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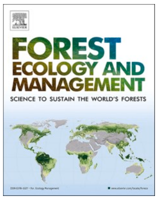

Timber stock recovery in a chronosequence of secondary forests in Southern Brazil: Adding value to restored landscapes

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ABSTRACT

The Brazilian Atlantic forest is largely covered by secondary forests, mostly regenerated after the abandonment of patches previously used for shifting cultivation. A characteristic of these secondary forests is the significant timber volume from fast-growing species at ages as young as 30–40 years. In this study, we investigated changes that occur in timber production of secondary forest during the first 50 years of succession. We inventoried 82 plots (10 × 20 m) in a chronosequence ranging from 2 to 50 years since agricultural abandonment in four municipalities located in Santa Catarina State, Southern Brazil. Our results showed that commercial tree species have rapid recovery of richness, basal area and stem volume in naturally regenerating forests. Commercial species represent about 51 percent of tree diversity, with 9 out of 12 dominant species being commercial timber species, with a stem volume up to 155 $m^3\ ha^{-1}$. Trees of commercial species with $\geq$15 cm in diameter are first observed after 20 years of succession, while trees $\geq$30 cm are found at 30 years of succession, and produce 126 $m^3\ ha^{-1}$ of stem volume. We highlight *Hyeronima alchorneoides, Miconia cabucu* and *Miconia cinnamomifolia*, as fast-growing dominant species that produce timber quality $\geq$20 cm in diameter after 20 years of succession, with volume reaching 200 $m^3\ ha^{-1}$ before 40 years of succession. We found that secondary forests are dominated by fast-growing and wood-producing species, with a rapid increase in timber stocks in the early stages of succession. These secondary forests are important biodiversity reservoirs in human-pressured landscapes, in addition to providing forest products and other ecosystem services. The management of secondary forests may be an alternative restoration approach that can accelerate the recovery of timber stocks, provide landscape diversity, and add more value to private forests.

1. Introduction

Around 50% of the world's remaining forests are secondary or degraded (Chazdon et al., 2009; FAO, 2020), and they play a significant social and economic role by supplying timber and non-timber forest products (Akindele and Onyekwelu, 2011; Barrance et al., 2009; Coomes and Burt, 2001; Guariguata, 1998; Moser et al., 2015). Secondary forests also provide ecosystem services, such as soil conservation, nutrient cycling, carbon sequestration and storage, and biodiversity conservation (Chazdon et al., 2009; Chazdon, 2014; Matos et al., 2020; Mukul and Herbohn, 2016; Silva Júnior et al., 2020). They are also recognized as a key element of traditional agricultural systems, such as swidden agriculture (Chazdon, 2012; Chazdon et al., 2020; Fantini et al., 2017; Piotto et al., 2009), a system that provides food and income to forest peoples (Adams et al., 2013; van Vliet et al., 2013). However, the management of secondary forests in ways that result in high-quality production of

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timber is largely overlooked.

In Brazil, approximately 26 million hectares of secondary forests were regenerated from deforested areas between 1986 and 2018, with 27% located in the Atlantic Forest biome (Silva Júnior et al., 2020). In this biome, one of the world's most threatened biodiversity hotspots (Soares-Filho et al., 2014), protection from further degradation and new deforestation has been achieved through top-down regulation (Brancalion et al., 2016). For example, efforts to restore Brazilian landscapes include the Brazilian Atlantic Forest Restoration Pact (AFRP), which aims to restore 15 M ha of degraded/deforested lands by 2050 (Crouzeilles et al., 2019). Other actions are aligned with global initiatives, such as the Aichi Target (Jørgensen, 2013) and the Bonn Challenge (IUCN, 2011). Under these circumstances, active restoration using timber species has the potential to reverse further degradation of overlogged forests (Cerullo et al., 2019), as well as restore cleared lands.

