secondary forests, mainly composed by early colonizers in successional forests and/or planted trees in restoration sites, determine how similar the regenerating trees communities are when compared to the observed functional composition patterns in reference mature forests. Community traits similarity was higher in sites where there is a higher amount of canopy tree basal area. We additionally show that the functional diversity of regenerating communities was lower in mid-successional forests (20-45 years) when compared with younger stands and with reference forests. Considering that functional similarity between regenerating communities and their reference forests is the desired target in order to recover ecosystem functions of the formerly existing forests, leaf functional traits of canopy trees that early colonize degraded areas and/or are planted for restoration must be considered as important features in the successional process, especially for restoration purposes.

Functional Composition and Diversity of Regenerating Trees Across Forest Age

Our results indicate an overall dispersion of trait community-weighted means in the successional forests, without clear trajectories along the age of successional forests for many individual traits, and also for functional diversity. However, seed mass, leaf dry-matter content, and the proportion of nitrogen and phosphorus on leaves (both LNC and LNC:LPC) showed significant relationships with forest age. Seed mass had the strongest relationship, showing a continuous increase in community mean values with forest age. This is in accordance with other papers that found a decrease in the proportion of small-seeded species with increased forest age (Warring et al., 2016). Large or heavier seeds are usually found in intermediate to advanced stages of succession, as they are usually associated with animal dispersal (Tabarelli et al., 2008), which takes longer to recover after disturbance. Leaf traits LDMC, LNC, and LNC:LPC also evidenced an expected change toward mature forest communities, showing a prevalence of more conservative attributes across successional time in moist tropical forests (Lohbeck et al., 2013; Fernandes Neto et al., 2019). Leaf nitrogen-phosphorus ratio increases with forest age, evidencing a potential nitrogen limitation in initial successional forests and a phosphorus shortage mainly observed in old-growth forests (Zeng et al., 2017). This ratio can be a useful indicator of nutrient limitation for productivity (Townsend et al., 2007). However, the transition state between nitrogen and phosphorus limitation is a ratio of 14–16, and our community values ranged from 11.7 to 15.8 (mean = 14.1), indicating almost no limitation for phosphorus, but maybe for nitrogen in some early-stage communities. For the other traits studied here (leaf

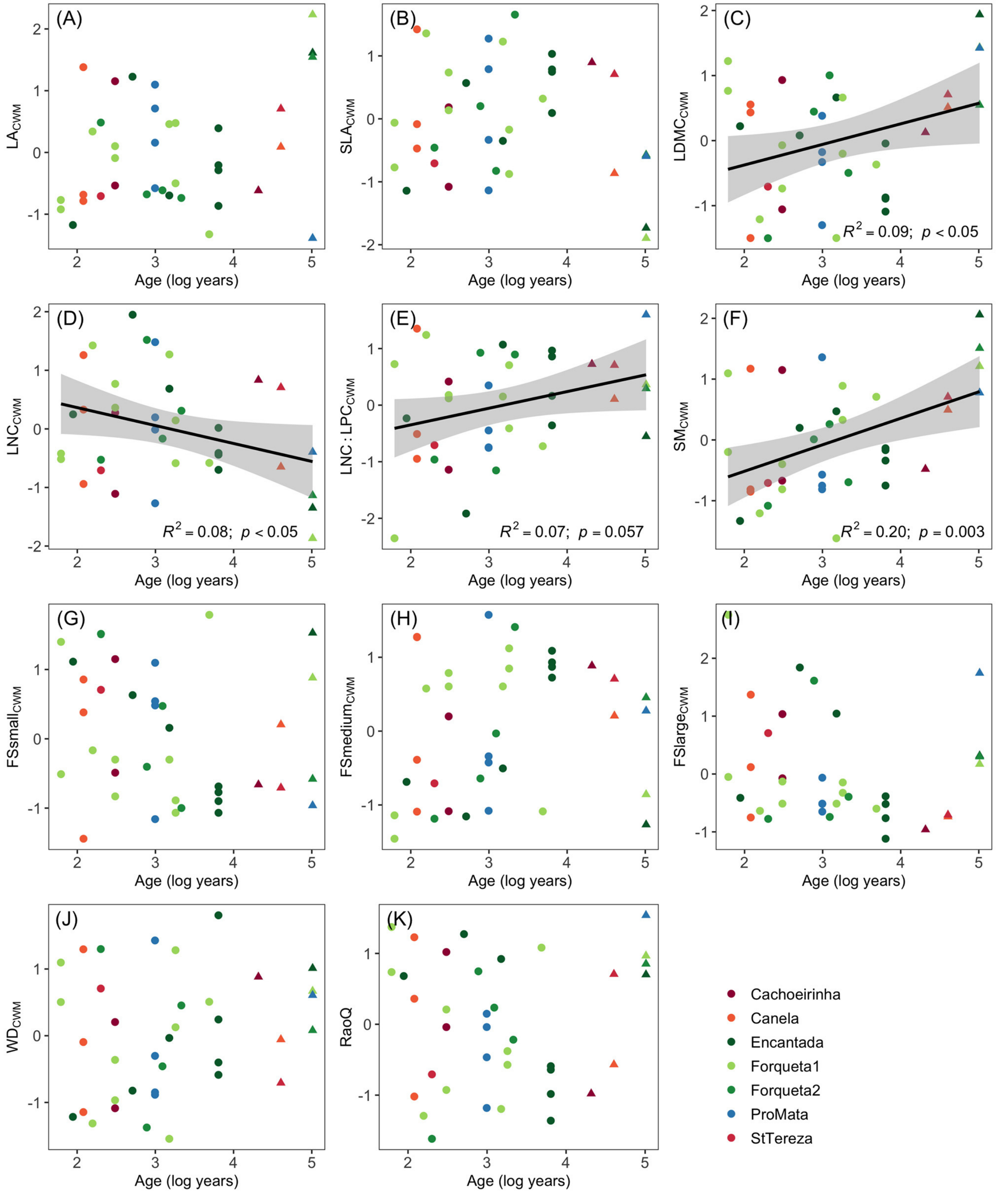

FIGURE 1 | Scatter diagrams of functional trait composition (CWM: community-weighted means; **A-J**) and diversity (RaoQ: based on all traits; **K**) from the tree regeneration component of secondary forests of southern Brazilian Atlantic Forest against the age since regeneration started. Successional secondary forest sites are Encantada, Forqueta1, Forqueta2, and ProMata (green-blue colors), while restoration sites are Cachoeirinha, Canela, and StTereza (warm colors). Values for the tree stratum of reference forests are also given and correspond to the oldest forests in the right-hand side of axis x (indicated in triangles). Regression lines indicate significant associations ($p < 0.05$ or $p = 0.057$ for **(E)**; see text for further information). LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LNC:LPC, leaf nitrogen-phosphorus ratio; SM, seed mass; FS, fruit size (sm: small; md: medium; lg: large); WD, wood density.

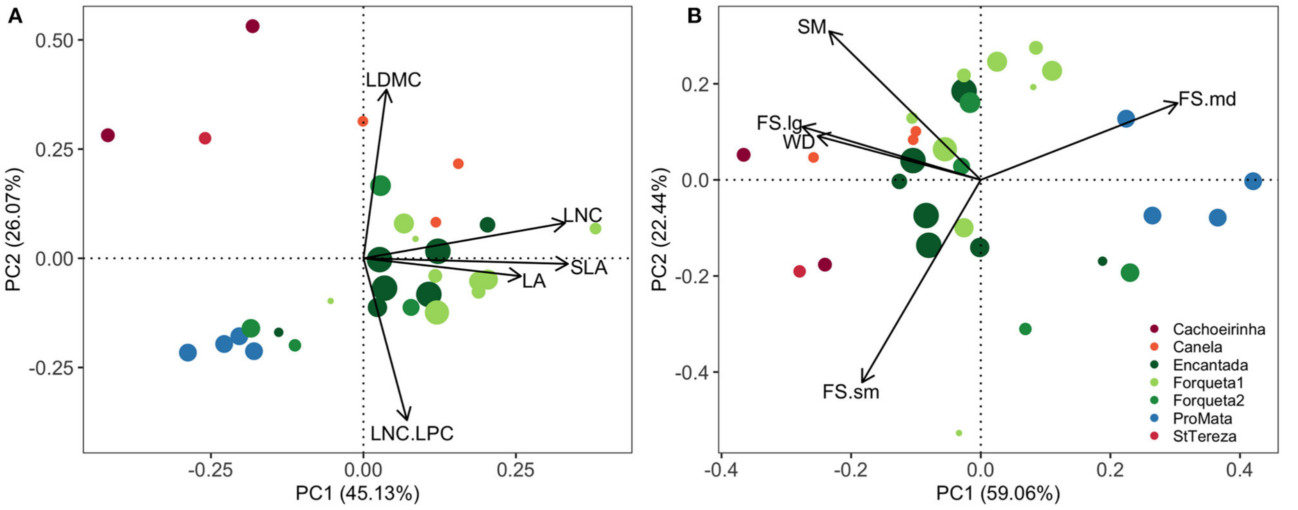

FIGURE 2 | Ordination diagrams of Principal Component Analysis (PCA) for community-weighted means of leaf **(A)** and reproductive **(B)** traits of canopy trees in secondary forests of southern Brazilian Atlantic Forest. Successional secondary forest sites are Encantada, Forqueta1, Forqueta2, and ProMata (green-blue colors), while restoration sites are Cachoeirinha, Canela, and StTereza (warm colors). Circle sizes indicate an increase in the regeneration age of each forest stand. LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LNC:LPC, leaf nitrogen-phosphorus ratio; SM, seed mass; FS, fruit size (sm: small; md: medium; lg: large); WD, wood density. The axes PC1 and PC2 of leaf traits, and PC2 of reproductive traits were considered as predictor variables of functional composition distance and diversity difference between the regeneration component of these secondary forests and their reference baseline (response variables: CWM.dist and RaoQ.diff in **Figures 3**, **4**).

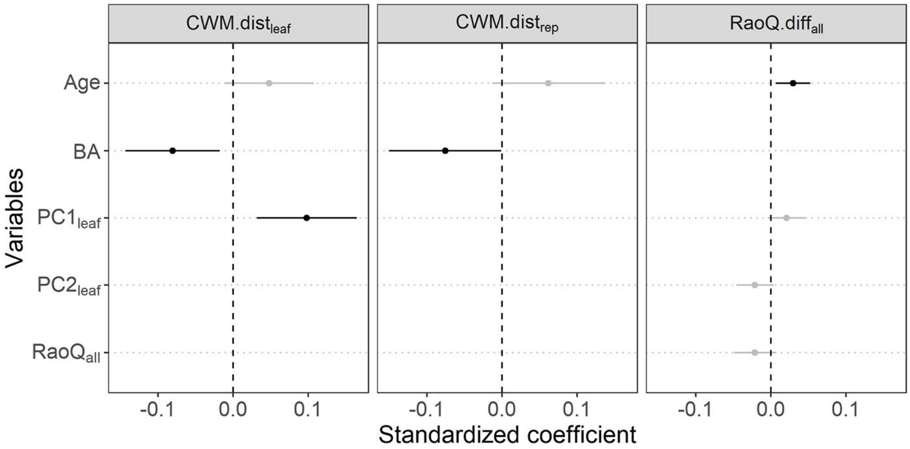

FIGURE 3 | Standardized coefficients of optimal linear mixed models selected for each response variable considered for secondary forests in southern Brazilian Atlantic Forest. Response variables are functional traits composition distance (CWM.dist in terms of leaf or reproductive traits) and diversity difference (RaoQ.diff) between the regeneration component of secondary forest stands and their reference baseline. Selected predictor variables are the age of forest stand since regeneration started (Age) and parameters derived from the canopy of studied secondary forests: total basal area of canopy trees (BA), distinct spectra of strategies ($PC1_{leaf}$ and $PC2_{leaf}$ shown in **Figure 2A**, with a clear acquisitive strategy gradient in PC1), and the functional diversity based on all traits (RaoQ.all). Points are the average estimates of the models and bars correspond to 95% confident intervals (CI). Variables that do not overlap zero (indicated in black) have significant effects on the response variable.

area, SLA, fruit size, and WD), we found a large variation across the studied forests, which prevented us to evidence any trend with forest age. One could improve community assembly predictions and understanding of natural regeneration process along with forest age development, by considering intraspecific trait variability. Plant functional traits vary among individuals of the same species, especially when environmental conditions change (Albert et al., 2010; Siefert et al., 2015), but here we were not able to account for intraspecific variability within the studied species.

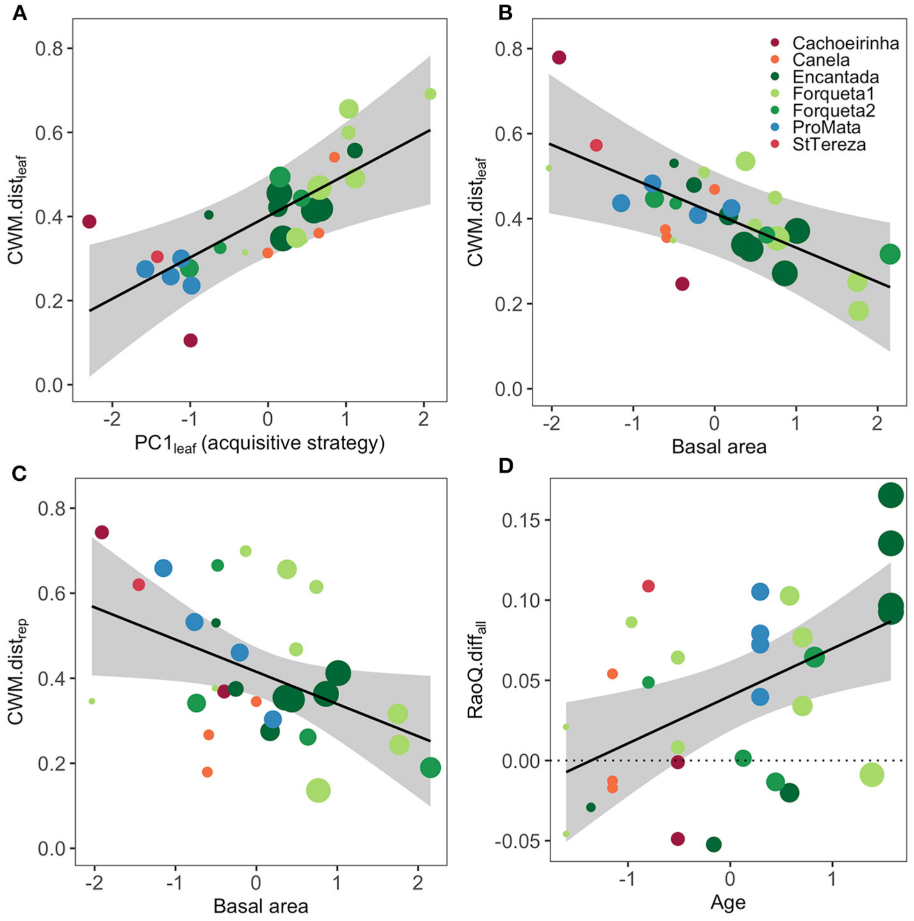

FIGURE 4 | Scatterplots of significant predictor variables of functional trait composition distances (CWM.dist) and functional diversity differences (RaoQ.diff) between the regeneration component of secondary forest stands and their reference baseline in southern Brazilian Atlantic Forest. Successional secondary forest sites are Encantada, Forqueta1, Forqueta2, and ProMata (green-blue colors), while restoration sites are Cachoeirinha, Canela, and StTereza (warm colors). Optimal models are presented in **Figure 3** and **Supplementary Table 5**. In plots **(A–C)**, values in axis y indicate the Euclidean distance between community-weighted means (CWM) of leaf traits (CWM.dist$_{leaf}$) and reproductive plus wood density traits (CWM.dist$_{rep}$) of the regeneration component of secondary forests and their respective reference baseline (i.e., comparisons were restricted to each site, see **Table 1**). In plot **(D)**, values in axis y indicate functional diversity differences: RaoQ.diff$_{all}$ = RaoQ$_{reference}$-RaoQ$_{regeneration}$; values close to zero suggest similar functional diversity between the regeneration component of secondary forest and their reference baseline. Regression lines indicate significant associations ($p < 0.05$; see **Supplementary Table 5**). Circle sizes indicate an increase in the regeneration age of each forest stand.

Time since abandonment in secondary succession and/or after restoration interventions is crucial for natural regeneration processes in tropical and subtropical forests. Tree stem density, biomass, height, and species richness can achieve similar values to old-growth forests in 30 to 50 years of forest regeneration (Guariguata and Osterag, 2001; Letcher and Chazdon, 2009; Poorter et al., 2016; Rozendaal et al., 2019), however successional trajectories can be either deterministic or stochastic. Temporal dynamic of successional trajectories varies widely within and between sites under similar land-use history, challenging the predictability even for structural features (e.g., stem density and basal area) in highly diverse tropical forests (Norden et al., 2015). This unpredictability might be associated with plot identity (i.e., involving processes that vary under local environmental conditions and interactions that occur inside each plot), which can overlap the contribution of age on successional dynamics (Norden et al., 2015). Random assembly patterns might be expected due to the high diversity of tropical and subtropical forests *per se* and to the often-patchy recruitment patterns of species (Fridley, 2013), especially when we think of low-abundant or rare species that predominate in these forest communities.

Determinants of Similarities in Functional Composition and Diversity Between Regenerating Trees and Reference Forests

Tree regenerating communities were more similar to reference forest values in terms of leaf traits as the canopy of established communities was composed mostly by species with conservative plant strategies: lower values of SLA, LA, and LNC. A study that experimentally tested distinct sets of planting trees (animal-dispersed *vs.* wind-dispersed tree species), aiming to restore tropical forests in Mexico, did not find differences in phylogenetic and functional diversity of early communities of recruits (eight years old), assuming that the initial composition did not influence community assembly (Li et al., 2018). Animal-dispersed species are often pointed out as an important component of forest recovery, due to their potential in attracting dispersers from nearby forest remnants and thus increasing the proportion of propagules' arrival (Boukili and Chazdon, 2017; Meli et al., 2017); leaf trait composition, however, is less frequently considered. Here, we found consistent influence of leaf attributes of the canopy on the functional composition of tree regenerating communities. Leaf functional traits of initial colonizers and/or of planted trees affect abiotic conditions—by altering shading patterns and nutrient content in litter and on the soil surface (Poorter, 2009; Rosenfield and Müller, 2020b; Teixeira et al., 2020)—and biotic interactions associated to competition for light and the use of soil resources (Kunstler et al., 2016; Muscarella et al., 2017). These conditions are relevant for mechanisms of tree establishment and growth and might be more relevant than the dispersal/arrival of individuals for the regeneration of secondary forests toward reference baseline values. Dispersal seems not to be a barrier to forest regeneration where the surrounding landscape still have forest remnants to serve as font of propagules and habitat for dispersers (Meiners et al., 2015), and our studied areas do not seem to be limited in terms of propagules arriving from surrounding forests (Zanini et al., 2014; Vicente-Silva et al., 2016; Rosenfield and Müller, 2019).

Functional composition distances between the regeneration component and the reference forests were also associated with the total basal area of the canopy stratum, a parameter of forest structure. Secondary forest stands with a greater sum of basal area of upper trees (canopy) had a regeneration component more similar to the expected target than less structured forests (i.e., with lower values of total basal area). The similarity was greater both in terms of leaf traits and reproductive plus wood density traits, indicating a secondary forest trajectory toward the expected target in terms of the functional composition and, consequently, ecosystem functionality. The functional composition of forest communities is often associated with ecosystem processes and temporal dynamics, representing the effect of the attributes of the most abundant species (mass-ratio theory), instead of the variability of traits (niche complementarity hypothesis), on ecosystem functions (Garnier et al., 2004; Van der Sande et al., 2018; Bordin and Müller, 2019; Rosenfield and Müller, 2020b). Greater similarity with respect to functional composition in these secondary forests may indicate that important ecosystem functions associated with these traits, and encompassing different compartments of the system (e.g., nutrient cycling, trophic interactions), may be recovering as well (Rosenfield and Müller, 2020a). Less structured secondary forests often fail to offer adequate conditions, such as more shadowed environments, for the establishment of secondary tree species (Holl et al., 2018). Regenerating trees in such communities might be composed by species with distinct strategies, e.g., pioneer species, thus increasing the distance from reference forests in terms of leaf and reproductive traits.

Differences in functional diversity values of tree regeneration communities in secondary forests when compared to reference values were predicted by forest age. The best model included functional composition and diversity variables, but only age was significant and with a low predictability power. Forest age was positively associated with the differences in RaoQ, indicating that early-stages of succession (6–12 years) have more similar values to reference forests (points close to zero located in the left side of **Figure 4D**) than mid-stage secondary forests (15–45 years), that still showed lower values of functional diversity in the regeneration component (positive values of RaoQ.diff; right side of **Figure 4D**). This is partially in accordance with a study that found decreasing values of functional diversity along succession (from 10 to 40 years) in tropical forests, but higher functional diversity in old-growth forests (Lasky et al., 2014). In this study, the pattern of decreasing functional diversity along succession was found when analyzing all traits together in a single index (similar to what was performed in our study), however diversity values based on single traits showed slight increases with stand-age (Lasky et al., 2014). In our study, RaoQ for all traits was highly correlated with RaoQ calculated for leaf traits and reproductive traits separately, so the observed pattern was consistent among the sets of chosen traits and not skewed by one or another selected set (Zhu et al., 2017).

The results found for functional diversity patterns can be related to transient community stages, where pioneer and secondary tree species co-occur in the regeneration component of early-stage successional forests without the dominance of only a few species. This leads to functional diversity values to be similar to the values found in the tree stratum of reference forests. High rates of species arrival and the absence of severe abiotic or biotic filters, arresting establishment, might be contributing to high functional diversity values in the early-stage secondary forests studied here. Along successional time, some shade-tolerant tree and treelets (e.g., *Cupania vernalis*, *Casearia silvestris*, *Mollinedia shottiana*, *Piper aduncum*, *Psychotria suterela*) eventually become more dominant in mid-stage forests, due to high colonization rate and low mortality in the understory. This dominance affects RaoQ values, which considers pair-wise traits' distance weighted by species abundance (Botta-Dukát, 2005). As self-thinning processes occur (Stephenson et al., 2011), decreasing the dominance of these species, there should be an increase in functional diversity, increasing the similarity with reference forests. However, functional diversity does not often vary across succession (e.g., Lohbeck et al., 2012; Böhnke et al., 2014), as the turnover of species along the regeneration time can maintain similar patterns of trait dispersion within communities.

CONCLUSION

A great portion of current subtropical and tropical forest coverage comprises secondary forests, which increases the role of these forests for biodiversity conservation and the provision of ecosystem services (Chazdon et al., 2009; Martin et al., 2013; Pichancourt et al., 2014). Even though many studies have shown that the recovery of forest structure parameters and even species diversity is possible in a relatively short time of succession (e.g., Guariguata and Osterag, 2001; Letcher and Chazdon, 2009; Poorter et al., 2016), species composition is hard to recover or restore (e.g., Dent et al., 2013; Suganuma et al., 2014; Rozendaal et al., 2019). Understanding whether functional composition and diversity of regenerating tree communities increase in similarity when compared to reference forests is essential in order to evaluate the potential return of ecosystem functions and services from these secondary forests. Our study offers an opportunity to understand the effect of first colonizers and/or planted species in the functionality patterns of regenerating tree communities in the understory of secondary forests originated from both passive and active restoration processes.

We provided some perspectives about the importance of forest structure and leaf trait composition of canopy species in the functional patterns of the future tree component of secondary forests (i.e., tree regeneration component). These perspectives go beyond any potential influence of climatic and soil conditions, as they concern natural regeneration of forests under sites that differ in terms of environment and species pool. Leaf trait composition of trees from the upper stratum influences the similarity of ongoing successional communities, indicating potential priority effects of initial assemblies on natural regeneration processes. Thus, despite the great potential of natural regeneration in tropical and subtropical moist forests, under the scope of ecological restoration, practitioners should consider leaf attributes that characterize plants with acquisitive strategies that grow fast to compose the set of species for early-stage communities, by planting or by thinning in the first years of recovery. This might turn initial canopy structure more similar to the observed in natural successional forests and might accelerate the increment of tree stem basal area. As we saw, forest stands with higher basal area of canopy trees can improve the functional similarity of regenerating trees with the expected functional target. In addition, the presence of species with conservative strategies in the canopy of early and intermediate successional forests seems to improve similarities of tree regeneration communities with target functional patterns; thus, species with such strategies (low SLA, LA, LNC) should also be considered in restoration plantings, especially after the planting of fast-growing species. Finally, the influence of recovery time on the regeneration of functional patterns along the successional and restoration processes is uncertain, making the monitoring of the tree regeneration component necessary to inform if, when, and where secondary forests are becoming functionally similar to their reference forest ecosystems.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: Most data are available as **Supplementary Material**; additional information might be available under request to the authors. Requests to access these datasets should be directed to Sandra Cristina Müller, sandra.muller@ufrgs.br.