In the Atlantic forest biome, a human-pressured landscapes, these proactive approaches may foster restoration by increasing the value of forested lands through the management of secondary forests. Secondary forests can be used for timber production from fast-growing species, reducing the pressure on the remaining natural forests (Fantini et al., 2019; Guariguata, 1998; Mesquita, 2000; Parrotta and Knowles, 2001). Despite this potential, few policies have been initiated to promote sustainable use of secondary forests, especially efforts to realize their potential for timber production (Fantini et al., 2019; de Oliveira et al., 2020). In part, this can be attributed to the fact that the current timber demand in the region is supplied by hardwood coming from old-growth forests of the Amazon (Barreto, 2006; Caires et al., 2019; Homma, 2011), and from plantations of the exotic species *Pinus* spp. and *Eucalyptus* spp. (Alarcon et al., 2010; Fantini et al., 2019), which cover an area of nine million hectares (IBÁ, 2020).

Studies on applied forest ecology are needed to support the management of secondary forests, but the scarcity of such studies has stalled efforts to scale-up restoration of these ecosystems. Most studies on secondary forest regeneration after swidden agriculture focus on understanding diversity, forest structure and biomass recovery through time (Adams et al., 2013; Aide et al., 2000; Coomes et al., 2017; Fantini et al., 2017; Liebsch et al., 2008; Lintemani et al., 2020; Piotto et al. 2009; Ribeiro Filho et al., 2015; Siminski et al., 2011; Wood et al., 2017). Other studies have focused on the natural regeneration of secondary forests as a strategy to restore forest ecosystems (Brancalion et al., 2019; Chazdon and Brancalion, 2019; Chazdon and Guariguata, 2016; Crouzeilles et al., 2020; Rozendaal et al., 2019; Siminski et al., 2021). Only recently has secondary forest, as source of timber production, started to gain attention based on data from forest management (Britto et al., 2017; Britto et al., 2019; Fantini et al., 2019; Oliveira et al., 2018; Piazza et al., 2017; da Silva et al., 2017). Such studies showed the significant volume of timber available in mid- to late-secondary forests and signaled the effectiveness of management in enhancing timber production and providing other ecosystem services (Fantini et al. 2019; Guariguata, 1998; Mesquita, 2000; Finegan, 1992). Although the principles of applied forest ecology are well established in the literature (e.g., Ashton and Kelty, 2018), further studies need to investigate the application of regeneration systems to Neotropical secondary forests.

Our study aims to examine the potential of timber production in secondary forests through changes they undergo during the first 50 years of succession. We asked (1) if secondary forests hold a diversity and timber volume of commercial species that would make their management attractive, (2) how the volume of commercial species changes through succession as compared to non-commercial species, and (3) when trees of commercial species reach a harvestable size during succession. With this study, we hope to promote the use of timber resources of secondary forests in the Atlantic forest and other tropical regions.

2. Methodology

2.1. Study area and data collection

The study was carried out in secondary forests located in the municipalities of Garuva, Guaramirim, Joinville and São Pedro de Alcântara, located in Santa Catarina State, Southern Brazil (Fig. 1). This region is characterized by a humid subtropical climate with warm summers (Cfa), average temperature of 20.7 °C, and annual precipitation of 1,800 mm (Alvares et al., 2014). The region is covered by the Brazilian Atlantic Forest, specifically Dense Ombrophilous Forest (DOF), which presents an evergreen canopy, abundance of epiphytes and palm trees (Gasper et al., 2014; Siminski et al., 2011; Vibrans et al., 2013). DOF mostly covers low to medium elevations ($<$1000 m elevation) of the eastern slopes of the mountain chain running along the Brazilian coastline, also known as the Serra do Mar Mountains (Morellato and Haddad, 2000). The characteristic soils of the region are Latosol Red-Yellow Alicus A Moderate, Podzolic Red-Yellow Alicus TB Moderate, Gleissol Low Humic Dystrophic and Alluvial Alicus Soils TB A Moderate (EMBRAPA, 2004). Currently, landscapes in this region have a mosaic of secondary and mature forests, monocultures of *Eucalyptus* and *Pinus* species, agricultural fields, pastures, and urban areas (Vibrans et al., 2012). Most secondary forests in the region have now regenerated after the abandonment of crop fields cultivated under swidden agriculture (Siminski et al., 2011).

For this study we used data from inventories carried out in naturally regenerated secondary forests, ranging from 2 to 50 years after the abandonment of the crop field. Secondary forests located in a mosaic of regenerating forest patches and agricultural lands were sampled in private lands, and landowners reported the land use history, including how long the land has been regenerating. The inventories were done using 82 plots (10 × 20 m), totaling 16,400 m^2 of sampling area (Table 1). For the purpose of statistical analyses, plots were categorized by floristic composition into three groups (hereinafter called successional pathways), according to the most frequently observed dominant species: 1. *Miconia cinnamomifolia*; 2. *Miconia cabucu*; 3. *Tibouchina pulchra* (Fig. 1). In each plot, we measured all living trees, palms, and tree ferns with diameter at the breast height (dbh) $\geq$ 5 cm. Each individual was measured for total height (m), commercial height (m) and dbh (cm) and identified to species level *in loco*, or a voucher specimen was collected for later identification by botanists in the FLOR Herbarium of the Federal University of Santa Catarina (UFSC), FURB Herbarium of the Regional University of Blumenau, HBR (Barbosa Rodrigues Herbarium) and BHCB of the Federal University of Minas Gerais. The species were classified according to the Angiosperm Phylogeny Website, version 14 (Stevens, 2017), and Species 2000 & ITIS Catalogue of Life (Roskov et al., 2019).

Species with potential timber use were classified into timber quality classes. To classify them, we used information from the literature (Carvalho, 2003, 2006, 2008, 2010; Coradin et al., 2011; Reitz et al., 1978; Schuch et al., 2008), the owners of the study areas, and an owner of a sawmill with more than 50 years of experience in timber harvesting and processing. Data on use and market price of timber from secondary species are difficult to obtain directly through enquiries because the management of these species is very restricted by current forest regulations. Since the vast majority of such timber in the market is illegal, dealers are not willing to disclose such information. First species were classified into commercial and non-commercial. Commercial species are those having marketable timber useful for any purpose other than charcoal. Commercial species were then classified according to their timber quality into three categories: low-quality timber (LQT), high-quality timber (HQT), and best-quality timber (BQT). The classification took into account information on timber use and market price (Appendix Table A.1). Even though we have compiled data on wood density from Chave et al. (2006) for Neotropical tree species and Oliveira et al. (2019) for species of the Subtropical Atlantic Forest, this