AUTHOR CONTRIBUTIONS

SM conceived the idea of the paper. RB, KB, JK, and MR participated in the collection of field data. SM, MR, KB, and JK performed statistical analyses. MR and KB prepared the figures. SM and MR led the writing of the manuscript. All authors contributed to the collection and compilation of functional trait data, discussed the results and thoroughly revised the manuscript, and contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.572864/full#supplementary-material

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Dynamics of Natural Regeneration: Implications for Landscape Restoration in the Atlantic Forest, Brazil

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This study aimed to understand post-agricultural natural forest regeneration in the Southern Brazilian Atlantic Forest and its possible role as a cost-effective, passive approach to forest restoration. The study characterized vegetation structure, floristic composition, and the dynamics of secondary forest chronosequences. Data were collected from 159 plots (10 × 10 m each) across forest remnants in Santa Catarina State, covering forest ages that ranged from 2 to 60 years of regeneration after swidden agriculture. Only areas with no signs of degradation were sampled in order to provide a description of vegetation characteristics that could be used to identify and monitor natural regeneration. A total of 11,455 woody plants were identified and classified into 334 species representing 71 families. As the succession process unfolds, the continuous turnover of species makes forests more diverse and structurally complex. Floristic similarity among forest types is observed during the early stages of succession, but decreases over time. Pioneer species dominate young secondary forests, representing about 40% of the basal area up to 10 years of regeneration. Shade-tolerant species start colonizing the sites at early ages; however, they become more important structural elements only after 30 years of succession. The observed patterns of forest structure and species diversity largely conform to the post-agricultural succession seen in many tropical forests. The high species diversity found in this study highlights the importance of natural regeneration as a strategy to restore ecosystems. Floristic data can be used as a reference for choosing suitable species for active restoration, as well as contributing to the design of integrated restoration strategies. We herein reinforce the potential of natural regeneration as part of large-scale restoration programs, which would be particularly attractive to family farmers by the low cost of supplies and labor.

Keywords: forest succession, secondary forest, passive restoration, swidden agriculture, chronosequences

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INTRODUCTION

The Brazilian Atlantic Forest region, home to more than 125 million people, contributes to 70% of the gross domestic product, and it is the center of the Brazilian industrial economy (Scarano and Ceotto, 2015). At the same time, the biome is considered one of the "hottest" of biodiversity hotspots, holding 2,420 vertebrates and 20,000 plant species, most of them with high levels of endemism (Rezende et al., 2018). However, historical fragmentation and loss of biodiversity have also made it one of the world's most threatened hotspots, as 84–88% of forest cover has vanished (Soares-Filho et al., 2014). In addition, many plant and animal species are endangered, the equivalent of 60% of the entire list of threatened species for both flora and fauna in Brazil (Joly et al., 2014). Maintaining the remnants of such species-rich biome has been a challenge for conservationists in a region marked by a permanent pressure for economic development.

Fast conversion of forest to other land uses and forest degradation represent a global phenomenon, calling for international organizations to establish programs to restore lost or degraded forest ecosystems. The Aichi Target, for example, set a goal of restoring at least 15% of degraded ecosystems (Jørgensen, 2013). The Bonn Challenge, another initiative, has set a global target of restoring 150 and 350 Mha of degraded/deforested lands by 2020 and 2030, respectively (www.bonnchallenge.org; IUCN, 2011). Aligned with these efforts, the Brazilian government in 2009 launched the Atlantic Forest Restoration Pact, an ambitious action plan to restore 15 Mha of degraded/deforested lands by 2050 in the Atlantic Forest region (www.pactomataatlantica.org.br/) (Crouzeilles et al., 2019).

To guide these efforts in restoring forest ecosystems, three main approaches have been used: (i) natural regeneration (passive restoration or spontaneous regeneration), which relies on the resilience of the ecosystem without, or after, removing the degrading factors; (ii) assisted regeneration, which prescribes the application of practices to facilitate recovery processes; and (iii) active restoration (plantation), which consists of intensive human intervention to accelerate recovery (Holl, 2020). The choice of restoration method should be based on site resilience, as well as the characteristics and goals of the project. Many authors suggest an integrated strategy whereby, for example, passive restoration, nucleation and plantation methods are combined to achieve high levels of species diversity, biomass productivity and ecosystem functions, while balancing inputs and costs (Vogel et al., 2015; Bechara et al., 2016; Meli et al., 2017; Trentin et al., 2018).

Assisted and active regeneration methods can be effective in accelerating restoration and reaching the final target ecosystem condition (Campoe et al., 2010; Rodrigues et al., 2011; Roa-Fuentes et al., 2015; Sujii et al., 2017; Brancalion et al., 2019a). However, costs are usually high (Benini et al., 2017; Crouzeilles et al., 2017) and mainly affordable only to large companies, such as the mining sector, or large-scale funded projects. Moreover, the success of restoration initiatives is not guaranteed by high levels of investment as outcomes vary from near-total success to complete failure (Souza and Batista, 2004; Crouzeilles et al., 2016; Toledo et al., 2018). Barriers to ecological restoration in highly degraded landscapes include lack of seed sources, poor germination, lack of colonizing fauna, weed infestation, as well as soil degradation (Garcia et al., 2016).

Survival of seedlings is one of the major limiting factors to action-based restoration initiatives (Holl, 2002; Grossnickle, 2012), leading to failure in forming a tree cover or maintaining the achieved characteristics of the ecosystem in the long run. This lesson was learned from one of the pioneer and large-scale restoration experiences in the Mata Atlântica region (Kageyama and Isshiki, 1992). The project succeeded in recovering a forest-like structure over a large deforested land, but the length of time it took for establishment of the forest, in addition to the failure of certain species to grow, forced reevaluation of the methodology (Souza and Batista, 2004).

Idealizing a quick restoration of ecosystem functions, legislators have demanded high species diversity as a requirement of restorations activities. For instance, the formerly enacted Resolution SMA 08/2008 regulated forest restoration projects in São Paulo State and required at least 80 species before a project could be considered complete (Secretaria do Meio Ambiente do Estado de São Paulo, 2008). Gomes et al. (2013) challenged the rationale of such requirement, arguing over such issues as the availability and variety of seedlings needed, the cost, and, mainly, the uncertain survival of many species. The authors also argued that even young, naturally regenerated forests frequently do not shelter such diversity of tree species.

Across the Brazilian Atlantic Forest region, as in much of the tropical world, socio-ecological systems demand low input of labor and supplies in exchange for optimal land/forest restoration projects. In Santa Catarina State, for example, 78% of farms are smaller than 50 hectares, and they are owned by family farmers (IBGE, 2019), most of whom cannot afford, or are not willing, to invest in the requirements mandated by environmental laws (Alarcon et al., 2010). Alarcon et al. (2017) reported that farmers in Santa Catarina State would agree to restore deforested land that they owned, but only in exchange for some monetary compensation. In such contexts, then, passive restoration becomes the most practical strategy.

Natural regeneration has been considered an effective nature-based solution for recovering tree biodiversity (Brancalion et al., 2019b; Rozendaal et al., 2019; Crouzeilles et al., 2020), and it may play an important role in the scale-up of landscape restoration to achieve multiple social and environmental benefits at minimal cost, especially in tropical regions (Chazdon and Guariguata, 2016). This approach can rapidly restore the forest at sites recently cleared, considering such factors as the presence of residual trees, seedlings and seed banks of local species, and biodiversity-rich forest across the landscape (Lamb et al., 2005). Moreover, the success of this approach in the Atlantic Forest region could possibly pave the way for reversing deforestation and degradation, mitigating water and food insecurity, improving livelihoods, and promoting ecosystem-based adaptation to climate change (Rezende et al., 2018).

Naturally regenerating forests can provide a wide array of ecosystem goods and services, as well as, support rural economies and livelihoods (Chazdon et al., 2020). Even young secondary forests, that are spread out in isolated patches could help mitigate climate change and recover species of high conservation concern, while, at the same time, improving landscape connectivity (Oliveira et al., 2019a; Matos et al., 2020), and working as a source of seed dispersal for the restoration process. Natural regeneration has also been suggested as a cost-effective method of achieving high carbon sequestration potential with multiple benefits for biodiversity and ecosystem services (Chazdon et al., 2016). Such combination of factors is frequently present in our region of interest since forest cover for Santa Catarina is estimated at around 30% (Vibrans et al., 2013a, 2020). Several studies have demonstrated the resilience of local native forests and their rapid regrowth, even after repeated swidden cultivation, a prevalent land use in the region until recently (Siminski and Fantini, 2007; Liebsch et al., 2008; Siminski et al., 2011; Fantini et al., 2017; Lintemani et al., 2019).

Professionals and researchers frequently evaluate degraded areas based on a mature forest model. Instead, the resilience of the forest at landscape scale should be taken into account, as well as, the potential of natural regeneration to re-establish a degraded ecosystem to a sound condition at a local scale. Therefore, it is important that practitioners recognize how these forests respond to human disturbances at multiple levels of ecological organization and spatiotemporal scales in order to respond to the threats posed and the potential opportunities offered by human-modified landscapes in the context of sustainability and regeneration (Joly et al., 2014; Arroyo-Rodríguez et al., 2017).

It is in this context that we evaluated different chronosequences of secondary forests to explore how attributes of regrowth change over time and across forest types in the Atlantic Forest. In a previous study in the same region, we focused on the average of floristic and structural variables in three forest types (Siminski et al., 2011). Now, we examine the data of individual plots that represent different forest ages in order to understand the dynamics of the diversity and structure of secondary forests through succession from 2 to 60 years. The values of species richness, diversity, density, basal area, and aboveground biomass were regressed against forest age to understand the dynamics of forest structure through succession. Species turnover was assessed through the proportion of ecological groups and the identity of the most dominant species. In order to better depict the importance of each ecological group for forest structure, we also regressed the relative values of plant density, basal area, and biomass. We designed our study in a way that examines how species composition, diversity and forest structure of naturally regenerated secondary forests change over time across forest types. Based on data analysis and information collected from vegetation surveys, we discuss the quantitative and qualitative aspects of secondary forests that can be used as indicators to evaluate and monitor natural regeneration in forest restoration programs.

MATERIALS AND METHODS

Study Areas

The study was carried out in 48 small farms located in the counties of Anchieta, Garuva, Concórdia, Três Barras, Caçador, and São Pedro de Alcântara in Santa Catarina state (**Figure 1**). These areas include in three different forest types recognized in the Mata Atlântica Biome, as defined by Brazilian Atlantic Forest Law 11.428/2006 (BRASIL, 2006): Seasonal Deciduous Forest (Anchieta and Concórdia), Mixed Ombrophilous Forest (Três Barras and Caçador) and Dense Ombrophilous Forest (Garuva and São Pedro de Alcântara) (Veloso et al., 1991).

Seasonal Deciduous Forest (SDF) occurs in the Uruguay River basin at elevations ranging from 200 to 600 meters a.s.l., where the predominant climate is Cfa (temperate humid with hot summers), according to Köppen's classification, with an annual precipitation of 1,600 to 2,000 mm (Alvares et al., 2013). It is characterized by a closed canopy dominated by species of Lauraceae, Asteraceae and emergent deciduous species, mostly Fabaceae (Siminski et al., 2011; Vibrans et al., 2012a; Gasper et al., 2013b).

Mixed Ombrophilous Forest (MOF) is usually distributed across plateaus ranging from 500 to 1,500 m a.s.l., with annual precipitation ranging from 1,600 to 2,100 mm. The climate is Cfb (humid temperate climate with moderately hot summers), according to Köppen's classification (Alvares et al., 2013). This forest is characterized by the presence of a supercanopy dominated by *Araucaria angustifolia* and a subcanopy rich in species of Lauraceae, Myrtaceae, Asteraceae, Solanaceae, and Fabaceae (Siminski et al., 2011; Gasper et al., 2013a; Vibrans et al., 2013b).

Dense Ombrophilous Forest (DOF) occurs across the coastal regions at elevations below 700 m a.s.l., where the climate is Cfa (temperate humid with hot summers), according to Köppen's classification. DOF is characterized as having the hottest temperatures among all forest types and an annual precipitation ranging from 1,500 to 2,000 mm (Alvares et al., 2013). DOF has an evergreen canopy dominated by Lauraceae, Melastomataceae, Fabaceae, Rubiaceae, and Myrtaceae, together with an abundance of epiphytes (Orchidaceae and Bromeliaceae) and palm trees (Siminski et al., 2011; Vibrans et al., 2013c; Gasper et al., 2014).

Data Collection and Analysis

We studied chronosequences of secondary forests from 2 to 60 years of age that had regenerated naturally on land previously cultivated under traditional swidden agriculture. We sampled only secondary forests originated from abandoned agricultural fields, with no signs of degradation, because they represent the majority of regenerating forests in the region (Lingner et al., 2020; Vibrans et al., 2020). We sampled only forests located within typical farms in the region (i.e., farms with a mosaic of regenerating forest patches, avoiding samples from isolated secondary forest patches). Our sampling did not take into consideration forest size, slope and aspect, or distance from mature forests; consequently, we did not measure such landscape variables in this paper. At each farm, we asked permission to inventory the forest. Then, the landowner was asked to explain the history of land use, and disturbance, including how long the land had been abandoned. Secondary forest in the region presents a sequence of stages recognizable from its physiognomy: shrubs, small trees, arboreal and advanced arboreal species (Siminski

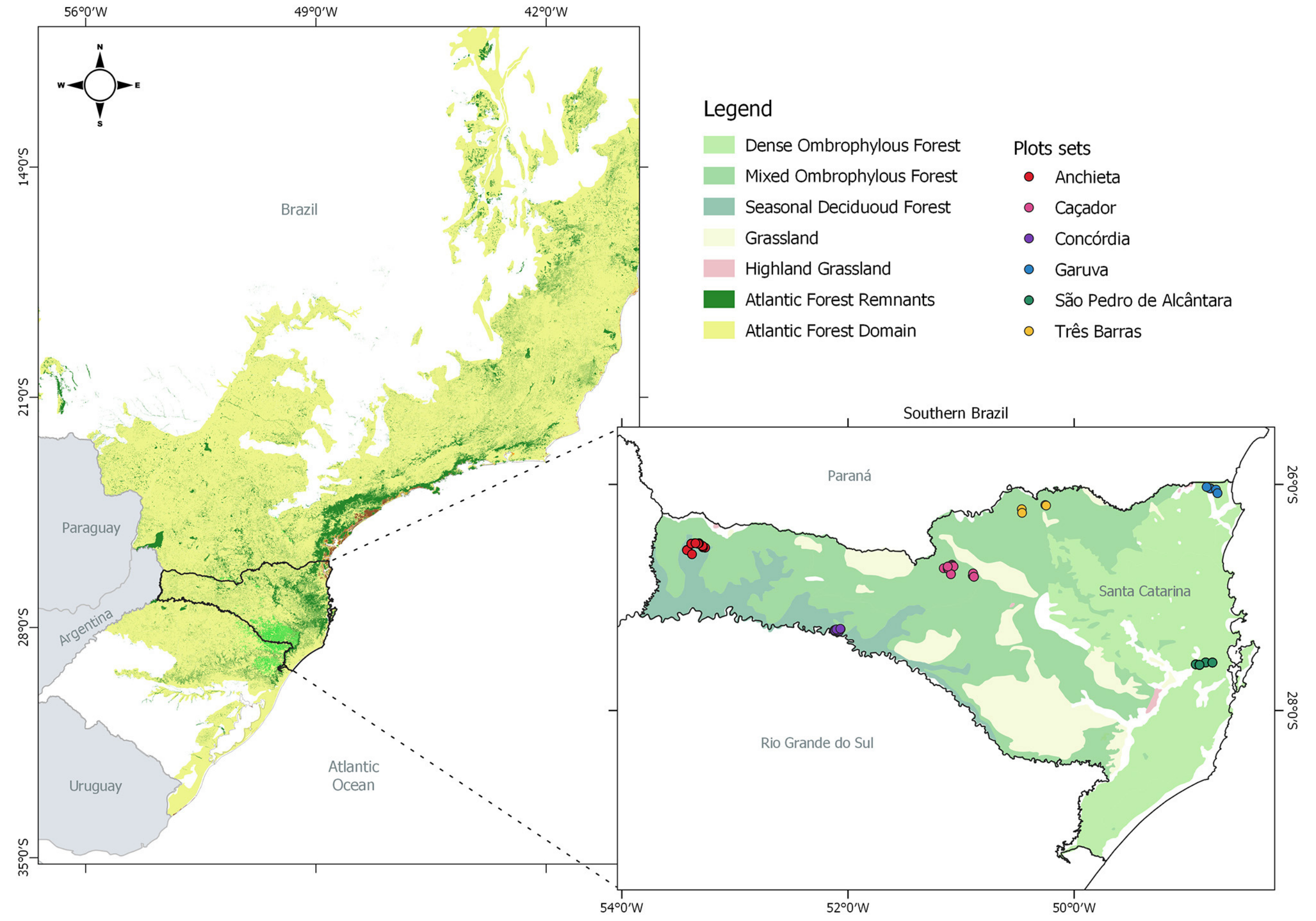

FIGURE 1 | Map of original and remnant Brazilian Atlantic forest. Map of forest types in Santa Catarina State (in detail) and location of the studied sites. Source: http://mapas.sosma.org.br/ (SOS Mata Atlântica, 2020); Application Area Map of Law n° 11.428/2006 (BRASIL, 2006); Klein's phytogeographic (SAR, 2005).

et al., 2011; **Supplementary Figure 1**). We tried to sample an even number of plots at each stage of succession. One plot was set at the center of a homogeneous forest patch, thus avoiding the edge effect on forest structure and diversity.

A total of 159 plots (10 × 10 m each) were inventoried in 2007 (a sampled area of 15,900 m^2), covering secondary forests at different ages in all three forest types: Anchieta (18), Garuva (20), Concórdia (20), Três Barras (8), Caçador (30), and São Pedro de Alcântara (63). In each plot, all woody plants higher than 1.5 m were identified to species level, either in the field or aided by taxonomists. Plants were identified using the classification updated on the *Angiosperm Phylogeny Website, version* IV (Stevens, 2017), as well as *Species 2000 & ITIS Catalog of Life* (Roskov et al., 2019). All individuals were measured for diameter (DBH, cm) and total height (m). Sampled species were classified into ecological groups (pioneer, early secondary, late secondary, and climax), following the criteria proposed by Budowski (1965), which were, in turn, based on bibliographic research (Carvalho, 2003, 2006, 2008, 2010; Santos et al., 2004; Mantovani et al., 2005; Martins, 2005; Klauberg et al., 2011; Vibrans et al., 2012b, 2013b,c; Ferreira et al., 2013; Barbosa et al., 2017). For simplicity, we will use the term "plants" to mean all individuals measured, irrespective of life form (shrubs, trees, palm trees, and tree ferns).

For each secondary forest plot, we calculated the following attributes of vegetation structure: plant density ($stems.ha^{-1}$), basal area ($m^2.ha^{-1}$), aboveground biomass (AGB, $Mg.ha^{-1}$), and importance value (IV) (Müeller-Dombois and Ellenberg, 1974). We also calculated the following attributes of species diversity: species richness (number of species) estimated by rarefaction curve (Mao et al., 2005) and bootstrap method (Smith and van Belle, 1984), rarefied species richness (Hurlbert, 1971), family richness (number of families), species richness, Shannon's diversity (H', nuts. ind^{-1}) and Simpson's diversity (1-D). Rarefied species richness was calculated down to the same number of individuals in the smallest plot (i.e., five individuals). In order to quantify the dominance of species in each forest type, within ecological groups, we calculated the importance value (IV). IV was calculated as the sum from (i) relative frequency; (ii) relative density; and (iii) relative dominance. It was estimated for each species, and the dominant species were selected for each forest type. Dominant species were defined as that set of species, the accumulated IVs which, when ranked from highest to lowest, reached 50% of the total for a given forest type (Finegan, 1996).

Diversity metrics and IV were estimated using the *vegan* package (Oksanen et al., 2019), *BiodiversityR* package (Kindt, 2020), the *FitoR* script (Dalagnol et al., 2013) in RCore Team (RStudio Team, 2019), and the RStudio interface (RStudio Team, 2019). Both rarefaction curve and species richness by bootstrap method were estimated using EstimateS 9.1.0 (Colwell, 2019). Forest biomass was estimated using the allometric equation for tropical forests proposed by Chave et al. (2014): $\mathrm{AGB_{est}} = 0.0559 \times (\rho \mathrm{D}^2\mathrm{H})$, where ρ is wood density, D is the diameter of stem, and H is the total plant height. Wood density was obtained from the database of Chave et al. (2006) for Neotropical tree species and Oliveira et al. (2019b) for species of the Subtropical Atlantic Forest.

Linear mixed-effects models were used to evaluate how forest structure (density, basal area and biomass) and diversity change over time (Gelman and Hill, 2007; Bolker, 2008; Zuur et al., 2009). For analysis of plant density ($\mathrm{stems.ha^{-1}}$), basal area ($\mathrm{m^2.ha^{-1}}$), and biomass ($\mathrm{MG.ha^{-1}}$), we transformed the values to meet the normality of the data and back transformed values are represented in **Figure 2**. We used square transformation and tested the normality with the Shapiro-Wilk test. Thus, one null model was established for each dependent variable: richness dataset, Shannon and Simpson index, density, basal area and biomass. The null model was calculated as: $y_i = \alpha + b_i + \varepsilon_i$, where y is the dependent variable, α is the intercept, b_i is the random effect, and ε_i is error (residual). Another model was established with fixed effect to test the significance among models using ANOVA with Chi-square statistics. This model was calculated as: $y_i = \alpha + \beta \times a_i + b_i + \varepsilon_i$, where y is the dependent variable, α is the intercept, β is the slope, a_i is the fixed effect, b_i is the random effect, and ε_i is error (residual). For each variable, the model has age as a fixed effect, and forest type is the random effect. Next, we evaluated how the contribution of the different ecological groups changes along succession. To accomplish this, we grouped all species into the four ecological groups described above and calculated their relative density, basal area, and biomass. We then analyzed the effects of age and ecological group (fixed effects) on the relative values of each response variable, using forest type as the random effect in mixed-effects models. For all variables individually, age and ecological group was included as fixed effect while forest type as random effect and ecological group was used nested within forest type as random slope. This model was calculated as: $y_{ij} = \alpha + \beta_1 \times a_{1ij} + \beta_2 \times a_{2ij} + b_j \times a_{2ij} + \varepsilon_{ij}$, where y is the dependent variable, α is the intercept, β is the slope, a_{ij} is the fixed effect, b_j is the random effect, and ε_{ij} is error (residual). First, we established the null model for each variable described above and tested the model with fixed effect. Forest type was the random effect. Ecological groups were used as the random slope, allowing the difference among groups to reflect variation on the slope. In total, we fitted five models to estimate relative values of plant density, basal area and biomass, with and without interaction among fixed effects, and with and without random slope nested with random effect.

We also applied a model selection procedure, whereby the models with the lowest delta-Akaike Information Criterion (ΔAIC) were chosen as the best model, for each dependent variable. The ΔAIC is the result of the differences among the AIC of the models fitted for each dependent variable (**Supplementary Tables 3**, **4**). For the best model selected we also calculated the conditional and marginal R-square, which explained the proportion of total variance through both fixed and random effects (**Supplementary Table 2**). The models were fitted with maximum likelihood to compare the null models and models with ANOVA. After selecting the best models for each variable, the distributions of each selected model were verified using the *visreg*( ) function of the *visreg* package (Breheny and Burchett, 2017). To plot the predictors for each model, we used the *bootMer*( ) function of the lme4 package based on the Perform model-based (Semi-)parametric bootstrap for mixed models with 1,000 simulations (Bates et al., 2015). The analyses were performed with the *lme4* package (Bates et al., 2015), *ggpubr* package (Kassambara, 2020), *bbmle* package (Bolker, 2020), *lmerTest* package (Kuznetsova et al., 2017), *MuMIn* package (Barton, 2020) in RCore Team (RStudio Team, 2019), and the RStudio interface (RStudio Team, 2019). For absolute and relative values, a line was fitted to each variable with the predictors of the chosen model (**Supplementary Table 3**), using the *ggplot2* package (Wickham, 2009), *viridis* package (Garnier, 2018a), *viridisLite* package (Garnier, 2018b), and *cowplot* package (Wilke, 2019).

RESULTS

Forest Species Composition and Diversity

A total of 11,455 woody plants were identified and classified into 334 species representing 71 families. The most common families were Myrtaceae (36 species), Fabaceae (32), Asteraceae (26), Lauraceae (24), Rubiaceae (20), and Melastomataceae (16) (**Supplementary Table 1**; see also **Supplementary Table 5** for plants with DBH > 5 cm). Secondary forests in the DOF region presented a higher number of species (220) compared to MOF (122) and SDF (127). Thirty-nine species were common to all three forest types, representing 11% of the registered species. The three forest types presented a high number of exclusive species: 137, 47, and 53 species, respectively, for DOF, MOF, and SDF. The five most abundant species were *Miconia cinnamomifolia*, *Myrsine coriacea*, *Tibouchina pulchra*, *Miconia cabucu,* and *Hieronyma alchorneoides* (DOF); *Baccharis dracunculifolia*, *Matayba elaeagnoides*, *Eupatorium vauthierianum*, *Cupania vernalis,* and *Schinus terebinthifolius* (MOF); *Baccharis dracunculifolia*, *Trema micrantha*, *Nectandra lanceolata*, *Dalbergia frutescens,* and *Cupania vernalis* (SDF) (**Table 1**). For exotic species, we registered 21 individuals of *Hovenia dulcis* in the sampled area, distributed in four plots (11%) of SDF forest and in one plot (3%) of MOF forest.

Family and species richness varied among plots in forests of the same age within each forest type (**Figures 2A,B**). In DOF, the median richness was 18 species, ranging from 2 to 52 species per plot. Median richness in MOF and SDF was smaller than that in DOF (median values of 10 and 12 species, respectively), as well as the maximum number of species per plot (respectively, 25 and 28 species) (**Supplementary Figure 2**). The number of species per plot increased rapidly from the early ages to 40 years

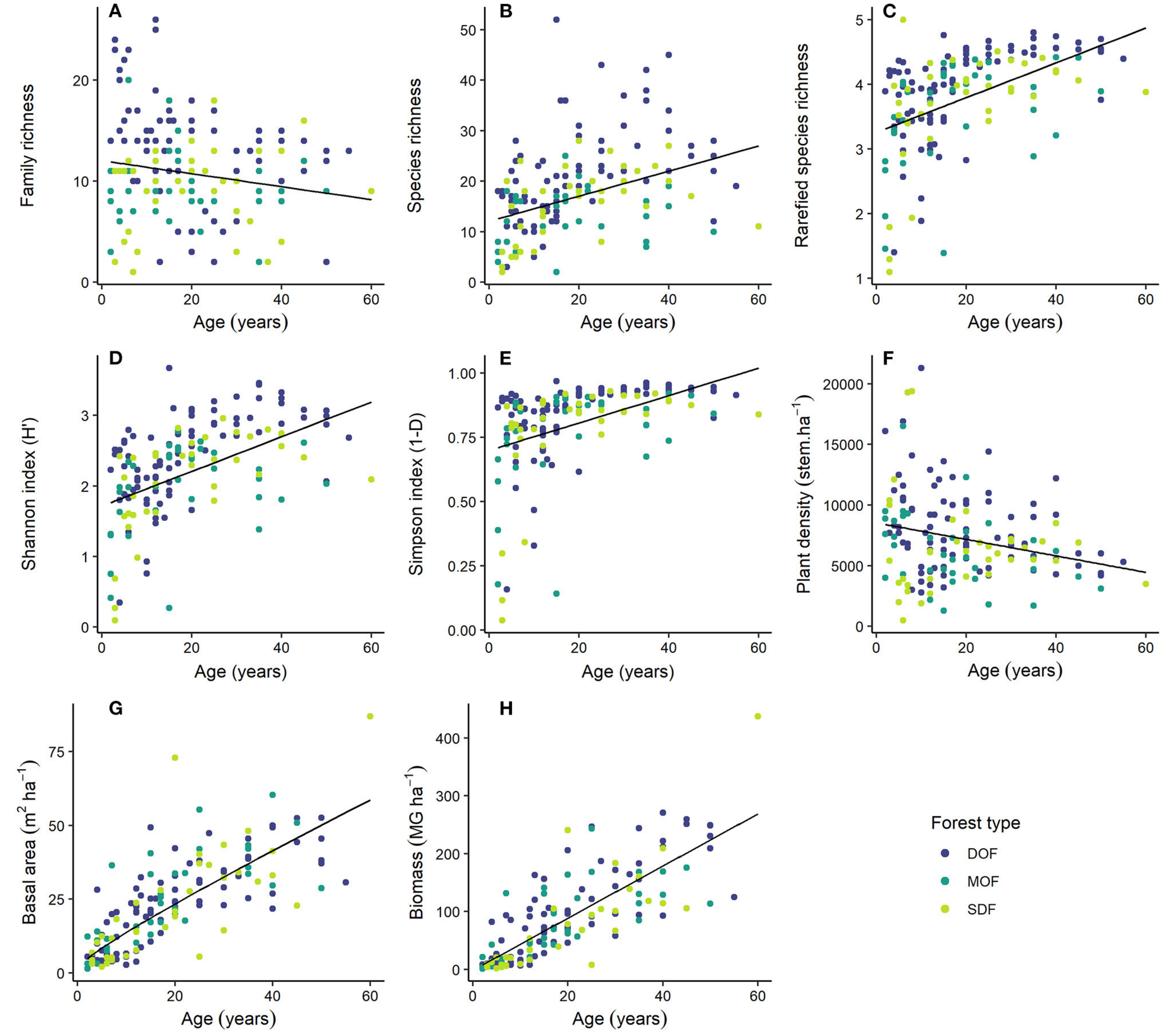

FIGURE 2 | Family **(A)** and species richness **(B)**, rarefied species richness **(C)**, Shannon **(D)**, and Simpson **(E)** diversity index, plant density [**(F)**; stems.ha^{-1}], basal area [**(G)**; m^2.ha^{-1}], and biomass [**(H)**; MG.ha^{-1}] in 2–60 years old secondary forests in three forest types of the Brazilian Atlantic Forest: Dense Ombrophilous Forest (DOF), Mixed Ombrophilous Forest (MOF), and Seasonal Deciduous Forest (SDF). Dots represent individual plots (10 × 10 m), but some overlapping occurs.

of succession in all the forest types. By the age of 20 years, most plots within forest types presented around 20 different species, but some plots in DOF reached more than 40 species. Family richness, on the other hand, showed no clear pattern of increase with forest growth in MOF and SDF. Median family richness in these forests was observed to be eight and 10 families per plot, respectively. In DOF, family richness was higher than that in the other forest types, with a median of 14 families per plot. Different from MOF and SDF, however, the number of families per plot in DOF was higher in young forests and decreased as forests aged (**Figure 2A**).

Species richness of the secondary forests studied varied with age and across forest types (**Figures 2B,C**). The rarefaction curves show that DOF had higher species richness than MOF and SDF when controlling for different number of samples (**Supplementary Figures 3A,B**). As an example, 100 species were found after sampling 6, 12, and 15 plots, respectively, in DOF, SDF, and MOF. The curves also suggest that our sampling did not find the maximum number of species expected in these forest types (87% in SDF, 85% in MOF, and 91% in DOF). When we analyzed rarefied species richness with a fixed number of five individuals per plot, the number of species increased rapidly in the first years of succession. At 6 years of fallow forest, we could reach a richness of five species (**Figure 2C**).

Shannon and Simpson indices also showed rapid increase of species diversity of secondary forests throughout succession

TABLE 1 | Species with highest importance values (IV) in the Dense Ombrophilous Forest (DOF), Mixed Ombrophilous Forest (MOF), and Seasonal Deciduous Forest (SDF).

Ecological group	Species	Importance value (%)[a]		
		DOF	MOF	SDF
Pioneer	*Myrsine coriacea*	4.8	3.1	-
	Cecropia glaziovii	1.6	-	-
	Dodonea viscosa	1.1	-	-
	Baccharis calvensces	1.0	-	-
	Baccharis dracunculifolia	-	6.1	6.8
	Mimosa scabrella	-	5.6	-
	Eupatorium vauthierianum	-	3.2	-
	Schinus terebinthifolius	-	2.3	1.7
	Sapium glandulatum	-	2.2	-
	Boehmeria caudate	-	-	1.5
Early secondary	*Miconia cinnamomifolia*	8.9	-	-
	Tibouchina pulchra	5.3	-	-
	Miconia cabucu	3.5	-	-
	Hieronyma alchorneoides	3.5	-	-
	Miconia rigidiuscula	2.1	-	-
	Vernonanthura discolor	1.5	-	-
	Jacaranda micrantha	1.5	-	-
	Tibouchina trichopoda	1.3	-	-
	Piper gaudichaudianum	1.3	-	-
	Piptocarpha angustifolia	1.1	-	-
	Casearia sylvestris	1.1	-	1.9
	Cupania vernalis	1.1	2.9	3.0
	Clethra scabra	1.1	3.7	-
	Trema micrantha	-	-	3.4
	Alchornea triplinervia	-	-	3.0
	Paraptadenia rigida	-	-	2.9
	Cordia ecalyculata	-	-	2.2
	Cecrela fissilis	-	-	1.7
Late secondary	*Euterpe edulis*	2.3	-	-
	Cabralea canjerana	1.0	-	-
	Matayba elaeagnoides	-	7.4	1.7
	Ocotea pulchella	-	2.9	-
	Ilex paraguariensis	-	2.2	1.5
	Nectandra lanceolate	-	-	6.8
	Nectandra megapotamica	-	-	6.3
	Dalbergia frutenscens	-	-	3.0
Climax	*Psychotria longipes*	1.8	-	-
	Cyathea schanschin	1.1	-	-
	Myrcia eugeniopsioides	1.1	-	-
	Cyathea vestita	1.1	-	-
	Ocotea puberula	-	9.2	-
	Strychnos brasiliensis	-	-	1.4
	Ocotea diospyrifolia	-	-	1.4
Sum of IV		50.2	50.8	50.2
Number of species		23	12	17

The species listed within each forest type accumulate IV up to 50% (from a base of 100).

[a] *Dominant species were defined as that set of species, the accumulated importance values (IVs) which, when ranked from highest to lowest, reached 50% of the total for a given forest type (Finegan, 1996).*

(**Figures 2D,E**). Some plots representing young forests showed low values of Shannon index, but most presented values between 2 and 3, mainly after 15 years of succession. The same pattern was observed for the Simpson index, except for a small number of plots representing young forests. Most forests older than 10 years presented values over 0.75.

Forest Structure

The chronosequence studied revealed the dynamics of the secondary forests that regenerated naturally in the three forest types, increasing in the complexity of forest structure (**Figures 2F–H**) and species succession (**Supplementary Table 1**). Plant density (height $\geq$ 1.5 m) varied strongly at early ages of succession, ranging from values as low as 200 plants per hectare to more than 20,000 plants per hectare (**Figure 2F**). In older forest patches, variation among plots decreased, along with plant density, which converged to values around 5,000 plants per hectare. The forest basal area increased with forest age, with values between 20 and 50 $m^2.ha^{-1}$ by the age of 20 years (**Figure 2G**). Following the same trend, biomass increased fast with forest age, reaching average values of 80 $MG.ha^{-1}$ around the age of 20 years, with 16 plots (10%) reaching values higher than 200 $MG.ha^{-1}$ after this age (**Figure 2H**).

We observed that species of all ecological groups in forests of all ages, from the youngest forests to those as old as 50 years (**Figure 3**; **Supplementary Tables 3**, **4**), kept the same pattern of behavior for plant density, basal area and biomass among the three forest types (**Supplementary Figure 4**). However, high variation was observed among plots insofar as the relative contribution of each group to the total number of plants per plot at each age. We also observed clear patterns of ecological groups in proportion to forest relative plant density through succession. More specifically, the relative plant density of pioneer species was very high at the beginning of succession, close to 100% in some plots, but decreased sharply up to about 15 years (**Figure 3A**). From that age, the relative density of pioneer species dropped more slowly, from 40% to even lower values. Early secondary species also decreased in their importance to plant density through succession, but high relative density of such species was observed in plots as old as 30 years. However, the relative density of this group in each plot displayed wide variation among plots of the same age, particularly in the youngest forests, ranging from almost zero up to 90% of the total number of plants. The relative density of late secondary and climax species increased as the forests aged. Still, their proportion was limited to ~60% of the total number of plants per plot in the oldest forests (**Figure 3A**). The contribution of each ecological group to the total basal area of each plot followed behavior very similar to that observed for relative plant density, especially for the pioneer and early secondary species (**Figure 3B**). Slightly different from the relative importance to plant density, late secondary and climax species contributed more to the basal area in several plots. In turn, the contribution of each group of species to the total biomass of each plot along the succession followed the same course as that observed for relative basal area. That is, as the

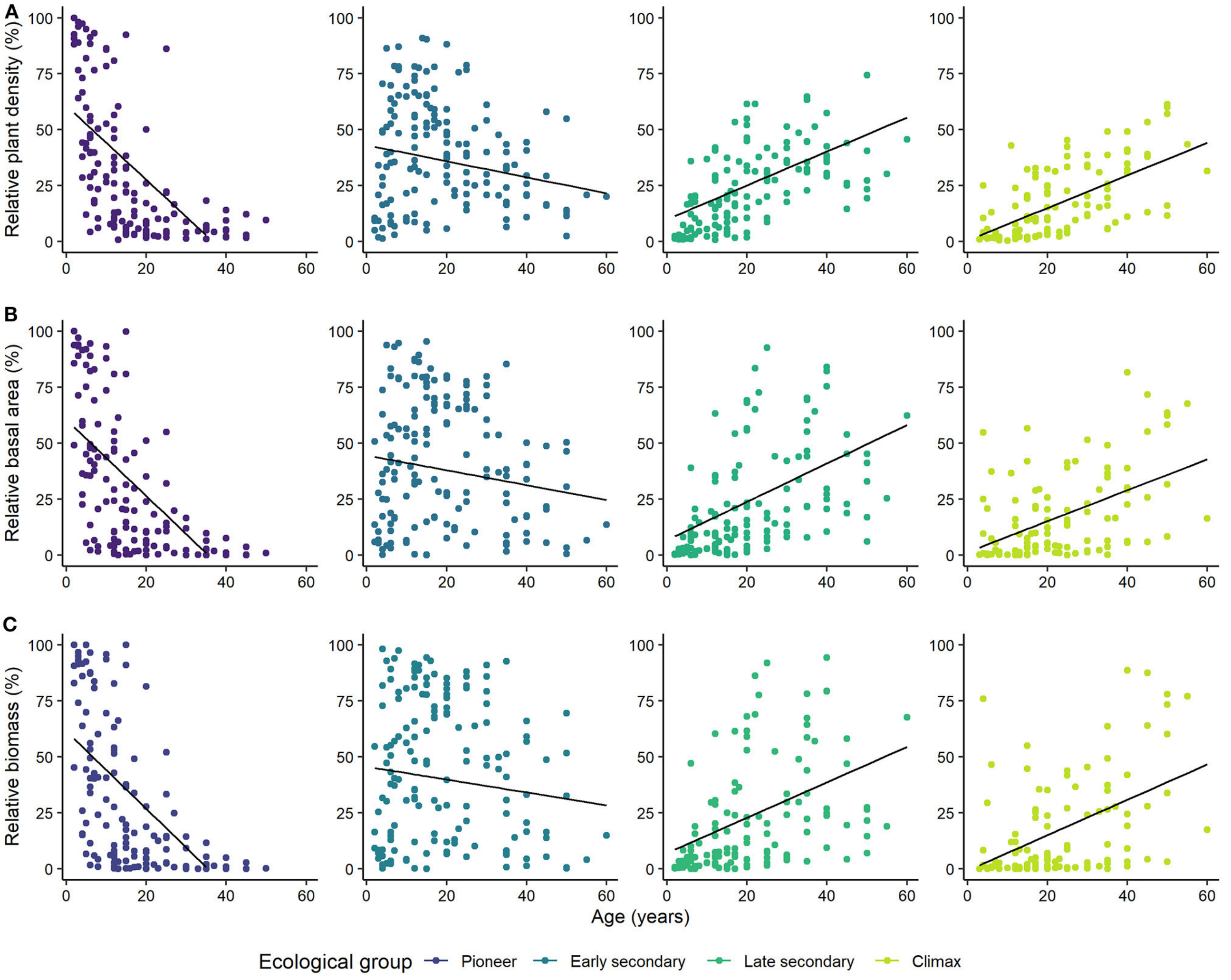

FIGURE 3 | Relative (% of the total per plot) plant density **(A)**, basal area **(B)**, and biomass **(C)** of plants grouped by ecological groups (pioneer, early secondary, late secondary, and climax) in 2–60 year old secondary forests in three forest types of the Brazilian Atlantic forest: Dense Ombrophilous Forest (DOF), Mixed Ombrophilous Forest (MOF), and Seasonal Deciduous Forest (SDF). Dots represent individual plots (10 × 10 m), but some overlapping occur.

relative biomass of pioneer and early secondary decreased, late secondary and climax species increased their share of the total biomass (**Figure 3C**).

The importance of each species to forest structure through succession varied within each ecological group and forest type (**Table 1**). Typical pioneer species, such as *Baccharis dracunculifolia* and *Myrsine coriacea*, were dominant in young forests and widely represented in all forest types. On the other hand, pioneers, such as *Cecropia glaziovii*, *Mimosa scabrella*, and *Schinus terebinthifolius*, were typical of DOF, MOF, and SDF forests, respectively. The early secondary species *Miconia cinnamomifolia*, *Tibouchina pulchra*, *Clethra scabra*, *Trema micrantha*, *Parapiptadenia rigida*, *Miconia cabucu*, *Hieronyma alchorneoides*, and *Alchornea triplinervia* also presented high density, dominance, frequency, or a combination of the three, becoming the most important species of the ecosystem and characterized by typical successional routes within a forest type. These are fast-growing arboreal species capable of forming a closed, or almost closed canopy, shading the environment and dramatically changing local abiotic conditions (**Supplementary Figure 1**). Important canopy species of secondary forests belong to the late secondary group, such as *Nectandra lanceolata, Nectandra megapotamica*, and *Ocotea pulchella*. This ecological group also presented important understory species, such as *Ilex paraguariensis* and *Euterpe edulis*. The importance of climax species was characterized by individuals tolerant to the already shaded environment of the forest, and the growth of this guild promoted a new increase in forest canopy diversity.

DISCUSSION

Dynamics of Natural Regeneration

Taken together, data from our chronosequences indicated that the natural regeneration of secondary forests followed a continuous process of succession from simple to more complex ecosystems. Biodiversity, as measured by richness and diversity indexes, and forest structure, as measured by basal area and biomass, increased through time in our chronosequence, results similar to reports of other studies at sites with a history of swidden-fallow land use (Saldarriaga et al., 1988; Tabarelli and Mantovani, 1999; Aide et al., 2000; Liebsch et al., 2007, 2008). The sampled secondary forest older than 40 years presented structural characteristics (density, basal area, biomass, and diversity) similar to the reference ecosystem, as informed by sites of old growth forests from the official Floristic and Forest Inventory of Santa Catarina—IFFSC (Vibrans et al., 2012b, 2013b,c; also available at www.iff.sc.gov.br).

The high number of species (220) found in DOF, compared to the other forest types was not surprising, as this region holds around 85% of all arboreal species found in Santa Catarina (Vibrans et al., 2013c; Gasper et al., 2014). However, in all cases, the numbers are remarkably high, considering that inventories were based on small plot size (10 × 10 m). Moreover, the high diversity among plots within forest regions was corroborated by the rarefaction curves and the estimator richness. In the DOF region, 100 species were found after taking inventory of only 10 plots, but the number of species grew to more than 200 without reaching a ceiling. In the other two forest types the numbers were smaller, but, again, the rarefaction curves point out that the ceiling for richness was never reached.

The values for diversity indexes found in our study may have resulted from the criteria used for plant inclusion (all plants higher than 1.5 m). The sampling method used, where non-contiguous plots were inventoried, may have raised the levels of diversity. The number of species with low abundance found in our inventories may also have increased the diversity indexes. In an inventory carried out in secondary forest in the same three forest types, Oliveira et al. (2019a) observed that ∼50% of the observed species were rare, having a diminished abundance and/or small area of occurrence. These results reveal the remarkable ability of the Atlantic Forest to hold its diversity of species, despite the reduction in remaining forest cover (Scarano and Ceotto, 2015). Our results show that the forests became more diverse through succession. The species diversity, as indicated by the Shannon and Simpson indices grew in the 1st years of succession. For example, by the age of 15 years, virtually all sampled plots presented a Simpson Diversity Index higher than 0.75. The diversity indices estimated for old-growth forests, as reported by IFFSC studies, show the Shannon Index ranging from 1.79 to 3.64 for SDF (Vibrans et al., 2012b); from 1.01 to 3.51 for MOF (Vibrans et al., 2013b), and from 2.00 to 4.20 for DOF (Vibrans et al., 2013c). It is well-known that species richness can increase rapidly in secondary forests (Aide et al., 2000; Liebsch et al., 2007, 2008; Letcher and Chazdon, 2009), while species composition and interactions recover at a much slower pace. In addition, non-arboreal life forms, like epiphytes, lianas, and ferns, will naturally colonize secondary forests (Guariguata and Ostertag, 2001; Colmanetti et al., 2015), albeit with lower diversity compared to mature or primary forest (Barthlott et al., 2001; Liebsch et al., 2008; Garcia et al., 2016). Liebsch et al. (2008) also verified an increasing number of animal dispersed, non-pioneer and understory species with time after disturbances, although the authors estimated around 1,000 to 4,000 years to reach the levels of endemism existing in mature forests in the Atlantic Forest. As illustrated by Rozendaal et al. (2019), while regeneration processes take, on average, five decades to recover the species richness typical of old-growth forest, it takes centuries to fully recover species composition. However, it seems that around 50 years after the start of succession, naturally regenerated secondary forests in our region formed a forest structure suitable for a wide variety of life forms other than trees.

Another way of evaluating the diversity found in our study is to look at the succession of ecological groups as the forests aged. The relative plant density of the different groups clearly changed over time, with pioneer species being replaced by the early secondary as the most important group and then, later on, by the late secondary and the climax species. These results imply a significant diversity of species, not only among plots of the same age, but also among plots of a different age. They also imply the mosaic of secondary forests across the landscape, a typical scenario in the studied regions, as described in the Floristic and Forest Inventory of Santa Catarina (Vibrans et al., 2012b, 2013b,c; www.iff.sc.gov.br).

Analyzing the behavior of ecological groups through the succession process, we show a pattern very similar to the general description of Neotropical secondary successions, as proposed by Finegan (1996). The presence of species from all ecological groups in young forests suggests that succession, as we illustrated in **Figures 3A–C**, also fits the Initial Floristic Composition model of Egler (1954). However, our understanding of forest succession in this study region is based on Klein (1980), who described post-agricultural secondary forests as those that present well-defined stages of succession, typically dominated by a few species. According to our interpretation, Klein‘s description agrees with the Relay Floristics model, a traditional view that developed from the work of Clements (Clements, 1916). In this sense, we believe that our data allow us to reconcile the ideas of Egler and Klein since each of the first stages of succession is well-marked by a dominant species, but the community is composed of many other species from all ecological groups, an approach close to that proposed by Drury and Nisbet (1973).

Our results on the chronosequences made evident a fast recovery of forest structure and a rapid restoration of community attributes. The basal area of the secondary forests increased fast in the first 20 years of succession (**Figure 2G**), the same pattern as that found in other studies in the Neotropics (Aide et al., 2000; Guariguata and Ostertag, 2001; Siminski et al., 2013; Chazdon and Guariguata, 2016). By that age, some forests may have reached the maximum basal area allowed by conditions of the site. Despite decreasing plant density, this growth resulted from the continuous replacement of shrubs and small trees by larger individual trees, the growing diameter of which contributed exponentially to the basal area. For the same reason, part of the large variation of basal area among plots in our data may have resulted from the small plot area we used, such that a single tree could have had a strong impact on the result.

Biomass accumulation can also be a main driver of plant community changes during tropical forest succession (Lohbeck et al., 2015). The studied secondary forests were highly productive, possibly owing to the coexistence of species that ensure a greater complementarity and facilitation among species in regenerated forests and the consequent efficiency in the use of available resources (Gardon et al., 2020). Among forest attributes, time since the beginning of restoration (forest age) and plant community composition play a relevant role in aboveground biomass stocks for ecosystem restoration. While fast-growing species present a higher contribution during the early years, the contribution of slow-growing species is significant at later stages of succession, as pointed out by Gardon et al. (2020).