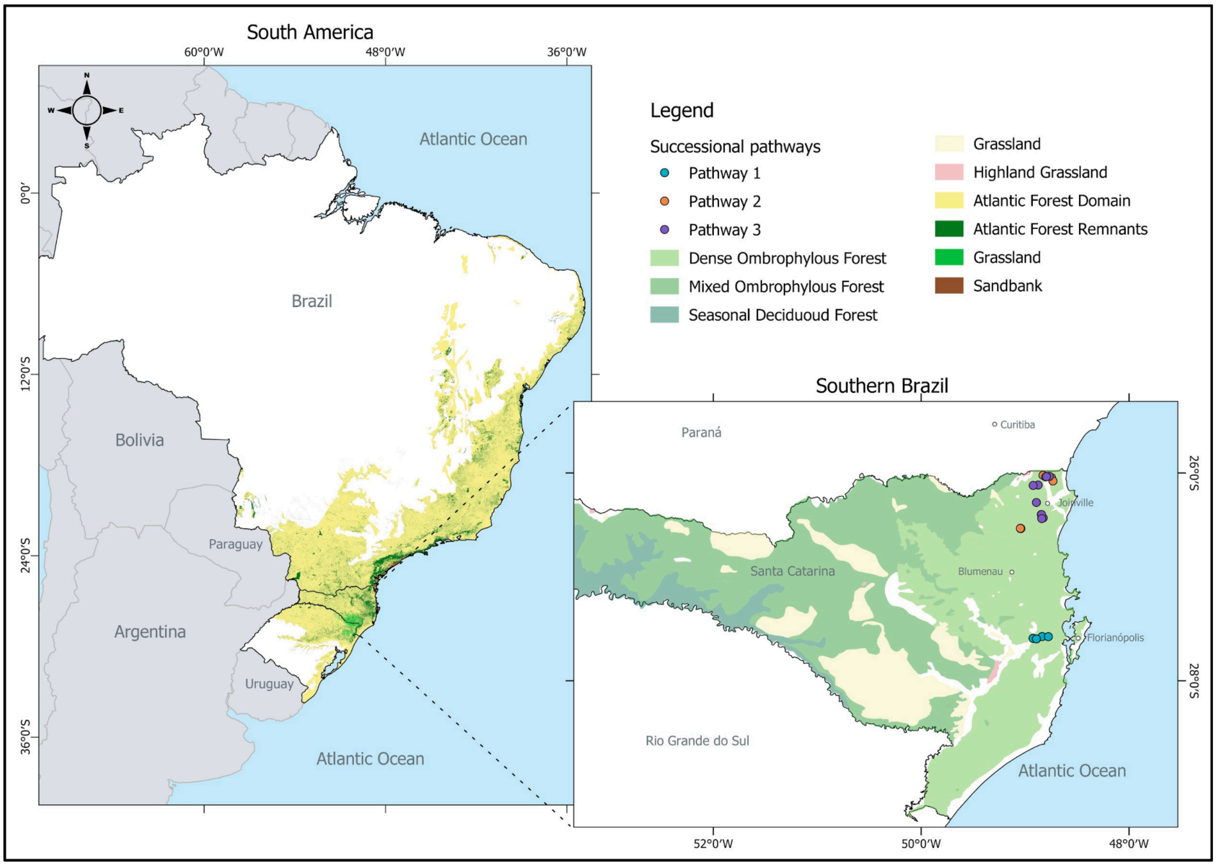

Fig. 1. Map of the original and remnant Brazilian Atlantic Forest in Brazil (left), indicating the forest type in Santa Catarina state. The location of the plots by successional pathways (1. *Miconia cinnamomifolia*; 2. *Miconia cabucu*; 3. *Tibouchina pulchra*) is provided in the detailed map. Source: http://mapas.sosma.org.br/ (SOS Mata Atlântica, 2020); Application Area Map of the Law n° 11.428/2006 (BRASIL, 2006); Klein's phytogeographic (SAR, 2005).

Table 1
Structure, volume, richness and species diversity in 82 plots of 200 m^2 in secondary forests of Dense Ombrophilous Forest in the Atlantic Forest, Brazil.

Parameter	Minimum	Maximum	Average	Stand. Dev.
Age (years)	2	50	–	–
DBH max	6.4	52.0	21.7	± 9.9
Density (stem ha^{-1})	100	3550	1455	± 835
Basal area (m^3 ha^{-1})	0.3	39.2	14.1	± 9.7
Tree volume (m^3 ha^{-1})	0.7	265.5	99.7	± 77.6
Stem volume (m^3 ha^{-1})	1.0	244.0	88.1	± 63.2
Species richness	2	26	11	± 6
Shannon index (H′)	0.137	2.752	–	–
Simpson index (1-D)	0.050	0.910	–	–

information was not used to group the species, because wood density does not necessarily determine either the timber use or price in the regional market. LQT mostly includes softwood species, but can also include species that present low workability and natural durability and that are used in less valuable products, such as pallets and crates. Their wood density ranges from 0.29 to 0.86 g cm^{-3}. HQT species produce wood with medium durability and easy workability. This wood is used as beams, box board, joist wood, molding, poles, wood flooring, wooden board, wooden ceiling, musical instruments, and furniture, thus achieving higher market value. Their wood density ranges from 0.34 to 0.92 g cm^{-3}. BQT species have the same uses as those of HQT, but their wood presents longer durability and easier workability, consequently reaching the highest market prices. The wood density of this species ranges from 0.32 to 0 78 g cm^{-3}. In most of our analyses, we also used the data on non-commercial species as these species may potentially be used for fuelwood.

2.2. Data analyses

For forest composition, we calculated species richness, Shannon's (H'), and Simpson's (1-D) diversity for each plot (Müeller-Dombois and Ellenberg, 1974). For analysis, species richness and diversity were considered separate for each group of species, both commercial and non-commercial. The importance value (IV) calculated for each species was used to determine the group of dominant species defined as that set of species for which the accumulated IV was 50% when classified from highest to lowest (Finegan, 1996). IV is the sum of relative density, relative dominance, and relative frequency. Species richness, diversity index and IV metrics were estimated using the *vegan* (Oksanen et al., 2019), *BiodiversityR* (Kindt and Coe, 2005) and *fitoR* script (Dalagnol et al., 2013) packages in RCore Team (RCore Team, 2019) and the Rstudio interface (RStudio Team, 2019).

For forest structure, we calculated tree density (stems ha^{-1}), basal area (m^2 ha^{-1}), tree volume (m^3 ha^{-1}), and stem volume (m^3 ha^{-1}) for each plot. We used volumetric models adjusted for species of the Atlantic Forest (Correia et al., 2017; Oliveira et al., 2018) to estimate total tree volume (TreeV) and stem volume (StemV) of each individual, including palm trees and tree ferns. TreeV represents the volume (m^3) of the tree from aboveground up to all branches $\geq$5 cm in diameter. StemV represents the commercial volume of the stem from aboveground to commercial height (i.e., up to the point of the first stem fork). Because of its importance, a specific model (Oliveira et al., 2018) was used for *Hyeronima alchorneoides*.

We studied structural changes in the forest through succession by grouping the individuals into three dbh classes: 5 $<$ 15 cm, 15 $<$ 30 cm, and $\geq$ 30 cm. Trees $\geq$ 30 cm dbh include most of the short-lived, fast-growing species with a harvestable size. Trees $<$ 30 cm in dbh can be harvested in the short- (for trees 15 < 30 cm in dbh) to mid-term (for trees 5 < 15 cm in dbh).

Linear mixed-effects models were used to determine the effect of time on richness, diversity indexes, density, basal area, and volume (Bolker, 2008; Gelman and Hill, 2007; Zuur et al., 2009). Successional pathway was included as a random effect as we are not interested in knowing its effect on the different variables. First, we regressed tree density, basal area, tree volume, and stem volume against forest age to analyze vegetational changes with succession. For these response variables, we transformed the values to meet normality using square root transformation and tested the normality with the Shapiro-Wilk test. Second, we regressed species richness, as well as Shannon and Simpson diversity, against forest age to analyze the potential contribution of secondary forest species to commercial use. Finally, we grouped trees by diameter classes (dbh class), species by commercial use (commercial, commercial dominant and non-commercial species) and timber quality (low, high and best), and tested if age has an effect on variation in density, basal area, total volume and stem volume when the above-mentioned categorical variables are included as a fixed effect in the models. For each response variable, we established the null model with random effect following this structure to RCore Team (RCore Team, 2019): $y \sim 1 + (1|\text{Pathway})$. After establishing the null model, we established the model with fixed effect to test the significance among models using ANOVA with Chi-square statistics. The model with fixed effect followed this structure: $y \sim \text{Age} + (1|\text{Pathwayn})$. For response variables analysed with categorical variable (dbh class, timber use and timber quality), we followed these structures: (i) $y \sim \text{Age} + \text{CVar} + (1|\text{Pathway})$ and (ii) $y \sim \text{Age} + \text{CVar} + (1|\text{Pathway/CVar})$. To analyse the effect of age and categorical variables (dbh class, timber use and timber quality), we used successional pathway as random effect and nested categorical variable as random slope. In this way, we analysed only the variance among them without analysing the effect. When species grouping was used as a random slope, we assumed that the difference among groups might reflect the variation in slope. We fitted five models to estimate richness, diversity index, tree density, basal area and stem volume with trees and species grouped. The models were fitted with and without interaction among fixed effects.