Implication for Landscape Restoration in the Atlantic Forest

This study shows that natural regeneration allows the restoration of forest structure and diversity. Here we discuss the local and landscape conditions that allowed a successful natural regeneration and that might be necessary to attain effective forest restoration. Additionally, we discuss indicators that can be used by practitioners to evaluate and monitor forest restoration through natural regeneration in the region.

The potential of natural regeneration to promote forest restoration, depends on local and landscape conditions that enable succession to proceed. First of all, the remnant forest cover in the State of Santa Catarina is high (around 30%, according to Vibrans et al., 2013a, 2020; Lingner et al., 2020). Because of the small size of the farms and the legal restriction against deforestation, these remnants are evenly spread across the State (Siminski and Fantini, 2007), forming a mosaic of secondary and mature forests, which helps to build connectivity among them, facilitating propagule dispersal (Crouzeilles et al., 2020). In addition, the regenerating sites studied show a striking resilience after land use for swidden agriculture, especially keeping soil in good condition (Lintemani et al., 2019), which is necessary in facilitating seed banks and stump sprouts to become important elements of the regeneration process after the land is abandoned. Another factor contributing to fast regeneration of forests may be the long fallow period, up to 30 years, as practiced by farmers in many places, like the Itajaí Valley and the Atlantic Coast (Klein, 1980; Siminski and Fantini, 2007). Such long fallow periods allow the soil to restore fertility (Lintemani et al., 2019) and physical properties. A long period of regeneration is also critical to allow the vegetation to become a source of propagules within the mosaic of regenerating forest and for sustaining an array of dispersers responsible for spreading the propagules to neighboring forest tracts. We recognize that natural regeneration in other regions or different previous land use may present a lower potential to restore degraded/deforested ecosystems (Stanturf et al., 2001; Holl and Aide, 2011; Chazdon and Guariguata, 2016; Crouzeilles et al., 2017; Holl, 2020; César et al., 2021), which can limit its application in specific cases.

In this study, we provide quantitative and qualitative indicators of forest recovery that can be used by practitioners to evaluate and monitor forest restoration within the three forest types herein examined. Quantitative information on forest structure and diversity can be retrieved directly from graphs, which indicate the average levels for the three forest types at all ages (fitted line). Additionally, qualitative information about canopy cover and species composition can help identify recovery dynamics. In the DOF region, for example, a closed canopy happens as early as 15 years after the beginning of succession when *Miconia cinnamomifolia* forms a nearly homogeneous canopy (Schuch et al., 2008) (**Supplementary Figure 1**). This event marks a transition from open ecosystems to intensely shaded forests, having a strong impact on pioneer species (**Figures 3A–C**). Many different successional routes are found in the Atlantic Forest, so each forest has its own species that drives the canopy coverage. Accordingly, this event happens at different times. For example, in the MOF region, the appearance of *Mimosa scabrella*, a fast-growing pioneer, may cause the formation of a closed canopy in forests as young as 10 years of age (Steenbock et al., 2011). The closing of the canopy favors climax tree species, and the process of vertical stratification of the forest starts. It also makes the environment suitable for other life forms like epiphytes.

Even under apparently favorable conditions, it is important to recognize that some limiting factors may impair or slow down the regeneration process. Lower resilience may be driven by low levels of seed dispersal and/or an absence of forest remnants, a common situation in some highly human-modified landscapes. A scenario with these limiting factors could fully, or partially, demand other restorative actions, such as plantation approaches, to help recovery of the dynamics of regeneration of forest structure, species composition and their interactions (Souza and Batista, 2004; de Melo and Durigan, 2007; Rodrigues et al., 2011; Suganuma and Durigan, 2015; Garcia et al., 2016; Pontes et al., 2019). When an active approach is needed, planted species contribute to internal seed dispersal, supplying seeds to assist secondary succession, as well as improve connectivity across the landscape (Rodrigues et al., 2011). In this sense, the floristic data presented in **Supplementary Table 1** can be used as a reference for choosing suitable species for active restoration. We identified those species most common in the early successional stages of regeneration, which will enhance the probability of success of large-scale plantations. We also identified a set of species that occur all across the study area, comprising another group of species suggested for active restoration, as they will potentially adapt to a variety of ecological conditions. Finally, our results made evident the importance of species unique to each forest type, which are critical for qualifying a restoration project.

Another important issue of concern is the occurrence of undesirable species. As pointed out by D'Antonio and Vitousek (1992), Fiore et al. (2019), and Weidlich et al. (2020), a negative association exists between these species and forest community structure and species assembly. In the DOF region, for example, the high susceptibility to fire of *Melinis minutiflora*, an aggressive grass that forms dense communities right after the abandonment of the land, may set succession back to the starting point more than once. In the SDF region, *Hovenia dulcis* may become an important element of the forest structure and composition (Dechoum et al., 2015). Colonization by *H. dulcis* is mostly associated with forest gaps, but the species is also able to invade closed-canopy forest fragments and persist in the more advanced communities (Dechoum et al., 2015; Padilha et al., 2015). However, whether invasive exotic species should be tolerated in restored forests is still a matter of debate in Brazil. Grazing cattle is another common threat to forest restoration all across the Brazilian Atlantic Forest because it may prevent the colonization of many plant species and slow down the pace of succession (Kilca et al., 2020). Fortunately, the problem can be reduced at low cost by building electrical or live fences, technologies already known by local farmers.

Monitoring forests undergoing a restoration process through natural regeneration is obviously crucial to determine the success of the initiative and, ultimately, to determine if the regeneration will flow unassisted. Indicators of potential for natural regeneration can be quantified and mapped, and frameworks can be used for that purpose and to guide decision makers on recognizing natural regeneration as an effective restoration strategy (Chazdon and Guariguata, 2016). Successful monitoring requires the practitioner to understand the whole picture of the succession process in the region (the landscape scale). The practitioners must also be able to recognize features of a particular community (local scale) that signal its qualitative progress.

Based on the data analysis and information of our study, we proposed a set of aspects we should have in mind when evaluating an area being restored through natural regeneration: (1) the matrix surrounding the site to be restored, e.g., predominantly rural or urban, extensive agricultural or industrial tree plantation zone, and proximity to advanced secondary and mature forests; (2) surrounding landscape that indicates frequent natural regeneration or impaired succession; (3) presence of diverse and well-structured regenerated late secondary forests in the region; (4) composition and structure of a given forest patch fit to a stage within a known successional route; (5) presence of juveniles typical of next stages of succession; (6) presence of factors that could delay or prevent succession, such as extreme isolation of the area, invasive species or cattle grazing; and (7) availability of low-cost modifications when limiting factors are present. Developing the skills to interpret the state of a secondary forest beyond the data from an inventory is a matter of training and experience, and training programs would help practitioners to fulfill such requirements.

CONCLUSION

In naturally regenerating forests, our results showed a continuous turnover of species and ecological groups and an increase in the complexity of forest structure over time. The forest types presented a floristic similarity at early stages of succession, but tended to differentiate over time. While initial succession is important to start forest structure restoration, advanced secondary forests showed the capacity to shelter increasing levels of diversity and likely provide a wider array of ecosystem services. Along with remnants of old-growth forests, these naturally regenerated secondary forests can play an invaluable role in rebuilding healthy ecosystems.

The success of natural regeneration in the region of our study is so conspicuous that we claim it should be the standard approach to restore degraded forest/lands. Because of its low cost, a restoration program based on natural regeneration could prompt landowners to set unproductive areas aside for forest regrowth, especially small farmers, who are otherwise unwilling or financially unable to engage in such programs. However, a combination of local and landscape factors also contributes to the high potential of natural regeneration, such as a significant number of mid and late secondary forests spread across the landscape, the relatively low intensity of previous land use, long fallow periods, and favorable climatic conditions.

The data on species composition, diversity and structure of secondary forests found in our study are valuable to define a set of objective parameters to evaluate and monitor restoration programs, building a reference framework to evaluate the success of restoration initiatives. We reinforce the potential of natural regeneration as part of large-scale restoration programs, which would be particularly attractive to family farmers because of their low cost of supplies and labor in the Atlantic Forest region.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

All authors agree to be accountable for the content of the work. The authors integrally contributed to the data evaluation and analysis, as well as the writing and discussion of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.576908/full#supplementary-material

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Indigenous Knowledge and Forest Succession Management in the Brazilian Amazon: Contributions to Reforestation of Degraded Areas

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The indigenous systems of agricultural and forest management in the Amazon are characterized by a deep knowledge of ecological processes, biodiversity, and the use and management of fire. The influence of these systems on the distribution of biodiversity includes semi-domesticated and domesticated species and landscapes, which have led to extensive anthropogenic or cultural forests. However, in many places, the livelihoods of indigenous peoples are being transformed by the intensification of agriculture and social, ecological, and economic changes, putting at risk the sustainability of production systems and food security and sovereignty of these peoples. In the last years, in the Xingu Indigenous Territory (XIT), the food production systems and the form of occupation of territories have changed, affecting the recovery of secondary forests, which now demand a too long period. The increase in the number and frequency of fires has aggravated this situation, due to a drier climate that has become predominant in the region. Changes in climate are attributed to deforestation in the neighboring municipalities, especially in the headwaters of the Xingu river basin. This study was conducted among the Kawaiwete (Tupi-Guarani) and the Ikpeng (Carib-Arara) peoples in the XIT, in the state of Mato Grosso, Brazil. The main objective was to develop alternative techniques of forest management based on indigenous and scientific knowledge more adapted to the new livelihood contexts, aiming to favor forest regeneration in areas dominated by shifting cultivation. We sought to answer the following questions: (I) How do forests regenerate during the fallow period? (II) How can local management improve forest regeneration? (III) Are there indicator species for secondary succession, soil recovery, and vulnerability to fires? (IV) Is the increase in the number of fires affecting the sustainability of the shifting cultivation systems? Our results show that some local practices based on indigenous knowledge have the potential to facilitate natural regeneration, such as choosing forest areas that have been recovered for agricultural use, limiting the number of cultivation cycles, protecting and selecting of individual trees during cultivation period, and attracting seed dispersers. Assisted natural regeneration strategies grounded on indigenous knowledge are promising ways to restore degraded lands of the XIT.

Keywords: Xingu Indigenous Territory, Kawaiwete people, Ikpeng people, local ecological knowledge, shifting cultivation, swidden fallows, assisted natural regeneration, indigenous forest management

INTRODUCTION

In the region of the Xingu Indigenous Territory (XIT), in the state of Mato Grosso (Brazil), several factors are affecting indigenous shifting cultivation systems, with consequences to the natural regeneration of forests. Changes in the type of occupation of the territory by indigenous peoples and in local rules that guide the use of agricultural environments may be the main causes of it. However, external factors, such as the intense and rapid change in land use around the XIT, which occurred in the last 50 years, have affected environmental conditions within the territory (Sanches and Villas-Bôas, 2008; Durigan et al., 2013; Sanches and Futemma, 2019). As a result of the increase in value of land for planting grains, there has been an increase in regional deforestation rates, which in turn has led to changes in the regional microclimate (Silvério et al., 2015), rainfall regimes, and levels of soil moisture (Nobre et al., 1991; Li et al., 2006; Morton et al., 2013), contributing to an increase in unintended fires (Nepstad et al., 2004; Brando et al., 2014; Alencar et al., 2015). With a drier climate, several accidents have occurred during the burning of areas to open traditional swiddens, leading to losses of forest areas. Thus, indigenous peoples in the XIT began to face challenges in finding strategies to ensure the sustainability of agricultural systems and adapting them to the new environmental context.

In many tropical regions, there is an increasing pressure to intensify indigenous productive systems (Denevan et al., 1984; Charlton, 1987; Denevan, 2001) as a result of delimitation of territories and population growth (Johnson, 1983; Freire, 2003, 2007; Toledo and Salick, 2006). In a political-economic context of accelerated cultural and social changes, the current challenge is how to reconcile or adapt traditional management practices while maintaining a sustainable use of these indigenous territories, which are increasingly circumscribed by the pressures of the surroundings (Le Tourneau, 2015; Jusys, 2018). Many indigenous productive systems in tropical forests are based on shifting cultivation, which depends on a fallow period for the regeneration of secondary forests and soil fertility (Ewel, 1986; Mertz et al., 2009; Ribeiro Filho et al., 2013, 2018). When subjected to agricultural intensification processes, the fallow time is shortened and may be insufficient to ensure sustainability, leading to forest degradation (Marquardt et al., 2013; van Vliet et al., 2013).

In the Amazon region, although the origin of anthropogenic forests is still under debate, evidence shows that there is an important contribution of indigenous food production systems and local communities to the generation and maintenance of biodiversity (Clement, 1999; Miller and Nair, 2006; Balée, 2010; Shepard and Ramirez, 2011; Sutherland et al., 2013; Tengö et al., 2014, 2017). Forest and agricultural management often leads to changes in species composition and in soils (Smith, 1980; Balée, 1993; Heckenberger and Neves, 2009; Arroyo-Kalin, 2010; Junqueira et al., 2011; Woods et al., 2013; Schmidt et al., 2014; Levis et al., 2018, 2020), and are based on a deep knowledge of ecological dynamics and on social and cultural rules (Berkes and Berkes, 2009).

The shifting cultivation practiced by indigenous Amazonian peoples depends on the multifunctional management of the landscape during the cultivation phase (van Vliet et al., 2012; Mukul, 2016), which includes the simultaneous cultivation of several cultivated/domesticated and semi-domesticated species (Hett et al., 2012). The combination of social and ecological dynamics leads to different successional trajectories (Wangpakapattanawong et al., 2010; Chazdon, 2014b; Chazdon and Uriarte, 2016; Uriarte and Chazdon, 2016). One of the most important aspects of indigenous adaptive management is the use of plants according to their potential to promote the natural regeneration of the forest and the recovery of biodiversity during forest succession in the post-cultivation fallow period (Wangpakapattanawong et al. op. cit; Chazdon, 2013), safeguarding fundamental species, including those used in material and immaterial culture.

However, despite the importance of the forestry and agricultural management of indigenous peoples for the diversification of Amazonian landscapes (Neves et al., 2003; Clement et al., 2015), less attention has been paid to forest recovery processes after agricultural cultivation (Moran, 1996; Jakovac et al., 2015; Hartman et al., 2016), including the development or regrowth of young plants (Tschakert et al., 2007; Jakovac et al., 2015; Uriarte and Chazdon, 2016). Likewise, little is known about the effects of the increase in population pressure, climate change, and the loss of environments and ecological knowledge in some local systems (Magnuszewski et al., 2015; Mukul et al., 2016a,b).

In this paper, we investigate agricultural management by indigenous people in two areas within the XIT that are undergoing processes of agricultural intensification and environmental changes (2013–2016). The areas belong to the Ikpeng and the Kawaiwete peoples. We seek to answer the following questions: (I) How do forests regenerate during the fallow period? (II) How can local management improve forest regeneration? (III) Are there indicator species for secondary succession, soil recovery, and vulnerability to fires? (IV) Is the increase in the number of fires affecting the sustainability of the shifting cultivation systems?

MATERIALS AND METHODS

The project *Fogo do Índio—Management alternatives adapted to climate change for the conservation of forests in the Xingu Indigenous Park* was conducted with a technical partnership formalized in 2016 between the non-governmental organization Instituto Socioambiental (ISA) and the Associação Terra Indígena Xingu (ATIX), which represents the interests of the indigenous peoples of the Xingu. The Cooperation Agreement contemplates strategic projects and activities in areas considered a priority to the indigenous peoples of the XIT, such as supporting initiatives aiming to raise awareness of and protect the Xingu peoples from the impacts of climate change. The construction of the project started in the Moygu Ikpeng village in response to internal demands resulting from a gradual increase in the number of fires in the XIT region, which caused several impacts on local livelihoods. All activities were conducted with the consent of the leaders and the people from the indigenous communities involved in the Moygu/Arayo Ikpeng[1] and Samaúma Kawaiwete villages, counting with a fundamental role of their elders. The main local interlocutors who acted in mobilizing communities and who had an active involvement in research activities are co-authors of this article.

The Xingu Indigenous Territory (XIT) and the Villages Analyzed in This Study

The XIT has an area of 2.8 million hectares and occupies a region of great biological and cultural diversity in the northeast of the state of Mato Grosso, Brazil, in the Parecis Plateau (Sanches et al., 2012). This region has distinct physiognomies that follow a gradual climatic and edaphic variability, and the species are characteristic of an ecological transition area (Radam Brasil, 1985). In this region, Evergreen Seasonal Forest predominates (Ivanauskas et al., 2008). However, there are also different savanna formations, among other wetlands and lowland swamps (Sanches et al., 2012). The predominant climate in the southern Amazon border is tropical rainy savanna (Aw), according to the Köppen classification (1948). Temperatures are above 18°C in two well-defined seasons: a rainy season (more than 1,200 mm of rainfall) and a dry season (less than 100 mm of rainfall). Seasons may vary between 4 and 7 months per year (Ivanauskas et al., op. cit.).

In addition to these natural characteristics, the XIT holds a significant part of the Brazilian sociodiversity. There are 16 indigenous peoples in this location[2]. Most of these peoples did not originally inhabit this region but were transferred there when the Brazilian government created the territory in 1961 (BRASIL, 1961). The limitation of land for establishing indigenous territories resulted in the loss of mobility for villages and farming areas of various peoples, leading to a scarcity of recovered agricultural land in the vicinity of villages.

In this study, two villages inhabited by different peoples were included: Samauma (Kawaiwete, with a population of 40 individuals) and Moygu/Arayo (Ikpeng, with a total of 300 individuals), both in the middle Xingu River region (**Figure 1**). Kawaiwete and Ikpeng livelihoods are similar regarding the way they perform subsistence activities such as hunting and fishing (Rodgers, 2002; Txicão and Leão, 2019). There are also similarities in the collection of forest products used for domestic and ritual purposes, in addition to forest-based shifting cultivation practices that complement their systems (Menget, 1981; Schmidt, 2001; Rodgers, 2013; Silva, 2016; Athayde and Lugo, 2018). However, these peoples have peculiar and distinct characteristics regarding their knowledge systems, the languages they speak, and their different origins, in addition to other characteristics of an ethnic and cultural nature (Dole, 2001).

The Kawaiwete people are the most populous in the XIT. They are widely distributed throughout the territory in more than 30 villages in the middle and lower Xingu River regions. They speak Tupi-Guarani and are originally from the Tapajós and Arinos river basins. Part of its population was transferred to the Xingu region in the late 1950s (Grümberg, 2004), while another part remained in its old traditional territory in the northwest of Mato Grosso (Athayde and Lugo, op. cit.). The Kawaiwete agriculture is one of the richest compared to those of other peoples in the Xingu (Villas-Bôas and Villas-Bôas, 1986) mainly because their food system presents a greater diversity of crops, among which peanuts (*Arachis* sp.), corn (*Zea* sp.), cassava (*Manihot* sp.), beans (*Phaseolus* spp. and *Vigna* spp.), broad beans (*Phaseolus* sp.), sweet potato (*Ipomea* sp.), yam (*Dioscorea* spp.), arrowleaf elephant ear (*Xanthosoma* spp.), pepper (*Capsicum* spp.), and tobacco (*Nicotiniana* sp.) (Grümberg, 2004) stand out.

The Ikpeng people, contacted in 1964 in the tributary region of the middle Ronuro River, were only transferred from their former territory to XIT in 1967 due to the risks of invasion by gold miners (Simões, 1963; Menget, 1981, 2001). The ethnic and cultural origins of the Ikpeng are related to indigenous groups in the northern Amazon and the Guianas, whose language is part of the Arara complex, a subgroup of the Caribbean family (Menget, 2001; Rodgers, 2002). Some of the rare records of Ikpeng agriculture show the cultivation of varieties of crops of beans, peanuts, and tubers (Menget, 1981). Corn (*Zea* sp.) is relevant in this system. It is used in the preparation of a type of baked bread (*pako*) and a fermented drink (*wonkinom-egr˙t*—beverage of the spirits), still prepared today for the end of the *Pomeri* feast (Rodgers, 2002), but that was not known by the peoples of the upper Xingu (Menget, 1981). Some of the agroforestry management techniques used by the Ikpeng were incorporated from the systems that already existed among peoples of the upper Xingu, such as cultivation of fruit trees in cassava swiddens, mainly pequi (*Caryocar* sp.) and mangaba (*Hancornia* sp.) (Carneiro, 1983 p. 68; Schmidt, 2006), as well as the

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[1] The Moygu and Arayo villages are in a same region in the middle Xingu River and thus, although there is a political separation, here we consider them as areas of common use.

[2] The inhabitants of the XIT are the Aweti, Kalapalo, Kamaiurá, Kuikuro, Matipu, Mehinako, Nahukuá, Naruvotu, Trumai, Wauja (Waurá), Yawalapiti, Ikpeng, Kawaiwete, Kĩsêdjê, Tapayuna, and Yudja (https://pib.socioambiental.org/en/xingu).

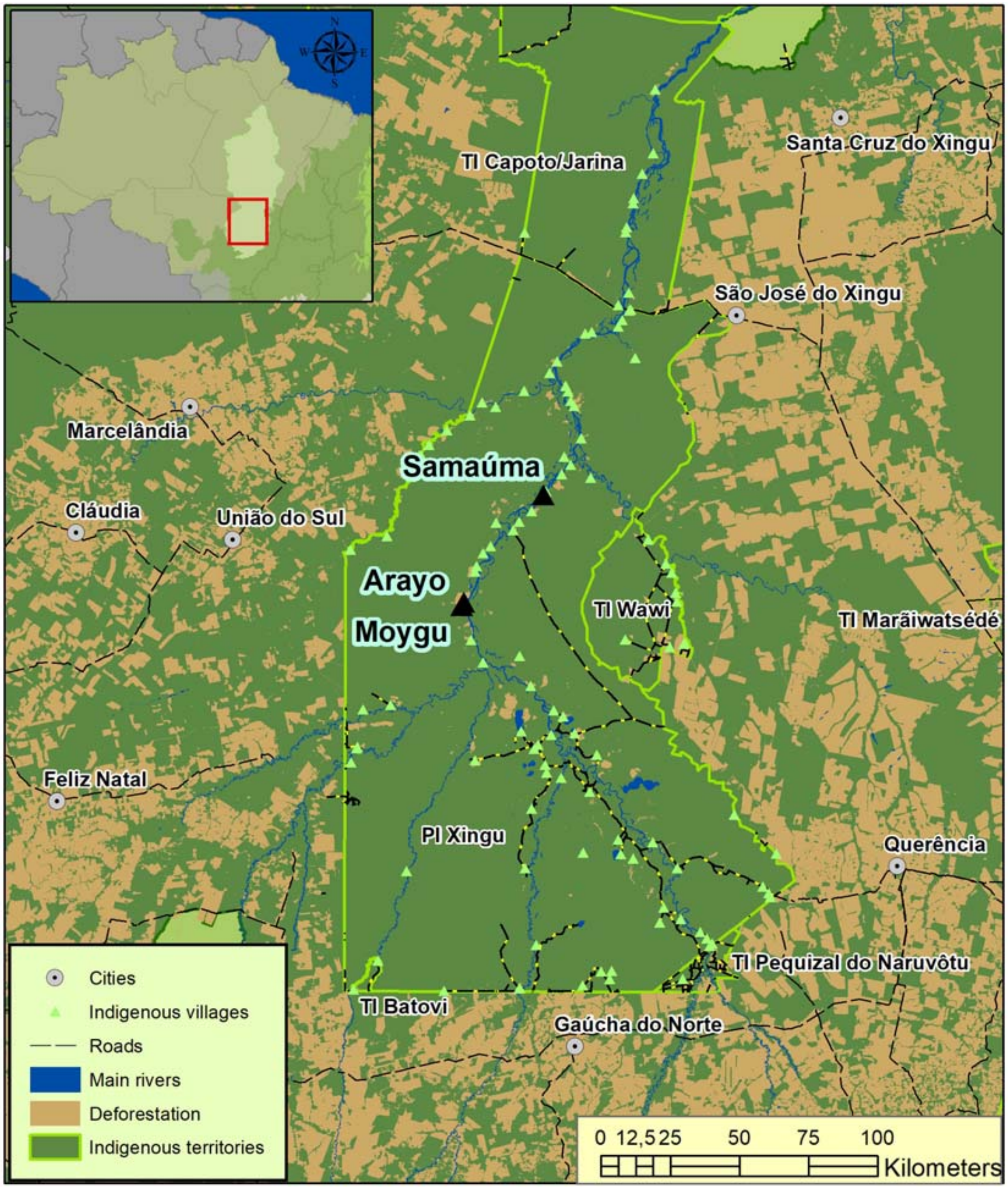

FIGURE 1 | Location of the Xingu River basin, and the villages of Samaúma Kawaiwete, Moygu Ikpeng, and Arayo Ikpeng within the boundaries of the TIX and surrounded by adjacent municipalities that have lost more than 66% of the forest cover in the last 40 years (*map by Ricardo Abad, courtesy Instituto Socioambiental, Xingu Program*).

cleaning of plots, as we present below (Item 3.2). Currently, the Ikpeng are distributed across four villages in the XIT, including the Moygu and Arayo villages, which are part of this study (**Figure 1**).

Inside the XIT, forests that grow on anthropogenic soils, called "Amazonian Dark Earth" (ADE), assume a strategic importance for the Xingu peoples (Clement et al., 2003; Schmidt, 2013; Schmidt et al., 2014). Its location is restricted to regions of stream headwaters or near ponds (Kern et al., 2003), coinciding with archeological remains (Smith, 1980; Neves et al., 2003). Although both peoples use the ADE, especially for crops more demanding in nutrients, mainly corn (*Zea* sp.), this soil is more important for the Kawaiwete people, as these lands are used for planting varieties of peanuts (*Arachis* sp.) and broad beans (*Phaseolus* spp.) (Silva, 2016).

Forests in soils of non-anthropogenic origin (nADE), also referred to locally as "red earth," are classified as "Perennial Forest Season—in true red-yellow Podzolic Soils" (Ivanauskas et al., 2008; IBGE, 2012). They represent the predominant landscape matrix in the XIT and, in addition to presenting different types of uses for these peoples, they are also prioritized for the cultivation of cassava varieties (*Manihot* sp.), which are the basis of local food. Among the Kawaiwete, some varieties are used in the preparation of the *puba* flour (Grümberg, 2004), while the Ikpeng cultivate varieties indicated for starch extraction to make *beiju—tariwe*—and others that are used to make a type of sweet porridge—the *perereba*.

The areas of the municipalities adjacent to the XIT have lost more than 66% of forest cover in the last 40 years (Nascimento et al., 2018; **Figure 1**). This is the main factor responsible for the greater vulnerability of forests in the region to fires, which have become more frequent (Nepstad et al., 2004; Brando et al., 2014; Alencar et al., 2015), affecting many plants species and strategic environments. The period of occupation of the villages in both locations coincides with the beginning of changes in the regions adjacent to the XIT.

Survey and Participation in the Project

The project activities were conducted between 2013 and 2016, in three stages: (I) co-construction of the project and adaptation of the intercultural research method; (II) data gathering on the successional process, agricultural and forest management techniques, and forest degradation and recovery indicators; and (III) in-field survey of the vegetation and indicators of successional stages, degraded areas, and vulnerability to fires (**Table 1**).

The project involved 67 people from both villages (100%) at its different stages. In Stage II, the interviews were undertaken with nine Ikpeng men (13% of participants), aged between 30 and 70 years old, and three women aged between 50 and 70 years old (4%). As the Samauma Kawaiwete village comprises a single family, we interviewed only three men, aged 39–70 years old (4%), and only one elderly woman, aged approximately 70 years old (1%). The other participants (61%) were directly involved in Stages I and III, including students from indigenous schools, girls and boys aged 15–18 years old, in addition to young people who aided in the interviews and translated the indigenous languages into Portuguese (**Table 1**). Here the indigenous names for species, types of management, and phases of forest succession were kept in the original language and written in italics.

(I) Co-construction of the project and adaptation of the intercultural research method:

The project was constructed in a participatory manner with the villages involved and adopted an intercultural research perspective. Participatory projects can provide information on the way natural assets are managed by a given community in a consensual way among all forest users (AFN, 2002) in a process of co-production of knowledge (Bergold and Thomas, 2012).

TABLE 1 | Methodological steps of the project.

People/village/population	Methods	No. of participants	Objectives	Data obtained
Stage I—Co-construction of the project and adaptation of the intercultural research method				
Ikpeng/Moygu (300 individuals)	Community meetings Workshops at the indigenous school Presentation of previous results	35	Construction and realization of the project Community understanding and involvement	Indicators used in the qualitative characterization of forests affected by fires and intensification processes
		23	Definition of participants and necessary materials	
Kawaiwete/Samauma (40 individuals)		9	Environmental changes in the region in recent years and the return of the forest	
Stage II—Survey of knowledge about the successional process, agricultural and forest management techniques, and forest degradation and recovery indicators				
Ikpeng/Moygu (300 individuals)	Semi-structured interviews	13	1. How do forests regenerate during the shifting cultivation cycle? 2. What are the local management techniques and traditional rules that facilitate forest regeneration; 3. Compromised plants and agricultural environments; 4. Species indicating secondary succession and Impacts on the sustainability of these systems with the increase in the number of fires	1. Identification of local concepts that favor or restrict forest regeneration; 2. Identification of the types of plants recovered in this process; 3. Identification of plants at initial, intermediate, final, or mature stages important to soil recovery
Kawaiwete/Samauma (40 individuals)		4		
Stage III—In-field survey of vegetation and indicators of successional stages, degraded areas, and vulnerability to fires				
Ikpeng/Moygu (300 individuals)	Trails monitored by impacted forests and agricultural fallows	5/12	1. Visit to cultivated areas and comparison of different intensities of land use; 2. Description of structure, composition, and types of plants and soils 3. Distinctive features between successional stages, time of use, history of fires	1. Vulnerability to fires and intensification of agricultural use; 2. Identification of plants in fallow in different periods of use and recovery 3. Uses of plants in material and immaterial culture
Kawaiwete/Samauma (40 individuals)		3/6		

Intercultural research was developed in partnership with the communities in order to access knowledge about local history, characteristics of natural environments and management techniques, and uses of plants, soils, and animals (Cabalzar, 2017). This approach allows relations among the different knowledge systems (scientific and local) to be more balanced and complementary, and based on local conceptions (Candau, 2012, p. 245). Intercultural studies have been used to access the local knowledge of other Amazonian indigenous peoples on the recovery of the agricultural fallows (Schmidt et al., 2010a) and participatory forest management (Schmidt, 2001; Schmidt and Ikpeng, 2006; Schmidt et al., 2010b).

Surveys on shifting cultivation systems were conducted through intercultural courses and workshops in the Moygu, Arayo (Ikpeng), and Samauma (Kawaiwete) villages (**Table 1**). The surveys sought to identify the main factors contributing to changes in the local systems in order to understand the regeneration processes of secondary forests according to local knowledge. To this end, the communities chose informants who had a renowned knowledge about the territory, as well as about changes in landscapes, to monitor and aid the field research.

(II) Data gathering on the successional process, agricultural and forest management techniques, and forest degradation and recovery indicators;

We conducted semi-structured interviews (Bernard, 2006) with 16 key informants chosen by the communities on issues related to the changes observed in the availability of land for cultivation, forest regeneration, and species used in material culture based on the following questions: *How swiddens were cultivated in the past and what has changed today? How does the forest grow again? What are the plants that emerge first? Which ones emerge after a few years? Which ones are essential to the recovery of the forest?* These information were essential for identifying the types of plants that are part of the initial, intermediate, final, or mature secondary forest formations, as well as for providing information on impact indicators based on the abundance or scarcity of certain plant species and other types of resources.

Most interviews were recorded in indigenous languages, later translated into Portuguese, and transcribed in full with the aid of some local young people[3]. During the interviews, we had the collaboration of indigenous teachers, especially from the Amure Ikpeng School, and of some students who participated in the surveys and discussions on environmental changes and possible forms of adaptation.

(III) In-field survey of vegetation and indicators of successional stages, degraded areas, and vulnerability to fires

The field survey sought to identify the predominant environments around both villages and to get to know the local landscape using "monitored trails" with the participation of experienced farmers chosen by the communities (Brondizio and Neves, 1996; Brondízio, 2006; Munari, 2009) (**Table 1**). The current and older agricultural areas were visited, allowing a qualitative characterization of secondary succession. The areas were characterized and classified according to regeneration phase (initial, intermediate, and final), establishing the trajectories of successional stages since the end of the cultivation period, according to the Kawaiwete and Ikpeng knowledge systems.

In the Samauma village, areas of anthropogenic ADE were visited between the initial and intermediate stages. Three swiddens were in production and three were in fallow. The more advanced stages, on the other hand, could not be located in the areas close to the village, and an oral description by the farmers on them was obtained. In the Moygu/Arayo Ikpeng villages, five swiddens in production on non-anthropogenic soils (nADE, red earth) were visited between the initial and intermediate stages, in addition to seven fallow areas. Likewise, visits to secondary forests were not made at more advanced stages, as they are far from the village and were described only orally. The oral description of forests at a more advanced stage aimed to characterize the reference environments.

The agricultural fallow areas were described according to the history of use—present fallow age and age at the last time it was cut—and the history of recurrence of fires (one, two, three or more times). However, it was not possible to locate and consider agricultural fallows that had not been impacted by fires, so that secondary "control" areas at more advanced stages could not be visited. For each of these areas, the characteristics of structure, composition, type of soil, and other aspects were collected and scientific illustrations were made. The plants from each successional stage were identified, as well as their uses in material/immaterial culture, to better understand how the losses caused by the changes could affect the cultural systems of the indigenous peoples under study.

The plants were identified in indigenous and scientific language, the latter with the support of Dr. Natalia Ivanauskas, a botanist specialist, who conducted the identification of several species from photographic images captured during field surveys. For this purpose, the APG IV botanical classification system (Iv et al., 2016) was used. As there was no collection of botanical material in the areas and the identification was conducted *in loco*, some of them are still preliminary. Unidentified species are here identified as (ni). The uses of plants were grouped into pre-established categories adapted from Cook (1995): (1) medicinal—including for humans and animals; (2) food—including drinks; (3) construction—including wood, fibers, and plants useful for the manufacture of canoes; (4) material—including handicrafts, hunting gear, paints, hygienic substances, toys, etc.; (5) fuel—firewood, torches, lighters; (6) social use—rituals, magic, smoking, hallucinogenic, drugs; (7) environmental use—including restorative plants, time markers, ornamentation; and (8) poison—including fish poison.

The areas under cultivation were visited to characterize the agricultural system and its influence on the regeneration of forests in the XIT. Through participant observation (Bernard, 2006), we identified together with experienced farmers, elders and leaders, techniques and practices used during the cultivation cycle and monitored some cleaning and product collection activities by recording practices, regenerating plants, and changes in the system. This survey considered local impact indicators, mainly regarding management and forest regeneration during the initial

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[3] The interviews were transcribed with the help of Rosana Gasparini (UNIFESP), Oreme Ikpeng and Kamatxi Ikpeng, and Tari Kaiabi and Myayup Kaiabi.

phase of fallow, when the forest is subjected to different historical and land use intensities (Defoer and Budelman, 2000; quoted in Marquardt et al., 2013), in order to identify species that "catalyze" forest regeneration (Chazdon, 2013).

To describe regeneration in areas used for cultivation, we defined a gradient of intensity of agricultural management and recovery of fallow areas based on descriptors of intensification of land use, such as (1) the number of fallow cycles, (2) the method for weeding during the cultivation period, (3) the age of the previous fallow when the forest was cut down, (4) the size of the area used, and (5) the dominant plants (Lawrence, 2004; Mertz et al., 2009; van Vliet et al., 2012; Jakovac et al., 2015, 2016a). These descriptors were recorded and discussed with some participants. Based on this information, lists of species were made according to different levels of land use intensity and the potential for regeneration of agricultural environments that remain in fallow, in addition to their vulnerability to fires. The information obtained in the Samauma Kawaiwete village (**Supplementary Table 1**) and in the Moygu/Arayo Ikpeng village (**Supplementary Table 2**) is presented below.

RESULTS

Regeneration of Forests During the Shifting Cultivation Cycle

The Kawaiwete recognize different landscape units during the shifting cultivation cycle according to the successional phases of secondary forests. The production phase includes the cultivation phases (*ko*), when selective cleaning is conducted; the harvest phase, lasting 2–3 years; and the final phase, when young plants of the forest begin to regenerate (*kofet jeapat*). The secondary forest then begins to grow, passing to the stage of new fallow (capoeira, in Portuguese) (3–15 years—*ojemowyt*), medium fallow "growing" (15–30 years—*ojemowyrete)*, until reaching the stage of fallow "*turning into a forest*" (30 and over 40 years old—*ojewyt koferete ramu*) (**Figure 2**).

In the anthropogenic dark earth (ADE), the true fallow (*koferete*) is considered the most important forest formation for agriculture as it is strategic to the most demanding crops. The forest at this later stage, with at least 40 years old, present a greater diversity of species, a closed canopy and stratified structure, a clean understory, and richer soils, which can exceed 25 m in depth, with a predominance of large trees (>40 cm DAP) and the presence of certain indicator plants. Among the species mentioned are *jatyta'yp* [*Maclura tinctoria* (L.) Engl], *jatua'yp* [*Guarea* cf. *guidonia* (L.) Sleumer], *pino* [*Attalea maripa* (Aublet) Drude], *tukumã* (*Astrocaryum aculeatum* G. Mey.), and *yky'ryp* (*Thyrsodium spruceanum*) (**Supplementary Table 1**). The following illustration represents the successional trajectory in the management of the shifting cultivation cycle in ADE according to the farmers interviewed in the Samauma village (**Figure 2**). Traditionally, for the Kawaiwete, the fallow should be reused for a new shifting cultivation cycle only after reaching the stage between 30 and 40 years (*ojewyt koferete ramu*).

Similarly, the Ikpeng also classify the secondary forest development phases into succession stages during the shifting cultivation cycle. In this case, we investigated the shifting cultivation cycle in non-anthropologenic earth (nADE), or in "red earth" (*akyun*), used mainly for the cultivation of cassava (*Manihot* sp.) and some fruit trees, although the Ikpeng also use dark earth environments (ADE, *iruktowowon*).

The old forests (*irwa*) are sought after for planting new gardens (*tukto)* and can be used for up to three production cycles (*ine)*. They are managed by selective cleaning, harvesting, and replanting techniques up to the end of the cultivation stage and the beginning of the new fallow stage (*irïnpïn*). The initial fallow stage (3–5 years, *awmtu)* is followed by the fallow stage (up to approximately 15 years, *tukto rïnpïn)*, advancing to fallow at an advanced stage of growth (15–30 years, *iprororetpïn)*, until reaching the secondary forest stage "*with a clean understory*" (30 years or older, *oremyegetpïn*) (**Figure 3**).

According to Ikpeng farmers, the gardens should preferably be opened at this last stage, which characterizes the most advanced stage of secondary forest growth, with trees already developed (>45 cm DBH) and a canopy height higher than 25 m. At this stage, some tree species are recognized as indicator species, such as *kumpang* [*Emmotum Emmotum nitens* (Benth.) Miers], *magra* (*Sacoglotis guianensis* Benth.), *motoe* [*Helicostylis tomentosa* (Poepp. and Endl.) J. F. Macbr.], *oyot* [*Dypterix odorata* (Aubl.) Wild.], *yego* (*Vochysia ferruginea* Mart.), *yemkat* (*Apeiba* cf. *tibourbou* Aubl.), *katepo* (*Hymenaea courbaril* L.), *raegï* (*Xylopia amazonica* R. E. Fries), *roromi* [*Dialium guianense* (Aublet) Sandw.], *muret* (*Byrsonima intermedia* A. Juss.), *ototo* (*Astrocaryum aculeatum* G. Mey), among others (Kampot Ikpeng, personal account, 2016). The fruiting stage of some species, such as *megriut* (*Inga marginata* Willd.), *katamaut* (*Inga thibaudiana* DC.), *potkïngis* (*Vitex montevidensis* Cham.), *tomela* (*Byrsonima crispa* A. Juss.), which attract birds and other animals, is also considered as an indicator of the maturity of the forest formation (*oremyegetpïn*) and of the appropriate time for the opening of a new swidden.

In this type of more developed formation, the soils are more structured ("fluffy," according to local speech; *oromãkura*) as a result of the accumulation of leaf remains, tree branches, and fruit peels on the soil surface, forming a darker layer (*yongonwulun*). However, finding fallow areas with these ideal characteristics of development stage for reuse is increasingly difficult in the current regional context. Close to villages, areas of fallows at early stages (*awmtu*) or slightly more developed (*tukto rïpïn*) predominate. **Figure 3** shows the succession trajectories of the Ikpeng shifting cultivation cycle according to farmers interviewed in Moygu and Arayo Ikpeng villages.

Techniques and Local Rules That Facilitate Forest Regeneration

The Kawaiwete traditionally manage swiddens to favor forest regeneration, for instance, by choosing the right places to open new plots, keeping some specific trees, cleaning the understory, and above all, limiting the number of years for cultivation at the same location contribute to forest recovery. As explained during the interviews, the most intensive cleaning should be conducted only at the initial stage of the swidden, when most plants are

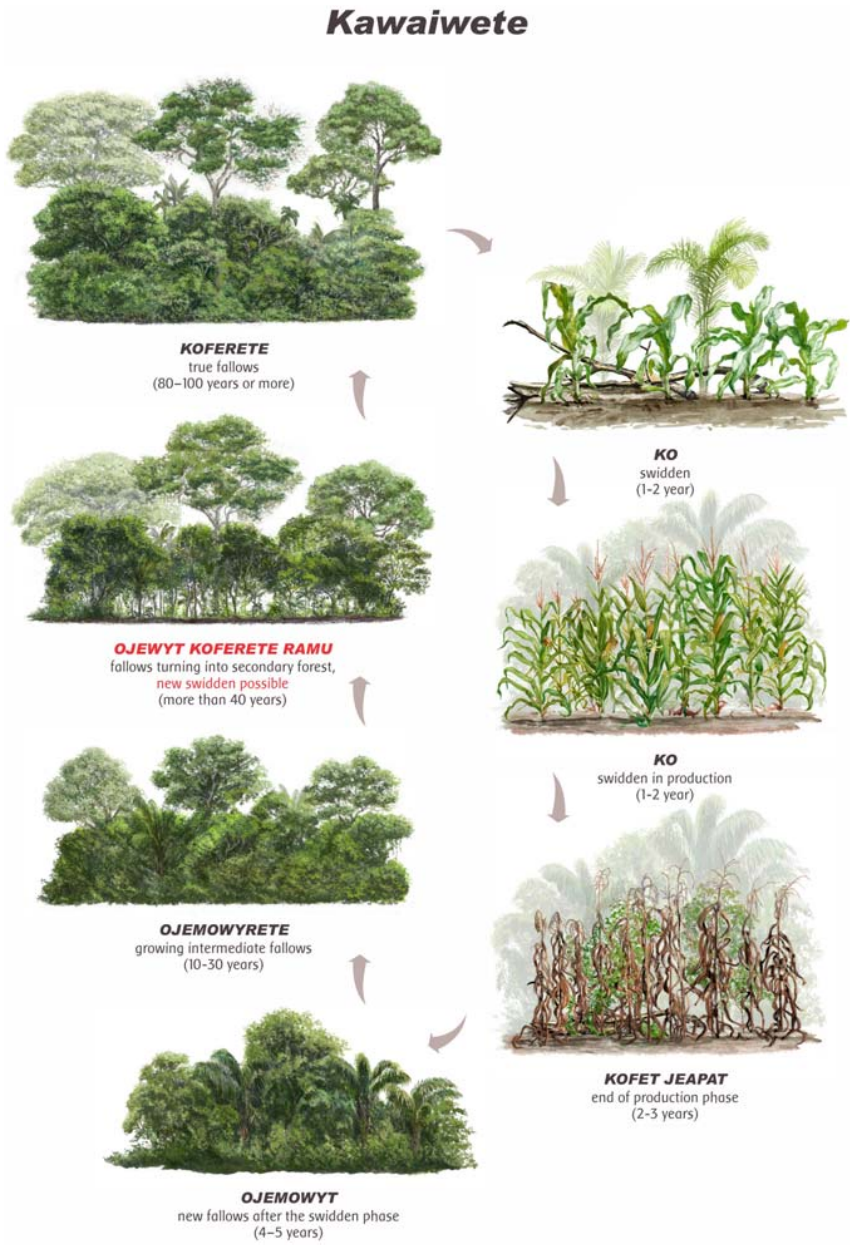

FIGURE 2 | Illustration of Kawaiwete maize (*Zea mays* L.) shifting cultivation cycle in anthropogenic soils (ADE). When the fallow reaches the *OJEWYT KOFERETE RAMU* phase (in red), soils and vegetation are considered as recovered and a new cycle may start (*Ilustração de Gustavo Marigo*).

eliminated so as not to hinder the development of crops, and species with specific uses are selected and kept, thus helping forest regeneration (**Supplementary Table 1**).

However, nowadays many farmers prefer to leave the swiddens very clean throughout the cultivation phase, so as not to hinder the growth of cassava roots or the peanut production, but they end up weakening the soil:

"*[.] No, no, they are all cut, that's why we clean the cassava, it's very clean, we remove everything that grows. This is also done with peanuts; it has to be kept very clean, we do not leave any young trees behind*" (Kape Kaiabi, personal account, 2016).

In cases where excessive cleaning has already occurred in previous cycles, the impacts can be even more drastic for regenerating areas. Although changes in management techniques are visible, it is not known exactly why they occurred. However, some farmers have shown resistance to changing the traditional way of cleaning, as they believe that it can hinder the development of cassava and compromise the feeding of their families. Some farmers also recognized that it is worth trying a more balanced management of swiddens and perform selective cleanings only around plants, decreasing clearing intensity gradually as crops develop, to favor forest regeneration during the fallow.

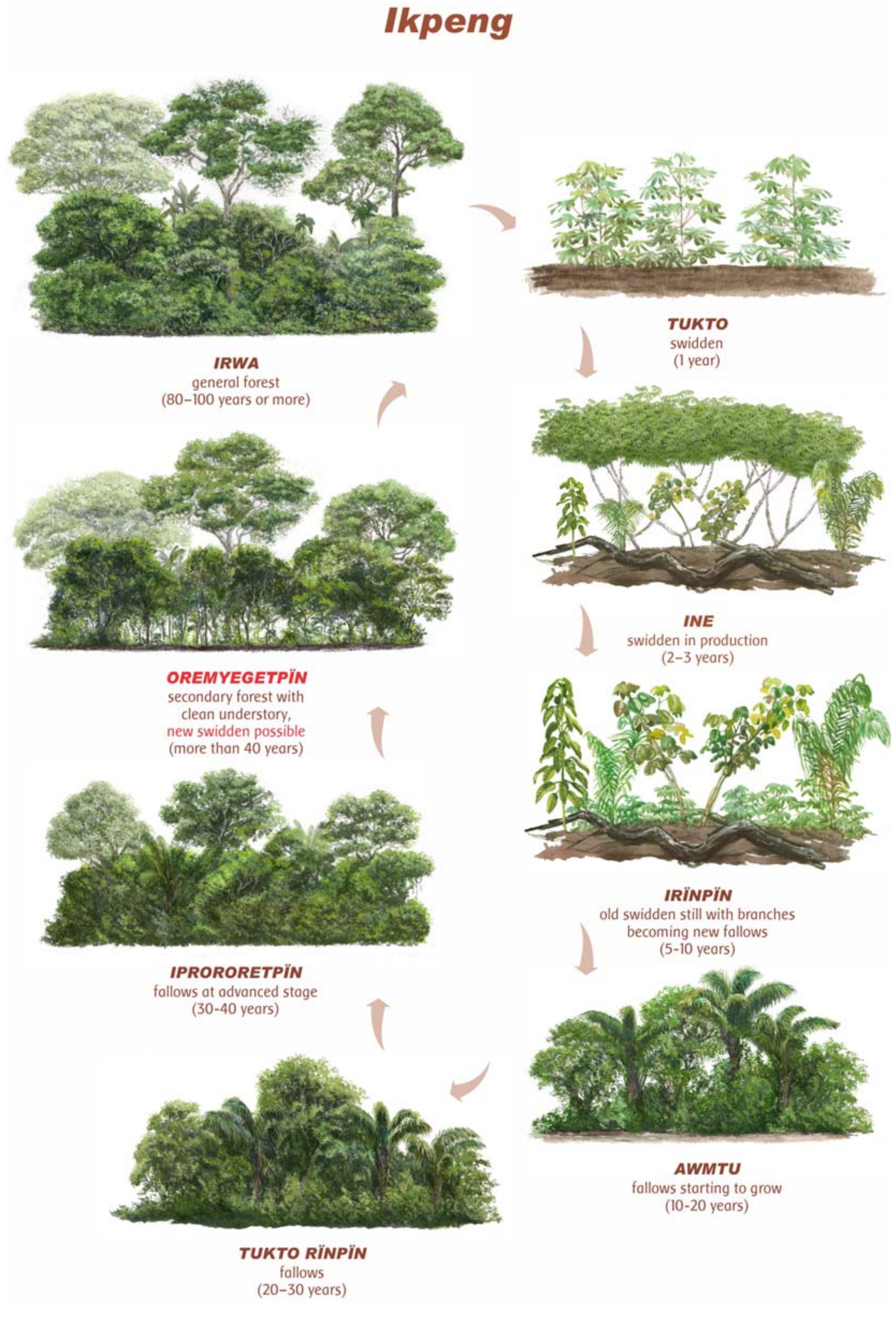

FIGURE 3 | Illustration of Ikpeng cassava (*Manihot esculenta* Crantz) shifting cultivation cycle in non-anthropogenic soils (nADE). When the fallow reaches the *OREMYEGETPÏN* phase (in red), soils and vegetation are considered as recovered and a new cycle may start (*Ilustração de Gustavo Marigo*).