In addition to selecting the best model for each response variable, we applied the selection based on the delta-Akaike Information Criterion (ΔAIC) where we selected the model with the lowest ΔAIC. The ΔAIC is the result of the differences among the AIC of the models fitted for each variable (Appendix Table A.5). The conditional and marginal R^2 was calculated for the model selected. These values explained the proportion of total variance through both fixed and random effects (Appendix Table A.6). The models were fitted with maximum likelihood to compare the null model and models with fixed effect with ANOVA. With the selection of the best model for each variable, the result was plotted using the *visreg*() function of the *visreg* package (Breheny and Burchett, 2017). The predictors for each model were plotted using the *bootMer*() function of the *lme4* package based on the perform model-based (semi-) parametric bootstrap for mixed-effect models using 1,000 simulations (Bates et al., 2015).

The analyses of linear mixed-effect models were performed with the *lme4* (Bates et al., 2015), *bbmle* (Bolker and R Development Core Team, 2020), *lmerTest* (Kuznetsova et al., 2017), *MuMIn* (Barton, 2020) and *visreg* (Breheny and Burchett, 2017) packages in RCore Team (RCore Team, 2019) and the Rstudio interface (RStudio Team, 2019) (Table A.5, A.6). In the plots, lines were fitted to each variable using the predictors of the chosen model (Appendix Table A.7), and the *ggplot2* (Wickham, 2009), *viridis* (Garnier, 2018) and *cowplot* (Wilke, 2019) packages were used.

3. Results

3.1. Changes in commercial species composition and diversity

We measured a total of 2,387 individuals in the sampling area, belonging to 202 species and 63 families (Appendix Table A.2). Among all species, 103 (51%) were commercial, while 99 (49%) were non-commercial. The indicators of diversity showed that commercial species increased with forest age, reaching the highest values around 30 years of regeneration (Fig. 2a–c). Richness of commercial species ranged from 1 to 18 species per plot with an average of 9 species. The diversity indexes increased over time from the age of 12 years for commercial species, reaching the value of 2.731 for Shannon's index (H') and 0.92 for Simpson's index (1-D) around 30 years of forest succession. Among the 12 species with highest importance value (IV), 9 are commercial species: *T. pulchra*, *M. cinnamomifolia*, *Myrsine coriacea*, *H. alchorneoides*, *M. cabucu*, *Miconia rigidiuscula*, *Pera glabrata*, *Vernonanthura discolor* and *Guapira opposita*. Together, these species accounted for 45% of the total importance value of the forest. The other three species, *Euterpe edulis*, *Cecropia glaziovii* and *Psychotria longipes*, are non-commercial timber species. *E. edulis* is a palm tree that produces non-timber products, while *C. glaziovii* and *P. longipes* are not utilized as a wood-producing species in the region (Appendix Table A.2 and A.3).

3.2. Changes in forest structure

Tree forest density ranged from 100 to 3,550 ind ha^{-1} through the chronosequence with an average of 1,455 ind ha^{-1} (±835 ind ha^{-1}) (Fig. A.1a). Tree density increased in the beginning of succession, reached a maximum approximately at 25 years of age, and then slightly decreased in older stands. The basal area increased throughout succession, ranging from 0.3 to 39.1 m^2 ha^{-1}, with an average of 14.1 m^2 ha^{-1} (±9.7 m^2 ha^{-1}) (Fig. A.1b). Young-secondary forests showed low tree volumes, but this variable increased fast after 10 years of succession, reaching a maximum value of 266 m^3 ha^{-1} (Fig. A.1c). Stem volume followed the same trends as those of tree volume (Fig. A.2d). The difference between tree and stem volume in mid-secondary forests can be as high as 28%, corresponding to the volume potentially useful as fuelwood.