In the Moygu Ikpeng village, the method of opening swiddens has also changed. In the past, there were fewer swiddens and the people always followed the guidelines of the village leaders to manage areas under recovery. As a result, it was possible to plan ahead the opening of new cultivation areas for the families. However, nowadays, the swiddens have become more individualized and often managed by young people with little agricultural experience, leading to the opening of secondary forest areas still at their early stages and without criteria. However, farmers also recognized that the method used for clearing swiddens can help the secondary forest to recover faster during the fallow and maintain important useful resources.

In the past, plots were cultivated for 1 year only, natural clearings were used, and cleaning was scarcely conducted during regeneration. Thus, such care helped the forest to recover faster, allowing it to be reused in a few years. According to the current Ikpeng rules, cassava swiddens can be used for up to three cycles of planting/harvesting. Nowadays there is no consensus on how to plant cassava and at the same time help the forest to regenerate. This has made it difficult to plan the use of agricultural fallows (Kampot Ikpeng, personal account, 2015).

These shifts in ancient Ikpeng agricultural management are attributed to the peoples of the upper Xingu, with whom they lived for several years after the time of contact (Menget, 2001), and may be causing changes in the local landscape: *"[.] We are currently cleaning the swiddens because we learned it from Kalapalo, Kamayura. Our old swiddens recovered quickly, a lot of raegï (Xylopia* sp.*) and yego (Vochysia* sp.*) grew naturally instead of cassava, do you understand?* (Amputxa Ikpeng, elder and farmer, personal account, 2015). However, the origin of this form of cleaning is not known, as well as the reason it occurs among the Kawaiwete.

Kawiago Ikpeng, an experienced farmer from the Moygu village, explained that the farmers themselves end up harming the forest regeneration by over-cleaning the plots. He also recognizes that the low productivity of cassava is due to the land itself, which became weak because fallows were reused at their initial stages of succession or because they were accidentally set on fire in previous periods:

"[.] The ancients did not live fixed in a same place. When they opened swiddens, they harvested, and soon moved to another village. Nowadays we live in the same place, we don't have woods anymore, it is too far away, that makes us use the swidden several times." (Kawiago Ikpeng, farmer, personal account, 2016).

Even so, some farmers manage their plots and fallows in ways that favor forest regeneration. Purat Ikpeng, a spiritual leader of the Moygu village, showed us a swidden plot that was at the final stage of cultivation (*ïrïnpïn*), still with some remaining cassava branches (**Figure 3**), where he performed only selective cleaning (*tukto tawengkeremtowo*). During the cultivation phase, he protected and let many types of trees to grow. The "real trees" (*yay were keni*) that were protected helped the regeneration of the fallows.

This selective cleaning system is based on two cultivation cycles, which may last between 2 and 3 years (30 months). The most intense cleanings take place in the first year, between 3 and 4 months of cassava growth. While weeding, farmers select the species that will remain in the system after selective cleaning. From the second year, the first-cycle cassava begins to be harvested and its branches are replanted taking advantage of the same location of the collected roots. At this stage, the regenerating trees that were left in the first year are already grown and can be pruned so that they do not hinder the second-cultivation cycle cassava. From the second year onward, regeneration trees are left to grow, the last cassava harvest takes place, and the regeneration phase of fallow begins with several species of trees already established.

After the third year, the swidden already has several trees important for local use, including fruit trees such as *pequi-do-xingu* (*Caryocar brasiliensis* Cambess.) and cashew (*Anacardium* sp.). Other species are *arakto* (ni)—for constructions; *ykwalapi* (ni)—medicinal use; *raegï* (*Xilopya amazonica* R. E. Fries) and *mopya* [*Attalea maripa* (Aublet) Drude]—wood and straw used in the construction of houses; *yepkuy* (*Himatanthus* sp.)—various uses, including paint fixing; *motoe* [*Helicostylis tomentosa* (Poepp. and Endl.) J. F. Macbr.] and *tomkorowo* (*Talisia* sp.)—highly prized foods, bait for hunting; and *ponmu* (*Cochlospermum* sp.)—medical use and fiber for the tucum oil press—*ototo* (*Astrocaryum aculeatum* G. Mey). **Figure 4**, adapted from Bahuchet and Betsch (2012) for the selective cleaning techniques used by the Wayãpi people of the Guianas, which are very similar, shows the technique used in the Moygu Ikpeng village.

Indicator Species for Secondary Succession, Soil Recovery, and Resistance to Fires

Certain trees or plants have cultural uses among the Ikpeng and Kawaiwete, but some also have functional characteristics that may favor the regeneration of secondary forests and the recovery of soils. Others are characteristic of certain sites (types of soil or successional stages), resistant to fires, or subject to certain levels of protection, among other characteristics that may favor a fast establishment in the cultivated areas.

In the Samauma Kawaiwete village, the forest species surveyed are organized into local categories: (I) adapted to the successional stages—initial, intermediate or advanced; (II) indicators of specific environments such as *koferete* (ADE) or "*trees that own fallows*" such as *kaarete* (nADE); (III) indicator of burnt forest *(ywokaiwet);* (IV) those that "*animate the regeneration*" and "*help the earth to become dark*" (*yja mama kaap)* or protected trees for being the "*owner of the swidden*" (**Supplementary Table 1**). For the recovery of *koferete*, plants called *yja mama kaap* are required, which care for and help to recover the soil because [.] "*they produce many leaves that fall quickly and the soil acquires a darker appearance, with good and more fluffy earth*" (Kape Kawaiwete, personal account, 2016).

In the past, during the opening phase of a Kawaiwete agricultural site, some adult trees were kept at the edges of swiddens to provide more shade and moisture to the lands, also serving as a source of propagules. These trees were called "*trees owners of the swidden*" and were not felled because, in addition to helping with regeneration, they had several uses in material culture. Among them, are the *jatua'yp* [*Guarea* cf. *guidonia* (L.) Sleumer], *jatuywa* (*Hymenaea courbaril* L.), *jatytayp* (*Maclura tinctoria* L. Engl.), *yangyp* (*Dinizia excelsa* Ducke), and *ykyr'yp* (*Thyrsodium spruceanum* Benth.) (**Supplementary Table 1**).

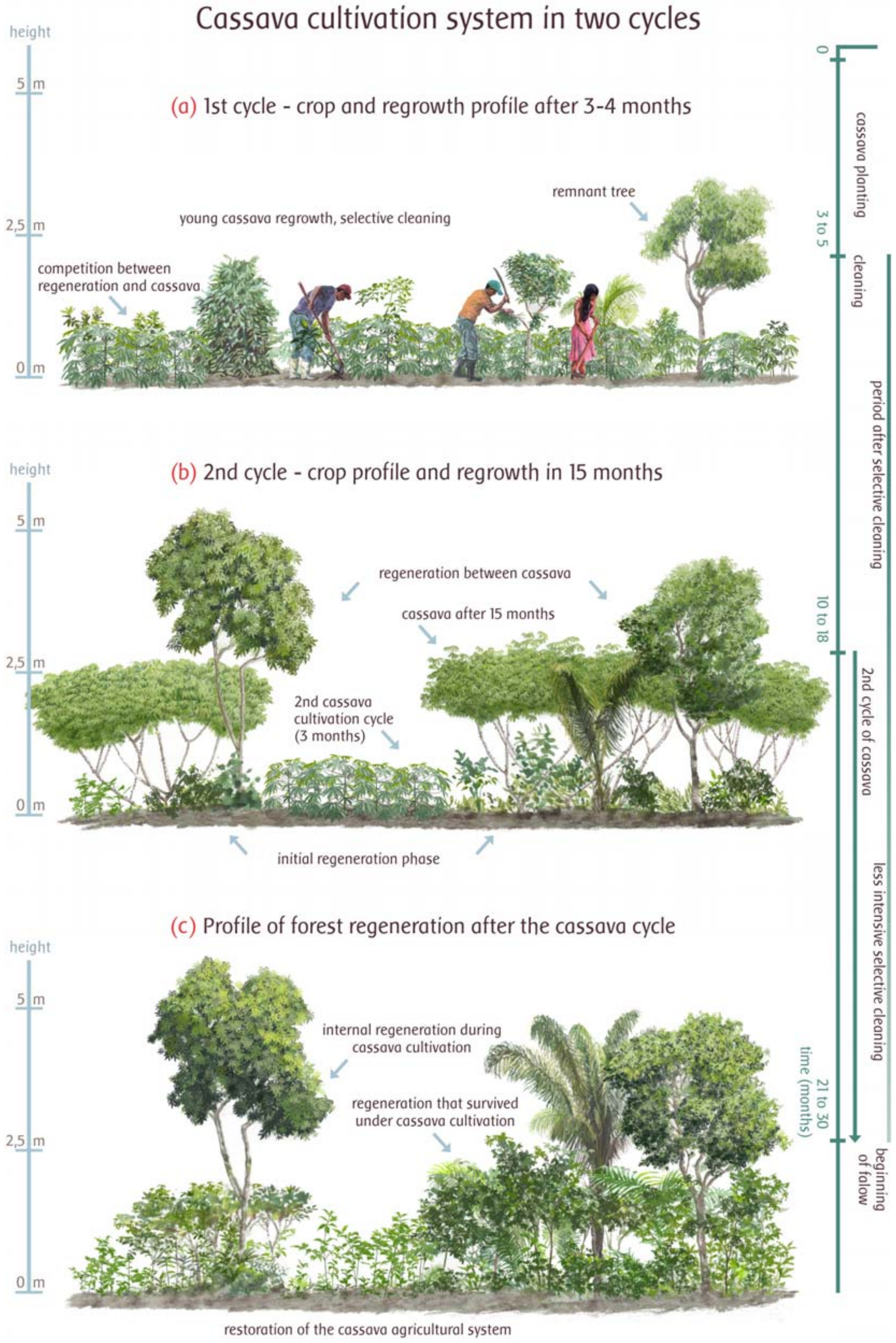

FIGURE 4 | Selective cleaning management (*tukto tawengkeremtowo*) and forest regrowth in the Ikpeng cassava (*Manihot esculenta* Crantz) shifting cultivation cycle. **(a)** When the plot is opened, certain tree species are tolerated and left in the plot. As the crop grows, selective cleaning is repeated after 3–5 months **(b)**. After the first harvest, cassava is planted again and left to grow among the young regenerating trees (2–5 m) that may be pruned to avoid competition (10–18 months). A less intensive selective cleaning is performed. **(c)** At the end of the cultivation phase (21–30 months) the protected trees help other regenerating secondary growth species to thrive (*Illustration by Gustavo Marigo—adapted according to* Bahuchet and Betsch, 2012).

According to Kape Kawaiwete, an elder farmer (personal account, 2016):

"[.] To me, they are left the jatua'yp; so when it bears fruit, the seeds are born in the middle of the swiddens. Jatua'yp is born in the middle of the swiddens; its seeds are red. These are those that the ancestors did not fell; so species returned, and fallows soon grew."

However, nowadays the practice is to cut all the trees down, even if such practices are recognized as enhancing recovery of fallows. This type of management has not been used in most Kawaiwete villages anymore and possibly in most villages in the XIT. As a result, secondary forests have become poorer in composition because certain types of plants are no longer found in the regenerating forest, such as *jatua'yp* [*Guarea* cf. *guidonia* (L.) Sleumer], *jatetayp* (*Maclura tinctoria* L. Engl.), *y'ga* (*Inga* spp.), and *ykyr'yp* (*Thyrsodium spruceanum* Benth.). Other useful trees used in medicine—*asiraryp* (*Zanthoxylum rhoifolium* Lam.), for collecting fruit—*ynga* (*Inga* spp.), *api* (*Pseudolmedia macrophylla* Trécul), and for wood—*yperoyp* (ni), *ykyr'yp* (*Thyrsodium spruceanum* Benth.), *yogyp* (*Dinizia* cf *excelsa*), *ajuyp* [*Ocotea leucoxylon* (Sw.) Laness], *ajuwyuun* (*Ocotea guianensis* Aubl.), *ywyiyp* (ni), *tukumãm* (*Astrocaryum aculeatum* G. Mey)—no longer exist (**Supplementary Table 1**). These species, with the exception of *Astocaryum* sp., do not tolerate fires and no longer regenerate spontaneously in changed or intensely burned areas. For Kape, a Kaiabi elder of the Samauma Kawaiwete village (personal account, 2016):

"[.] *The land is finished; the land and the trees that existed no longer do; it is not the same as before. Jatyta'yp is a sign of where there is dark earth; there is no more dark earth; there is no jatyta'yp, there is no jatua'yp; the trees that existed before do not exist anymore.*"

For the Ikpeng of the Moygu and Arayo villages, the most conserved forests at advanced stages of succession (*irwa otepnïnpo)* contain trees considered as vulnerable, which cannot withstand impacts (such as frequent fires), and/or have relevant uses for material culture. Among them are *poret* (Annonaceae) and *raegï* (*Xylopia amazonica* R. E. Fries), which are highly sought after and used for building traditional houses. They are increasingly rare in areas close to the villages. Currently, there are also no more species that indicate the recovery of forests, such as *muret* (*Byrsonima intermedia* A. Juss.), *katepo* (*Hymenaea courbaril* L.*), tïrampo* [*Guarea* cf. *guidonia* (L.) Sleumer], *kumpang* [*Emmotum nitens* (Benth.) Miers], and *yego* (*Vochysia ferruginea* Mart.) (**Supplementary Table 2**). The *yego* is considered a sacred tree for the Ikpeng people. It is used as a bench for the initiation of children during the festivity *panango atpotpot* (piercing children's ears, one of the stages of the festive event Pomeri; Rodgers, 2002, 2013), as well as for building traditional houses.

Like the Kawaiwete, Ikpeng farmers also used to protect some trees during the opening of swiddens in the past and recognized their value, as explained by Oporike (Tome) Ikpeng, a leader of the Moygu Ikpeng village: *"[.] These trees were kept in the swiddens because they had a strong spirit; it wasn't just anyone who could cut them down"* (Oporike Tomé Ikpeng, personal account, 2016).

During the cultivation phase, the "*real trees*" (*yay were keni*) were tolerated in swiddens by means of selective cleaning. They indicated that fallows were following their successional recovery, so that the forest could be reused for agriculture, yielding a productive yield. Among them were *katepo* (*Hymenaea courbaril* L.), *kuryum* (*Enterolobium schomburgkii* Benth.), *oyot* (*Dipteryx odorata* (Aubl.) Wild.), *pitpirak* (*Qualea* cf. *paraensis* Ducke), *raegï* (*Xylopia amazonica* R. E. Fries), *yeron* (*Ocotea leucoxylon* (Sw.) Laness.), and *txiworo* (*Trattinickia* cf, *rhoifolia* Wild.) (**Supplementary Table 2**). Other tall trees, which form a wide canopy and favor a quick shading of the area, protecting regenerating plants, are called "*mother trees*" (*okewï*) and "*grandmother trees*" (*iramrungmo*). Other species are important because they "*call the other plants*" (*awmtu*), such as *kumpang* (*Emmotum nitens* (Benth.) Miers), *kuryum* (*Enterolobium schomburgkii* Benth.), and *katepo* (*Hymenaea courbaril* L.) (Pura Ikpeng, Makawa Ikpeng, personal account, 2015). Finally, some plants "*are [also] born by the spirit oyng,*" a non-human entity who plants many trees for the forest to be reborn (Totopiat Ikpeng, personal account, 2015).

Totopiat Ikpeng, the main spiritual leader of the Moygu village, when questioned about how forests regenerate, explained very slowly: [.] *"everything has its owner. the owner of the river—orongo—the owner of the land—momtïng. and the owner of the bush in general—oyoreta."* In his understanding, [.] *"the forest needs oyng, the spirit that freshens the earth and helps the forest to grow back—orong ewyangtenopni. When he cries, the tears make the earth moist*[4]. *Plants are born together, kerekere-umi, ogolak, which is next to the kayakpo, tïrampo, pïrigu, mawa. These are plants that oyng gives birth to it to first refresh the earth*" (Totopya Ikpeng, personal account, 2015).

As noted, in addition to presenting some priority uses, many of these plants have functional characteristics in the recovery of secondary forests. However, the Ikpeng have observed that many species that re-sprouted in disturbed secondary areas (*engrotet*) are no longer sprouting due to the increase in the number of fires and the excessive cleaning in agricultural areas during the cassava cultivation cycle.

Impacts on the Sustainability of Systems With the Increase in the Number of Fires

The availability of recovered areas for opening new plots is increasingly critical. In choosing the area for cultivation, in addition to other indicators, the main criterion is the stage of development of fallows measured by the forest structure and tree sizes. The lack of good lands in areas close to Kawaiwete and Ikpeng villages implies the clearing of secondary forests that are still very young, with less than 5–10 years in fallow age, indicating an intensification of the traditional system.

However, even areas that remain for longer periods in fallow, between 10 and 15 years, have their recovery affected by the history of fires or previous uses. As a result, many species characteristic of secondary forests—and that are important

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[4] Relating to morning dew.

for forest regeneration and soil recovery—no longer grow spontaneously nowadays. Examples such as *jatua'yp* (*Guarea* cf. *guidonia* (L.) Sleumer), *jatetayp* (*Maclura tinctoria* L. Engl.), *y"ga* (*Inga* spp.) for the Kawaiwete and *katepo* (*Hymenaea courbaril* L.), *kuryum* (*Enterolobium schomburgkii* Benth.), *oyot* [*Dipteryx odorata* (Aubl.) Wild.], *pitpirak* (*Qualea* cf. *paraensis* Ducke), *raegï* (*Xylopia amazonica* R. E. Fries), *yeron* [*Ocotea leucoxylon* (Sw.) Laness.] and *txiworo* (*Trattinickia* cf*, rhoifolia* Wild.) for the Ikpeng.

For this reason, important resources characteristic of late stages of regeneration become less accessible, rare, or even extinct in areas close to human occupations, like (*Pseudolmedia macrophylla* Trécul), [*Guarea* cf. *guidonia* (L.) Sleumer], (*Xylopia amazonica* R. E. Fries), (*Inga* spp.), (*Talisia* sp.), (*Byrsonima crispa* A. Juss), and (*Vochysia ferruginea* Mart.).

DISCUSSION

The indigenous peoples of the Amazon exert an important influence on the structure and composition of its forests through the succession management conducted during the cleaning and gardening of plots (Irvine, 1989; Pinedo-Vasquez et al., 2012). Practices conducted during cultivation or fallow management can favor forest recovery. In addition to selective clearing, the frequency and duration of other processes, such as the protection of useful species, seed dispersal and attraction of fauna, selection of desirable phenotypes and cultivation of propagules, may favor a greater concentration of useful plants and to improve soils (Levis et al., 2018).

The agroforestry management includes food attractive to animals for hunt and, therefore, the fauna plays an important role by contributing to the dispersion of seeds that are brought from other forested areas close to swiddens (Denevan et al., 1984; Zent and Zent, 2012; Bahuchet et Betsch, op. cit.; Thomas, 2014). Areas in fallow create wetter and more fertile microhabitats than areas that are open and thus drier (Uhl et al., 1981; Uhl, 1983). Seeds dispersed by animals are more likely to establish themselves and accelerate the initial recovery of the area (Unruh, 1988). Several of these species also serve as food for humans. They are multiplied in backyards, gardens, or even dispersed in displacements during collection activities. Fire management, at low intensities and frequency, when combined with these other practices, may also lead to an improved soil fertility, a process that indirectly favors forest recovery (Junqueira et al., 2011; Levis et al., 2017).

However, in several regions of the Amazon agricultural intensification processes in indigenous lands are taking place, either by changing habits to more sedentary livelihoods, circumscription of their original territories by legal delimitation (Vickers, 1983; Denevan, 2001; Freire, 2003, 2007) or illegal advancement of miners and loggers, a need for access to schools, health centers or urban areas, as well as the advancement of the agricultural frontier and the impacts of large construction works (Jusys, 2018; Fa et al., 2020).

In the two cases studied here, the reality is no different. In the past, both the Kawaiwete and the Ikpeng presented patterns in the use of the territory characterized by the frequent mobility of villages, which were moved when the local natural resources were depleted. This lack of mobility, in the long run, results in an increase in pressure on secondary formations, with impacts to local livelihoods. Inside the XIT, it has become increasingly difficult to observe older villages changing place, as this decision depends on the availability of specific environments that are rich in dark earth and that are close to the main river channel, which must be negotiated with other indigenous people.

The lack of mobility is directly related to the time and space necessary for the continuity of the shifting cultivation and territory management system, making difficult a full recovery of secondary forests and leading to the intensification of agricultural use (Uriarte and Chazdon, 2016; Chazdon, 2017), in addition to surpassing the limits of the system (van Vliet et al., 2012). The history of intensification of land use with the increase in cutting and burning practices leads to a reduction in soil fertility, which ends up causing a decrease in species that depend on seeds to regenerate to the detriment of those that have the ability to regrowth and are more adapted to this new context. This leads to a decrease in species diversity in managed landscapes, as Jakovac et al. (2016a) observed in other regions of the Amazon. With the increase in the number of cultivation cycles, the frequency of cleaning also increases, and, in this way, the system may reach a state of interrupted succession, where regeneration starts to rely more on re-sprouting to compensate for the loss of species that reproduce by seeds (Jakovac et al., 2015). The factors that contribute to these changes are often difficult to understand, since the systems are dynamic and correspond to different sociocultural contexts (Wiersum, 2004; Mansourian et al., 2019).

Local Transformations and Forest Regeneration

From the circumstances presented, in the studied Kawaiwete and Ikpeng villages there is a conjunction of local factors of change that are being aggravated by regional transformations. In the past, the processes of clearing and cultivating Kawaiwete and Ikpeng swiddens followed specific rules that, although still present in local knowledge, had their application hampered by changes in the form of occupation of the territory. Currently, the period during which plots are left in fallow varies from 5–10 years. The history of previous uses of the same plots and accidents with fires aggravates this situation, which impairs the processes of vegetation regeneration, soil recovery, and recovery of key species in this process.

With less mobility in villages, in addition to occasional forest fires, agricultural areas already show signs of soil degradation even before they are cultivated, affecting the regeneration of many forest species during the fallow phase. The decrease in the size of plots close to the Kawaiwete and Ikpeng villages leads to the cutting down of secondary forests even at initial stages of regeneration (up to 10 years). These often present little biomass, individuals with a baseline DBH area below 5 cm, and heights up to 3 m, where fast-growing trees and low longevity predominate. In other words, the criteria used in the choice of new swidden plots does no longer take into account aspects of forest structure or other local indicators as in the past. As a result, many species characteristic to these areas—which are important for forest regeneration and soil recovery—no longer appear spontaneously. For this reason, the resources characteristic of late stages of regeneration become less accessible, rare, or even extinct in areas close to human occupations.

The decision of using initial stages seems to be related to the ease of access to areas or to their practicality, since the branches and thin shrubs do not need much effort to be cut down, unlike swiddens cleared in a more developed fallow or the older and more distant forests (**Figures 2**, **3**). For the same reasons, agricultural areas may end up being reused for cultivation cycles of less demanding species, such as manioc, beyond the limits dictated by traditional local rules (two to three cycles). Limitations in the available workforce may be one of the factors that lead to this decision, making it easier to work in a nearby area and in a fallow of thin trees instead of having to look for more distant areas with thick trees where the human-hour work would be more demanding. However, the effect of using young fallows may be the opposite, as there seems to be a relationship between low productivity in swiddens and an increased need for work. When poorer soils start to predominate, the need for weeding and for cultivating other sites in order to compensate for the low yields of the swiddens increases, as Jakovac et al. (2016b, 2017) also reported.

On the other hand, some indigenous families began to seek other areas of old forests for the most demanding crops that need recovered soils, mainly maize (*Zea* sp.), peanuts (*Arachis* sp.), banana (*Musa* sp.), broad beans (*Phaseolus* spp.), sweet potato (*Ipomea* sp.), and yam (*Taro* sp.). The dependence on more distant places demands more physical effort and inputs, including those from outside the village, because people need vehicles and fuel to transport production either by tractor or motorboats. In other cases, the loss of resilience in red earth systems made farmers use dark earth (ADE) plots for less demanding crops, as observed in the Samauma village. These soils, which were previously indicated only for demanding crops and grown only once, are now reused for planting cassava, without enough fallow time after the cultivation of corn and peanuts, for example. As Junqueira et al. (2010) reported, although the ADE is more fertile and allows for a more intensive use when compared to the nADE, a prolonged and intensive cultivation period without respecting the fallow period may compromise regeneration and cause soil degradation (Junqueira et al., 2016).

Impact of Fires on the Sustainability of the Kawaiwete and Ikpeng Systems

Fires started to occur more intensely in the Kawaiwete and Ikpeng villages mainly due to environmental changes that occurred in the last decades in the XIT region (Nepstad et al., 2004; Morton et al., 2013; Brando et al., 2014). As already explained, the loss of forest cover in the Xingu river basin changed the microregional rainfall regime and seasonal events that were recognized by the indigenous peoples; it also led to an increase in the flammability of forests inside the XIT. Fires alter the structure and composition of forests and more vulnerable tree species do not resist, becoming rare or disappearing from these areas, such as observed by Chazdon et al. (2009) and Rozendaal et al. (2019). The degree of vulnerability of species to fire defines their survival in affected areas. Depending on the intensity and recurrence of fires, tree species can (1) extinguish locally, (2) remain stable, (3) be stimulated by regeneration, or (4) re-sprout, starting to dominate the forest formation in an opportunistic way. Participants recognized the degree of vulnerability of plants to fires during the interviews, as their importance to the forest regeneration processes (**Supplementary Tables 1, 2**).

As a result, fallows or secondary forests around the villages have become poorer in composition (less biological and cultural richness) due to frequent fires, leading to the loss of raw materials and conditions that were previously more favorable for the establishment of species that are considered by indigenous people as key regeneration species, such as the "regeneration-animating" plants (*ywakamaap* for the Kawaiwete) and "real trees"—*yay were kenin*—used in the material and immaterial culture of these peoples.

Traditional Kawaiwete and Ikpeng Forest Management Practices

The changes reported by the Kawaiwete and the Ikpeng in the traditional management of swidden plots corroborate research conducted in other tropical regions, that points to shorter fallow periods due to limitations in access to traditional territories and increase in pressures for demographic or for socioeconomic reasons (Johnson, 1983, p. 52; Thrupp et al., 1997; Marquardt et al., 2013). For the Ikpeng people, as already mentioned, agricultural areas were traditionally cultivated only once. This is no longer possible due to the permanence of villages in a same place, leading nearby areas to be frequently reused, as Jakovac et al. (2017) also observed for farmers in the Amazon.

Regarding the impacts on the regeneration of fallows, the Kawaiwete and Ikpeng local knowledge seems to value preventive care during cultivation phases aiming to prevent the forest from being degraded, instead of resorting to concepts or ways of restoring exhausted environments. In this sense, traditional local knowledge seems to indicate rules or "care" in the way environments should be managed based on resilience limits, as observed for other places (Lugo, 1995; Camacho et al., 2012; Chazdon, 2014a; Magnuszewski et al., 2015; Chazdon and Guariguata, 2016; Brancalion et al., 2016; Mukul, 2016; Vásquez-Grandón et al., 2018).

The experiences reported here indicate that the Kawaiwete and the Ikpeng manage to favor forest regeneration while the field is being cultivated (Marquardt et al., 2013). According to the observed agricultural rules and practices, some tree species were not cut during the opening of plots as a way to protect seed-bearing species during the fallow time. According to research conducted in tropical regions, this practice contributes to ensure fertile agricultural areas, as it favors forest regeneration (Abdoellah et al., 1993; cited in Balée, 2010; Chazdon, 2014a). Karen farmers in Thailand, for example, left between 20 and 40 trees in swiddens at an average of 244/ha (Schmidt-Vogt, 2001). As a result, the structure and composition of the forest changes following a process that is similar as that of domesticating landscapes (Denevan et al., 1984; Wiersum, 2004; Clement et al., 2015).

The careful cleaning of areas surrounding crops, with little removal of regenerating plants, can also favor the recovery of the forest (Rodrigues, 1993; Silva, 2016, p. 146). As the Kawaiwete and the Ikpeng, the vast majority of indigenous and traditional people that practice forest-based agriculture use "selective cleaning." Some plants are protected and favored during soil preparation, resulting in the spontaneous development of useful species (Denevan et al., 1984, Descola, 1988; Denevan, 2001; Bahuchet and Betsch, 2012; **Figures 4**, **5**). However, this traditional technique is not followed by all the Kawaiwete and Ikpeng farmers nowadays, despite apparently presenting good results. Likewise, some regenerating species could also be pruned during the crop growth phase, such as manioc, instead of being uprooted (Johnson, 1983; Wiersum, 2004; Uprety et al., 2012; Pye-Smith, 2013; Peltier et al., 2014; Chazdon, 2017; FAO, 2018). The use of nitrogen-fixing species, as is the case observed in the Samauma village, is a strategy widely used by tropical forest farmers (Unruh, 1988; Chazdon and Guariguata, 2016, p. 717), and, in a way, is related to the *yja mamakaap* ("*trees that grew together*") of the Kawaiwete[5].

Finally, according to the perception of many indigenous peoples in the Amazon, the regeneration of forests also seems to assume a mythical and spiritual dimension. Some concepts refer to domains that are claimed by human and non-human beings (Rodgers, 2002; Fausto, 2008; Oliveira, 2016). In this case, forests are understood as a large plantation of creative spirits (Descola, 1996), as the peoples of the XIT. Thus, the plants over which the spirit *Oyng* cries to refresh the earth are plants that should be considered in forest recovery projects (**Supplementary Table 2**).

Assisted Natural Regeneration (ANR) as a Way of Managing Indigenous Shifting Cultivation Systems in the XIT

In the Kawaiwete and Ikpeng villages, traditional agroforestry management is being replaced by techniques that take into account the practicality and ease of access to areas, with food production as a priority, rather than a good regeneration of fallows. As the more mature forests are far away from villages, there is no alternative but to reuse the same area several times, even if this means degrading the secondary forest. Therefore, as it seems, it is not just a question of disregarding techniques that favor regeneration, but of the lack of local conditions to put these techniques into practice. Therefore, the mere recovery of some rules that previously governed the access to resources may not respond to the challenges for the maintenance of production systems more adapted to the current reality (Denslow, 1980; Wiersum, 2004; Uprety et al., 2012; Chazdon, 2013, 2017; Tengö et al., 2014).

The Ikpeng believe that the best way to recover areas affected by the increasing episodes of recurrent fires in recent years would be to leave the forests to recover on their own. According to preliminary assessments considering the species identified here, the restoration of burnt forests can take place with few interventions, since many areas impacted by the fires are close to the remnants of more enclosed forests, which favor the flow of seeds[6]. To this end, the forest should be protected from fires and there should be investments in broad firebreaks and in local agreements, in addition to monitoring the growth of species characteristic of more advanced stages in fallow areas. However, there are cases where it becomes necessary to create favorable conditions for the maintenance of the productivity and the resilience of these systems (Hames and Vickers, 1983, p. 25).

The methods used by the peoples in the XIT are methods of assisted natural regeneration (ANR), as Wiersum (2004); Walpole (2010), Marquardt et al. (2013); Chazdon (2014a), and Thomas (2014) described. The main methods are: (1) tolerate adult trees at the borders of swiddens in such a way that they begin to produce seeds that regenerate the cultivated site, (2) limit the crop cycles so as not to affect the potential for the establishment of regenerating plants, (3) select individuals during cleaning at the cultivation phase, which favors the regeneration of useful and functional species, (4) use fire protection techniques, and (5) know functional plants that favor regeneration processes. In this regard, the ANR should be considered a tool to promote livelihoods within the context of traditional forest management (Butic and Ngidlo, 2003; Wiersum, 2004; Walpole, 2010; Marquardt et al., 2013; Thomas, 2014).

One of the main reasons for forest degradation is the depletion of soils (Chazdon, 2003), when the resilience limits are exceeded and prevent forest succession (Jakovac et al., 2016a,b). Therefore, cultivation systems with accumulated ash and coal from controlled burning (Schmidt et al., 2014) may improve soil structure and fertility and accelerate the recovery of fallows (Junqueira et al., 2010). On a local scale, ANR processes must also consider the previous legacies of agricultural management because they influence the structural, compositional, functional, and dynamic attributes of regenerating forests (Uriarte and Chazdon, 2016).

ANR strategies also include the sociocultural values of the communities involved and may include approaches to recover traditional indigenous ecological management practices, in which their knowledge can support management strategies and silvicultural practices (Coomes et al., 2000; Sajise, 2003; Uprety et al., 2012). In this regard, it is essential to maintain the social structures that govern these mechanisms of agricultural production and landscape conservation aiming to achieve a long-term production stability (Bahuchet and Betsch, 2012).

Transforming degraded lands into improved fallow lands may represent a large investment in labor and harvests could be very low during the first seasons, as Marquardt et al. (2013) argued. However, in situations as the XIT, where there is a limitation in the availability of fertile lands and difficulty in moving the villages, this form of "adaptive management" may improve the conditions of weakened or degraded soils,

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[5] This concept was also identified in the Capivara Kawaiwete village, where a group of similar plants were called "trees owner of fallows," necessary for the recovery of the dark earth (*koferete*).

[6] The analyses of results were conducted with the support of Dr. Daniel M. Vieira of EMBRAPA-CENARGEN 8.

FIGURE 5 | Three-year-old cultivation plot (*irïnpïn*) submitted to selective cleaning management (*tukto tawengkeremtowo*) in Moygu village. See young trees that were left to grow for different purposes: medicinal— (*arakto* (ni), *ykwalapi* (ni); construction—*raegï* (*Xylopya amazonica* R. E. Fr.), *mopya* (*Attalea maripa* (Aubl.) Drude); ritual—*yepkuy* (*Himatanthus sucuuba* (Spruce ex Müll. Arg.) Woodson); food and food for hunting—*motoe* (*Helicostylis tomentosa* (Poepp. and Endl.) J. F. Macbr.), food, food for hunting and ritual—*inot* (*Caryocar* cf. *Brasiliensis* Cambess); among others (*Photo by Marcus V. C Schmidt, Moygu Village* 2008).

which limit the natural regeneration of forests (Wiersum, 2004; Joslin et al., 2011; Pinedo-Vasquez et al., 2012). Farmers remembered that in the past, the fields were smaller, circular, and separated by a forest matrix (Eden and Andrade, 1987; Chazdon, 2003, 2014b, 2017; Chazdon et al., 2009; Ferguson et al., 2003). These aspects almost no longer exist in the oldest and most populous villages in the XIT. Thus, other factors should also be considered in future ANR strategies, such as the size of the cultivated area, the presencxe of remaining trees in the surroundings, the number of years of use, and the control of fires in areas under recovery (Uriarte and Chazdon, 2016).

To overcome these challenges and move to more sustainable cultivation systems there is a need to bridge local knowledge systems with scientific knowledge systems and co-produce knowledge adapted to uncertainty and environmental change

(Armitage et al., 2011; Tengö et al., 2017). Ikpeng and Kawaiwete younger generations are open to innovations and some initiatives are being implemented with external organizations to try and overcome the knowledge gap, such as the agroecology high school program in the Ikpeng village[7], the *muvuca* seed-planting system by ISA[8] and the *Prevfogo* fire-fighting training program by the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA)[9]. Knowledge co-production and adaptive management are processes mediated by institutions that need to create the conditions for "social learning, defined here as the iterative action, reflection, and deliberation of individuals and groups engaged in sharing experiences and ideas to resolve complex challenges collaboratively (Diduck et al., 2005; Keen et al., 2005)" (Armitage et al., 2011, p. 995). However, at this stage, the agroecology program and the *muvuca* system have not yet incorporated the local knowledge of older generations on shifting cultivation, forest regeneration and fallow indicators discussed here, and are based on external forest restoration models that need to be adapted. The *Prevfogo* has been more successful in training local fire fighters and cultivators on fire management techniques adapted to the new environmental conditions, but needs to be upscaled to include all the villages in XIT.

CONCLUSION

Maintaining agricultural productivity in indigenous lands in the Amazon is a priority, especially considering the increase in deforestation rates and in the number of fires in the Xingu Indigenous Land (XIT). In areas where processes of agricultural intensification have led to the degradation of lands for cultivation, it is necessary to involve indigenous farmers in forestry landscape recovery initiatives considering their ancient knowledge in order to understand the causes and consequences of the permanence of these shifting cultivation systems.

Our results show how traditional practices can favor the regeneration of forests after disturbances according to the knowledge of the Kawaiwete and the Ikpeng peoples. Traditional knowledge can provide important information about the functional and ecological roles of pioneer species during natural regeneration (Reyes-García et al., 2018). However, the potential for natural regeneration is influenced by the intensity of land use. The more conserved the forests, the greater the power of recovery of forest remains in the landscape (Uriarte and Chazdon, 2016). We suggest that the restoration of degraded areas in villages in the XIT should use ANR techniques grounded on indigenous knowledge. This implies the adaptive co-construction of knowledge on cultivation systems that value and strength traditional practices of these indigenous peoples, as well as assimilate new practices comprising a more "agro-forestry-restorer" profile, and fundamentally a greater control of fires.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical approval was not provided for this study on human participants because this article represents part of the results of a project developed by a non-governmental organization—Instituto Socioambiental (ISA) that works in partnership with indigenous peoples in this area of study. ISA develops activities to protect and defend the rights of these peoples and carries out collaborative and intercultural research projects on the impacts of fires, in order to identify strategies to favor the conservation of forests in Indigenous Territory. This project was carried out through a formal partnership with these peoples, represented by local associations and indigenous representatives participated in the project and are co-authors of the text that is being submitted for this Frontiers special. The indigenous authors participated in the conception of the research and in the elaboration of the text. They are very pleased to be recognized and represented in this scientific article and the results value their knowledge of their people. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

MS author of the project and research, conducted interviews in the communities and surveys in the forests of Xingu, and specialized in intercultural research and knowledge co-construction processes. YI professor and researcher, was responsible for the mobilization and planning of research between Ikpeng villages, helped in the interviews and translation of local knowledge about environmental changes, indigenous management, and forest regeneration. TK researcher from the village Samauma Kawaiwete, was responsible for mobilizing the people who participated in the project, in field surveys and in interviews about the knowledge of the forest, environmental changes, and the agricultural management of his people. RS technical reviewer of the scientific text and played a fundamental role in structuring the text. KO technical and administrative support to carry out the project in the Indigenous Territory. CA supervisor of MS, has reviewed and reorganized the manuscript after Frontiers first review, has contributed with theoretical inputs to the interpretation of data, as well as revised the manuscript's translation to English. All authors contributed to the article and approved the submitted version.

FUNDING

This project was carried out through a non-governmental organization (Instituto Socioambiental), the project was carried

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[7] Integrated Technical High School in Agroecology, linked to the State Secretariat of Education of Mato Grosso (Seduc/MT).

[8] https://www.sementesdoxingu.org.br/site/muvuca-que-vira-floresta/

[9] https://www.ibama.gov.br/ultimas-2/2043-forca-tarefa-combate-14-incendios-no-parque-indigena-do-xingu

out with funds from the National Fund for Climate Change, of the Ministry of Environment, linked to the federal government. Although MS now linked to the University of São Paulo, as a doctoral student, this project was not linked to any university. The research was funded by the Climate Change National Fund of the Brazilian Ministry of Environment. The grant (Agreement 813130/2014) was awarded to Instituto Socioambiental (ISA).

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.605925/full#supplementary-material

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Natural Regeneration After Gold Mining in the Peruvian Amazon: Implications for Restoration of Tropical Forests

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Context: Gold mining is the most destructive activity in the natural forests of the Madre de Dios region in the southeastern Peruvian Amazon. Understanding the natural regeneration process of these degraded areas is necessary to develop forest restoration projects in such conditions.

Aims: We aimed to evaluate forest recovery and identify the successional and structure patterns of vegetation governing natural regeneration over time.

Methods: Structure, composition, richness, diversity, and successional status were evaluated in abandoned artisanal gold mine areas in Madre de Dios, southeastern Peru. Vegetation data were recorded in 61 plots of 250 m^2 established in five sites varying from 1 to 19 years of abandonment. Vegetation in abandoned areas was compared with six undisturbed forests evaluated in previous inventories.

Results: In the mining lands, tree density and basal area recovered quickly, while species richness and composition were slow. Forest recovery is an initial stage of transition from pioneer to early secondary species until at least 19 years after abandonment. The most abundant and frequent species were the fast-growing species *Ochroma pyramidale* and *Cecropia engleriana.* These species could be considered potential candidates to promote restoration plans. Pioneer species represented 63% of the number of species in plots of 1–4 years, 57% in plots of 5–7 years, and 50% in plots of 8–19 years. Early and late secondary species represented 34 and 16%, respectively, of the number of species in plots of 8–19 years. Abandoned mining and reference plots present less than 5% of species in common.

Conclusion: Our results highlight a slow natural regeneration process in areas for up to 19 years after gold mining. Species from different successional statuses were identified as potential candidates for recovering vegetation in such areas. Our findings may have important implications for further research focusing on the ecological restoration in tropical forests severely degraded by gold mining.

Keywords: degraded area, forest disturbance, forest succession, Madre de Dios Region, natural regenaration, artisanal gold mining

INTRODUCTION

The southeastern region of Peru comprises one of the largest areas of preserved Amazon forest encompassing almost 30% of the total protected areas of the country (SERNANP, 2019). This region is recognized worldwide as part of the Tropical Andes Biodiversity Hotspot due to its high species diversity (Rodrigues, 2013). However, artisanal gold mining in the region is the principal driver of deforestation (Joshi et al., 2015). In the Madre de Dios region, gold mining-related deforestation was approximately 1,000 km^2 between 1984 and 2017 (Swenson et al., 2011; Asner et al., 2013; Caballero Espejo et al., 2018), and it was responsible for the highest annual deforestation rate since 2011, 80 km^2 $year^{-1}$ on average (Caballero Espejo et al., 2018). Forest loss appears as extensive wastelands with superficial soil layers removed, large mounds of sand, and artificial bodies of water (Mosquera et al., 2009; Kalamandeen et al., 2020). Long-lasting impacts also include mercury-polluted air, soil, and water (Scullion et al., 2014) that severely limits forest recovery (Mosquera et al., 2009).

Forest recovery strongly depends on the initial degree of degradation (Chazdon, 2008). In tropical forests, results from chronosequences analyzed in abandoned sites impacted by agricultural and pasture activities showed that regenerating forests can attain many of the structural characteristics and woody species richness comparable with old-growth forests within a few decades (Guariguata and Ostertag, 2001). In contrast, in gold mining areas, the recovery is slower and more complex and may not even occur because the impacts not only alter the vegetation but also soil characteristics (Peterson and Heemskerk, 2001; Lamb et al., 2005; Ren et al., 2007; Kalamandeen et al., 2020).

Old-growth or secondary forests surrounding the degraded areas function as important seed sources that facilitate forest recovery following mining (Rodrigues et al., 2004). Their spatial distribution as well as their proximity to degraded areas usually defines the composition and structure of natural regeneration (Pereira et al., 2013; de Rezende et al., 2015; Sloan et al., 2016). Nevertheless, management strategies are needed to promote forest recovery in highly degraded areas. Active restoration accelerates forest recovery in less resilient areas (Stanturf, 2005; Chazdon, 2008; Rodrigues et al., 2009).

In the Peruvian Amazon, most of the areas degraded by gold mining are surrounded by old-growth forests (Joshi et al., 2015), suggesting favorable landscape-scale conditions for natural regeneration (Chazdon and Guariguata, 2016). Although variation in secondary forest structure and composition following agriculture and pasture abandonment has been widely studied (Chazdon et al., 2007; Feldpausch et al., 2007; Norden et al., 2015), quantifying the structural and compositional parameters and the time of recovery in abandoned gold mining areas remains poorly known. Considering the urgent need to restore landscapes across the tropics, it is important to understand how vegetation recovery in such lands occurs over time.

In this study, we aimed to evaluate vegetation recovery to help develop restoration strategies of tropical forests under gold mining impacts. We analyzed (i) the relationship between vegetation structure status with the age of abandonment and (ii) the species richness, diversity, and successional patterns as a function of site age; and (iii) compared the floristic composition between abandoned and reference forests evaluated in previous inventories. We also sought to identify pioneer and secondary forest species to enrich or accelerate natural regeneration in abandoned gold mining areas.

MATERIALS AND METHODS

Study Areas

The study was conducted along the mining corridor of Madre de Dios Department, southeastern Peruvian Amazon (**Figure 1**). The corridor extends along the Madre de Dios River and Interoceanic Highway (PE-30). The forest is classified as seasonal tropical moist (Román-Dañobeytia et al., 2015; Dueñas and Garate, 2018). Mean annual rainfall is 2,300 mm and mean annual temperature is 27°C (SENAMHI, 2008).

Most of the artisanal gold miners are informal and/or illegal because they either lack the proper permits to operate or work outside authorized mining concessions (Scullion et al., 2014; Daley, 2016; EJAtlas, 2018). Miners primarily exploit riverbanks and primary forestlands (Damonte et al., 2013). Widespread tree mortality is observed in the abandoned mining areas, possibly due to sediment mobilization and anoxic or desiccating conditions and perhaps because of heavy metal contamination (Asner et al., 2013).

Five abandoned sites were located: “Tres Islas,” “Laberinto,” “La Pampa,” “Sarayacu,” and “Huepetuhe” of 220, 900, 2,000, 1,200, and 2,200 ha in area, respectively (**Figure 1**). Reference forests included the Universidad Nacional Amazonica de Madre de Dios (UNA) (Escalante, 2017; Carhuarupay, 2018), Inotawa (INO) (Mamani, 2012; Báez, 2014), Chonta (author’s database), and three plot metadata collected by Forest Plots

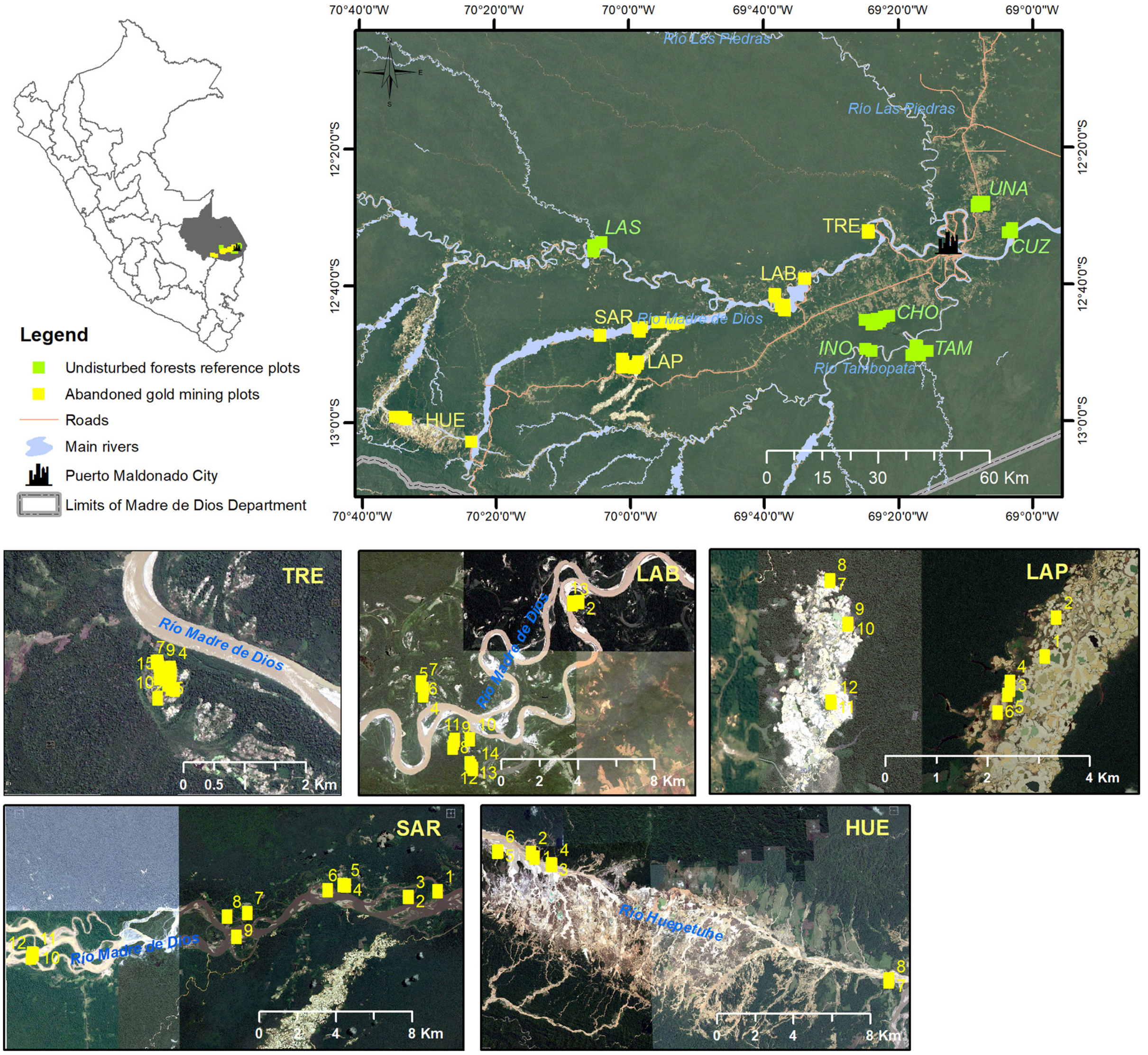

FIGURE 1 | Location of the study region including the abandoned gold mining plots (TRE, Tres Islas; LAB, Laberinto; SAR, Sarayacu; LAP, La Pampa; HUE, Huepetuhe) and undisturbed forest reference plots (UNA, Forest of the Universidad Nacional Amazonica de Madre de Dios; INO, Inotawa; CHO, Chonta; TAM, Tambopata plot zero; LAS, Jacaralia Los Amigos; CUZ, Cuzco Amazonico). The numbers within the images indicate the plot number.

(ForestPlots, 2014): Tambopata plot zero (TAM), Jacaralia Los Amigos (LAS), and Cuzco Amazonico (CUZ).

Data Collection

Abandoned Mining Sites

Sixty-one plots of 250 m^2 (10 × 25 m) were randomly established in five mining sites (between 8 and 15 plots per site). The plot ages were determined by interviews and confirmed by examining satellite images between 1990 and 2016. In each plot, three size classes of woody species (all trees and shrubs) were recorded, identified, and measured, and botanical material was collected: small trees (10 cm diameter-at-breast-height, dbh), saplings (5–10 cm dbh), and seedlings ($\geq$ 1 m height and $<$ 5 cm dbh). The identification and classification was performed by botanists at the Alwyn Gentry Herbarium (Universidad Nacional Amazonica de Madre de Dios) and the San Marcos Herbarium (Universidad Nacional Mayor de San Marcos). The classification was based on the Angiosperm Phylogeny Group (Chase et al., 2016), and the scientific names were updated and standardized based on the data from Missouri Botanical Garden[1].

Reference Forest

Table 1 shows the number and characteristics of plots in reference sites. In each plot, all trees $\geq$ 10 cm dbh were identified at the species level, and their height and dbh were measured.

The species of abandoned mining and reference plots were also classified by their successional status (pioneer, early

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[1] http://www.tropicos.org/

TABLE 1 | Plot characteristics in abandoned mining and reference sites.

Abandoned mining sites (*)	**Age since abandonment (years)**											**Total area (ha)**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**10**	**15**	**19**	
	No. of plots, 250 m^2 (10 × 25 m)											
Huepetuhe		3	4	1								0.2
La Pampa	2	1	1	1	2	3	2					0.3
Laberinto			1	1	2	1	1	2	2	3	1	0.35
Sarayacu		4		3	1	1	1		2			0.3
Tres Islas							5		7	3		0.375

Reference sites	**No. of plots**	**Plot area**	**Total area (ha)**	**Date of evaluation**	**References**
UNA	32	10 × 100 m	3.2	2017	Escalante, 2017; Carhuarupay, 2018
INO	4	10 × 500 m	2	2012	Mamani, 2012; Báez, 2014
CHO	8	10 × 200 m	1.6	2014	Author's database
TAM	9	100 × 100 m	9	2008–2011	
LAS	1	100 × 100 m	1	2008	Lopez-Gonzalez et al., 2011
CUZ	4	100 × 100 m	4	2008	

(*) Abandoned mining plot data include species information collected and described in Cutire and Ramirez (2017) and Sajami (2017). UNA, Forest of the Universidad Nacional Amazonica de Madre de Dios; INO, Inotawa; CHO, Chonta; TAM, Tambopata plot zero; LAS, Jacaralia Los Amigos; CUZ, Cuzco Amazonico.

secondary, late secondary, or climax) based on a literature review of ecological studies in the Amazon rainforests (e.g., Gandolfi et al., 1995; Guariguata and Ostertag, 2001; Pitman et al., 2001; Gama et al., 2002; Souza et al., 2002; Da Silva et al., 2003; da Santos et al., 2004; do Amaral et al., 2009; Orrego and Zevallos, 2014; Dueñas and Garate, 2018).

Data Analysis

We classified plots into three groups by age of abandonment: 1–4, 5–7, and 8–19 years, with 22, 19, and 20 plots, respectively, based on a principal component analysis of mean diameter and height of seedlings, saplings, and small trees and the number of seedlings, saplings, small trees, pioneer, early secondary, and late secondary species by plot (**Supplementary Figure 1**). Three plots of La Pampa (two of 1 year and one of 2 years) did not have any individuals.

Linear regression analysis, plotting the age of site abandonment against species richness, basal area, and density of plants, for each successional status, was used to describe the pace of forest regeneration. Data correspond to 61 plot observations including pioneer, early secondary, and late secondary species. Analyses were performed in SAS Software, Version 9.4 (SAS Institute Inc, 2013).

Rank-abundance plots (Daly et al., 2018) were used to graphically depict the abundance distributions of species in each age group after mining, for each reference forest. For these analyses, log 10 data transformation was performed. The relative abundance of species (%) by successional status was calculated. Shannon diversity index (H') (Magurran, 1988) and the effective number of species (ENS) calculated as ENS = $\exp(H')$ (Jost, 2006; Daly et al., 2018) were determined to compare plant communities among age groups and reference forests.

Rarefied species richness curves (Chazdon et al., 1998) were constructed to compare expected species for each age group after mining and reference old-growth forests. Ninety-five percent confidence intervals derived from 100 permutations were also calculated. Rarefaction curves are robust to estimate species richness, and they are recommended for unbalanced sampling design (Magurran, 1988).

The Importance Value Index (IVI) was also calculated (Lamprecht, 1990). The ranking of the highest 10 species according to their IVI was graphed for each site. Analyses were performed in Past 3.2.1 (Ryan et al., 2001) and Origin 2018 (OriginLab Corporation, 2018).

RESULTS

Forest Community Overview

We recorded 3,129 stems from 71 species of woody plants. Three plots (1 and 2 years since abandonment) from La Pampa did not have any individuals. In addition, 35 species were classified as pioneers, 23 as early secondary, and 13 as late secondary. Seventy percent of individuals corresponded to seedlings (61 species), 20% to saplings (43 species), and 10% to small trees (21 species).

In the reference plots, we recorded a total of 11,067 stems from 948 species of trees. Ninety-eight species were classified as pioneers, 314 as early secondary, 475 as late secondary, and 61 as climax.

Forest Structure, Species Richness, Diversity, and Successional Status Over Time

Total stem density was 2,155, 2,200, and 1,798 ind. ha^{-1} for 1–4, 5–7, and 8–19 years after mining, respectively. Pioneers had the highest stem density in all age groups, representing 96, 89, and 69% of total stem density in plots of 1–4, 5–7, and 8–19 years post-abandonment, respectively. The relative density of early and late secondary species increased with abandonment age, from

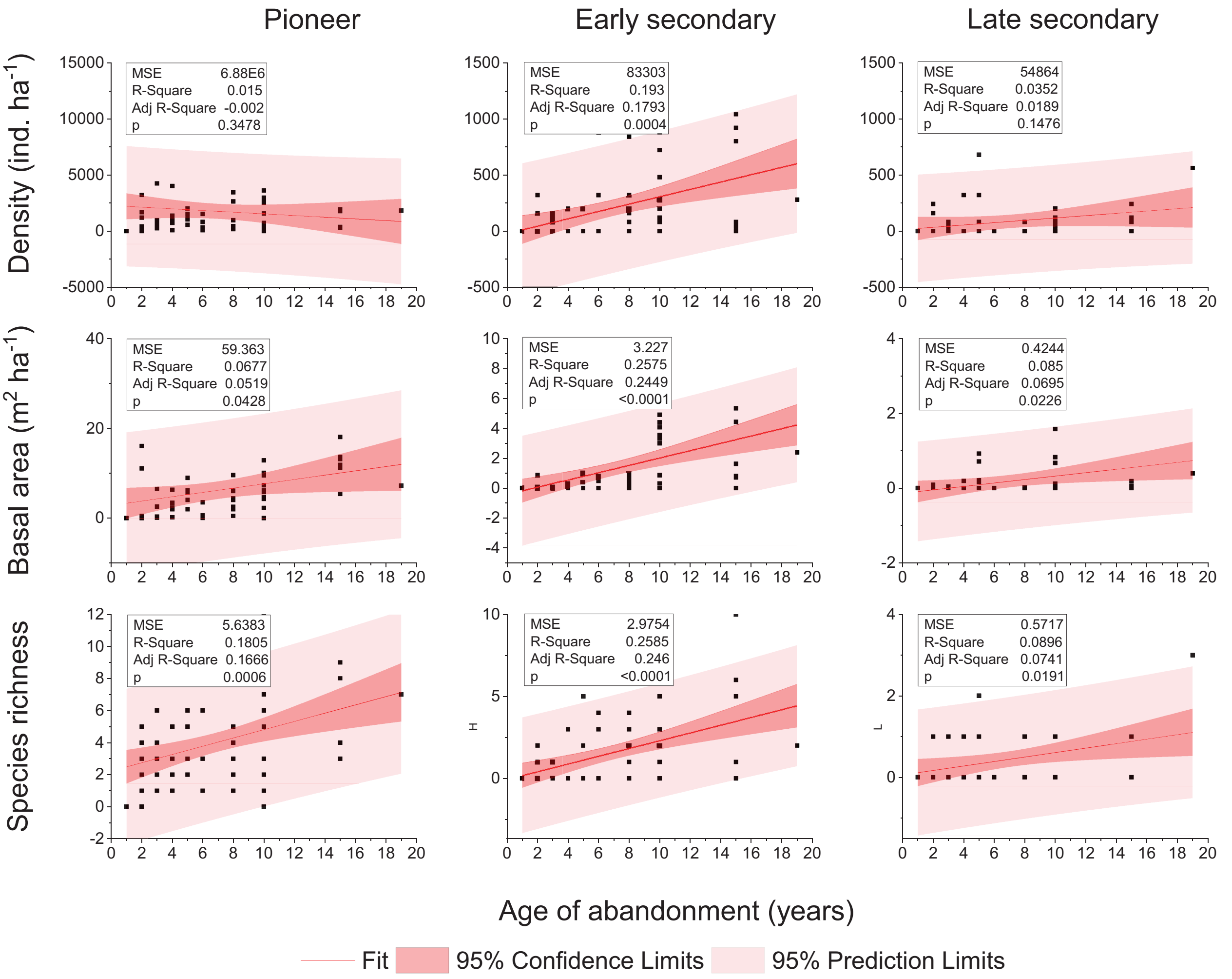

FIGURE 2 | Relationships observed between the age of abandoned mining plots and density, basal area, and species richness for each successional status. Data correspond to 61 plot observations including pioneer, early secondary, and late secondary species. Linear regressions and correlation statistics are also shown.

4.3% of total density in recently abandoned mines to 31% in the oldest plots. Small trees increased from 4 to 17% in plots of 1–4 and 8–19 years post-abandonment, respectively.

The pioneers *Ochroma pyramidale* and *Cecropia engleriana* showed the highest stem density across all ages. The stem density of *O. pyramidale* decreased with site age, from 1,235 ind. ha^{-1} (1–4 years) and 998 ind. ha^{-1} (5–7 years) to 328 ind. ha^{-1} (8–19 years). The plots of 5–7 years presented the highest density of *C. engleriana*, 364 ind. ha^{-1}, while plots of 8–19 years presented the lowest, 132 ind. ha^{-1}.

Reference plots presented an average stem density of 551 ind. ha^{-1} only for trees and small trees (≥10 cm dbh). The species with the highest density were *Iriartea deltoidea*, *Pseudolmedia laevis*, and *Euterpe precatoria*.

Stem density, basal area, and species richness increased positively and significantly with increasing age of abandonment, and this pattern was consistent with the successional status. The exceptions were the density of pioneer and late secondary that did not vary by increasing the abandonment age (**Figure 2**).

Steep curves for small trees, saplings, and seedlings at 1–4 years in the dominance–diversity curves graph indicate communities with high dominance of very few species in recently abandoned areas. Similar patterns were observed for saplings and small trees at 5–7 years (**Supplementary Figure 2A**). On the other hand, curves for seedlings at 5–7 and 8–19 years show a relative uniformity in the distribution of individuals among the species of the community. These results indicate a more diverse species assemblage for seedlings and saplings.

Rarefied species richness (30 individuals) ranged from 8 to 10 species in abandonment plots (**Supplementary Figure 2C**) and 23–25 species in reference plots (**Supplementary Figure 2D**). The ENS and H' show that the diversity in all size classes increased positively with abandonment age, although diversity is lower compared with the reference plots (**Table 2**).

The plant community across abandoned plots was dominated by pioneer species followed by early secondary species. Late secondary species were slightly proportionally higher in plots of 8–19 years of abandonment compared with the other plot

TABLE 2 | Richness and diversity for the abandoned gold mining and reference forests plots in Madre de Dios, southeastern Peru.

			ENS	H′
Abandoned gold mining plots	1–4 years	Seedlings	6	1.79
		Saplings	2	0.59
		Small trees	1	0.28
	5–7 years	Seedlings	12	2.44
		Saplings	7	1.94
		Small trees	4	1.32
	8–19 years	Seedlings	19	2.92
		Saplings	14	2.66
		Small trees	9	2.24
Reference forests	CHO		110	4.70
	CUZ		91	4.51
	INO		95	4.55
	LAS		74	4.30
	TAM		162	5.09
	UNA		98	4.58

ENS, effective number of species; H′, Shannon index; UNA, Forest of the Universidad Nacional Amazonica de Madre de Dios; INO, Inotawa; CHO, Chonta; TAM, Tambopata plot zero; LAS, Jacaralia Los Amigos; CUZ, Cuzco Amazonico.

ages (**Figure 3A**). The plant community in reference plots was dominated by early and late secondary species and a small set of pioneer and climax species (**Figure 3B**).

Forest Composition

The IVI shows that *O. pyramidale* and *C. engleriana* are the dominant species across all abandoned plots, ages, and size classes (**Supplementary Figure 3A**). Furthermore, other pioneer species such as *Piper* sp. (seedlings), *Schizolobium parahyba* (saplings), *Guazuma crinita*, and *Senna silvestris* (small trees) presented high IVI in plots of 8–19 years of abandonment. *Inga thibaudiana* was the only non-pioneer species ranked among the 10 highest IVI in areas 5–7 and 8–19 years of abandonment.

In reference plots, the IVI shows that *I. deltoidea*, *E. precatoria*, *P. laevis*, and *Bertholletia excelsa* are the most important species in almost all areas. Forty-five, 40, 10, and 2% of the species in the reference plots corresponded to late secondary, early secondary, climax, and pioneer, respectively (**Supplementary Figure 3B**).

Shared Taxa

Plots younger than 7 years post-abandonment shared 29% of similarity (**Supplementary Figure 3**). This pattern was observed in both La Pampa and Huepetuhe plots. The oldest sites, Laberinto and Tres Islas, shared 35% of the species. Abandoned mining and reference plots presented less than 5% of species in common. *Ficus maxima*, *Jacaranda copaia*, *S. parahyba*, *Terminalia oblonga*, *Trema micrantha*, *G. crinita*, *O. pyramidale*, *Cecropia* sp., *Inga* sp., *Piper* sp., and *Triplaris* sp. were the main species observed in both abandoned and reference plots. Some of them were recorded in the oldest abandoned mining plots (Laberinto and Tres Islas) as seedlings and saplings.

DISCUSSION

Forest Recovery Following Gold Mining

Considering the concerns about the recovery of vegetation in abandoned gold mining lands, we show that structural and compositional parameters presented different patterns of recovery, likely reflecting the biotic and abiotic local variations in the sites and historical land-use changes. Our results point out faster recovery of forest structure than recovery of species composition and species diversity. This is a relevant finding since in some cases the recovery of forest structure following gold mining in Amazonian forests is close to zero or extremely slow, as in Suriname (Peterson and Heemskerk, 2001) or Guyana (Kalamandeen et al., 2020).

The density and basal area of early secondary species increased with age since abandonment. Contrary to expected, the stem density of pioneers and late secondary species did not vary with plot age. Considering that basal area represents a conservative estimate of the total biomass (Gilman et al., 2016), this has accumulated rapidly in most plots and showed a positive increase as the plot age increased. These results highlight the value of naturally regenerating sites for promoting the provision of ecosystem services related to carbon storage and sequestration (Rozendaal et al., 2019). Other studies argue that carbon storage from regenerating forests may not reach levels of old-growth forests until many decades later (Denslow and Guzman, 2000; Mascaro et al., 2012).

Although species richness increased positively with abandonment age, it represented only 9–19% of that reported in reference forests. This result has been also described in other studies across the Amazon Basin (e.g., Lozano Baez, 2013; Valois-Cuesta and Martínez-Ruiz, 2017; Kalamandeen et al., 2020). Changes promoted by mining activities are even more intense than other human-induced land conversions such as agriculture and pastures (Fujisaka et al., 2000; Guariguata and Ostertag, 2001).

In the oldest abandoned plots, pioneer species had four times the stem density and almost twice the richness relative to early secondary species. These values were even higher when compared with late secondary species. Despite the dominance of the pioneers, the richness, basal area, and stem density of the early and late secondary species increased over time. Consistent with previous studies (Peterson and Heemskerk, 2001; Rozendaal et al., 2019), these floristic and structural changes indicate a transition from pioneer to early secondary species at least until 19 years after abandonment. The dominance of early–late secondary species can take a few more decades (Rodrigues et al., 2004; Van Breugel et al., 2013), whereas the progression of secondary into old-growth forest can take centuries (Peterson and Heemskerk, 2001; Sharma and Chaudhry, 2018; Rozendaal et al., 2019).

Factors Influencing Forest Recovery Patterns

The high abundance of pioneer species can be related to their seed dispersal strategies (Rozendaal et al., 2019) and their fast growth

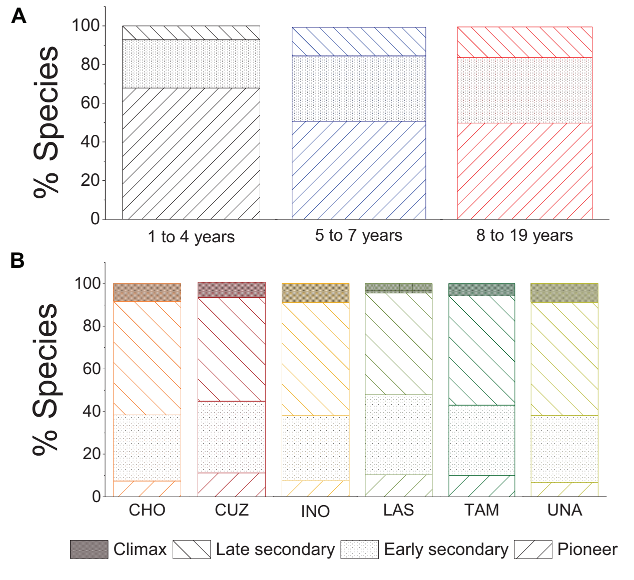

FIGURE 3 | Percentage of species by successional status in abandoned mining plots **(A)** and reference plots **(B)**. UNA, Forest of the Universidad Nacional Amazonica de Madre de Dios; INO, Inotawa; CHO, Chonta; TAM, Tambopata plot zero; LAS, Jacaralia Los Amigos; CUZ, Cuzco Amazonico.

(Kalamandeen et al., 2020), while the low abundance of early and late secondary species could be due to soil removal (e.g., tailing ponds and mining pits) (Peterson and Heemskerk, 2001; Román-Dañobeytia et al., 2015; Kalamandeen et al., 2020).

However, we observed improvements in some soil characteristics over time (% sand and nutrients) (**Supplementary Table 1**), although the soil quality remained below that of reference forests. Despite the severe impacts on soil conditions, the complexity of the vegetation increased slightly with the abandonment age. The surrounding old-growth forests can probably function as a continuous source of seeds and contribute to increasing diversity over time (Fujisaka et al., 2000; Rodrigues et al., 2004).

Forest Composition in Abandoned Gold Mining Areas

Plant composition in almost all abandoned plots and plant size classes show that the dominant species are the fast-growing *O. pyramidale* and *C. engleriana*. Similarly, abandoned fallows in central-eastern Peru are dominated by *T. micrantha* and *Cecropia membranacea* (Fujisaka et al., 2000). In many other degraded lands across the Amazon basin, the presence of *Cecropia* spp. is common in natural regeneration but *O. pyramidale* (Mesquita, 2000; Mesquita et al., 2001; Rodrigues et al., 2004; Kalamandeen et al., 2020) is not, even though *O. pyramidale* is naturally distributed in these areas (ITTO, 2019).

The composition of the surrounding forests plays an important factor in driving the floristic composition of the plots. *O. pyramidale* and *Cecropia* spp. are abundant in riverbanks in the Madre de Dios region, and *G. crinita, S. parahyba*, and *Calycophyllum spruceanum* are common species in secondary forests and even in primary forests of this region (Gentry, 1982; Phillips and Gentry, 1993; Reynel et al., 2003; Dueñas and Garate, 2018).

Implications to Forest Restoration

The slow pace of natural regeneration observed after 19 years of mining abandonment suggests the need for active restoration strategies with soil reclamation efforts to accelerate forest recovery. The combination of strategies can assist the restocking of transitional succession species speeding up the succession process (Evans et al., 2013; Román-Dañobeytia et al., 2015; Orozco-Aceves et al., 2017).

In the southeastern Peruvian Amazon, however, considering that active restoration with soil reclamation costs 2,100–3,500 US\$ ha^{-1} during the first year of activity (Román-Dañobeytia et al., 2015) and that the areas degraded by gold mining sum up to 80,000 ha, only during 2007–2017 (Caballero Espejo et al., 2018), this strategy imposes financial challenges. Therefore, it is necessary to evaluate the relative effectiveness of different restoration strategies, ranging from passive (e.g., natural regeneration) to more intensive ones (e.g., mixed plantations of native species with soil reclamation). In older sites, natural regeneration followed by enrichment with late-successional species could further accelerate the successional process.

Despite not formally testing the tolerance of specific species to soil conditions, we observed that several tree taxa were found continuously at high densities despite the extensive soil disturbance. *O. pyramidale* and *C. engleriana* colonized and dominated areas 19 years after abandonment, which could have created a favorable structure for the establishment of early secondary species in older areas, providing shade and contributing to organic matter (Mesquita et al., 2001). Both could be key species in facilitating forest succession in recently abandoned mining lands. *G. crinita*, *S. parahyba*, and *C. spruceanum*, pioneer species co-dominating the oldest areas, could also be considered as potential species to be used in restoration strategies, as they have timber value (Reynel et al., 2003). Tree plantations using timber species have been recognized as a cost-effective alternative to convince landowners to recover or catalyze successional processes in degraded lands (Lamb et al., 2005; Rodrigues et al., 2009). *I. thibaudiana*, a non-pioneer species found in abandoned 5-year-old plots (**Supplementary Figure 3A**), commonly grows under broad environmental conditions (Schierenbeck et al., 1997), and similar to other *Inga* spp., it recovers and enriches soils through nitrogen fixation (do Vale et al., 2014; UICN, 2019).

CONCLUSION

After gold mining in Madre de Dios, forests regenerating demonstrated a high potential for biomass recovery throughout the regeneration process and a high conservation value in degraded landscapes. Stimulating their natural regeneration and testing some restoration strategies (e.g., soil reclamation, species enrichment) to accelerate forest recovery in such areas are fundamental to complement the biodiversity conservation provided by surrounding reference forests.

DATA AVAILABILITY STATEMENT

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

AUTHOR CONTRIBUTIONS

RC-L, DOR, FF, JPV, PZP JM-P, and DR conceived the research idea. RC-L, JPV, and PZP collected data. RC-L, DOR, and DR performed statistical analyses and wrote the manuscript, with contributions from FF, JPV, PZP, and JM-P. JM-P and PZP made the determination of successional status of all plant species of the areas. All authors discussed the results, commented, and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.594627/full#supplementary-material

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