Small trees (dbh 5 < 15 cm) presented the highest density in young forests, but their number decreased with succession (Fig. 3a). The mid-sized (dbh 15 < 30 cm) and largest trees (dbh ≥ 30 cm) appeared only after 5 and 13 years of succession, respectively. However, their contribution to the basal area increased fast (Fig. 3b). The proportion of stem volume of the smaller trees remained stable throughout succession, while the volume of larger trees increased as the forests aged (Fig. 3c). After 30 years of forest succession, the stem volume of trees ≥ 30 cm in diameter increased and reached 126 m^3 ha^{-1}. The stem volume of small trees showed no correlation with forest age (Fig. 3c), while the stem volume of larger trees increased fast. An even higher contribution of mid-sized trees was observed until approximately the age of 25 years when most of the commercial volume could be attributed to larger trees.

Commercial species showed higher density, basal area, and stem volume when compared to non-commercial species (Fig. 4a–c). Among the 103 commercial species, 9 are considered dominant, which represents 75% of all dominant species (45% of the total IV) (Table A.3.). Density of commercial dominant species decreased as succession progressed, while commercial and non-commercial species followed an opposite trend. The stem volume of commercial species reached up to 140 m^3 ha^{-1}, corresponding to 74% of the stem forest volume, while for dominant species, the stem volume was 155 m^3 ha^{-1} (Table A.3).

3.3. Changes in volume and quality of timber species

Overall, commercial species represented an important proportion of the forest tree diversity at all forest ages. The proportion of species by

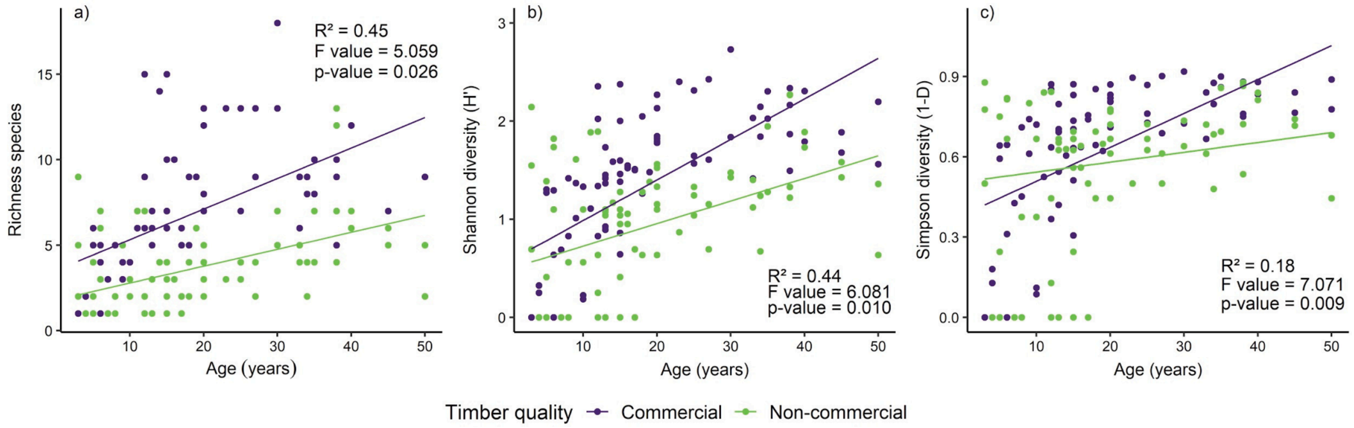

Fig. 2. Richness species, as well as Shannon and Simpson diversity, of commercial and non-commercial species in secondary forests 2–50 years old. Data include trees, palm trees and tree ferns. Each dot represents the total values for the respective timber quality in a single plot (dots overlapping may occur). R^2 is the variation explained by the full model (fixed + random), i.e., the conditional R^2 for linear mixed-effects models, and the other value (F value and p-value) is the summary of the model.

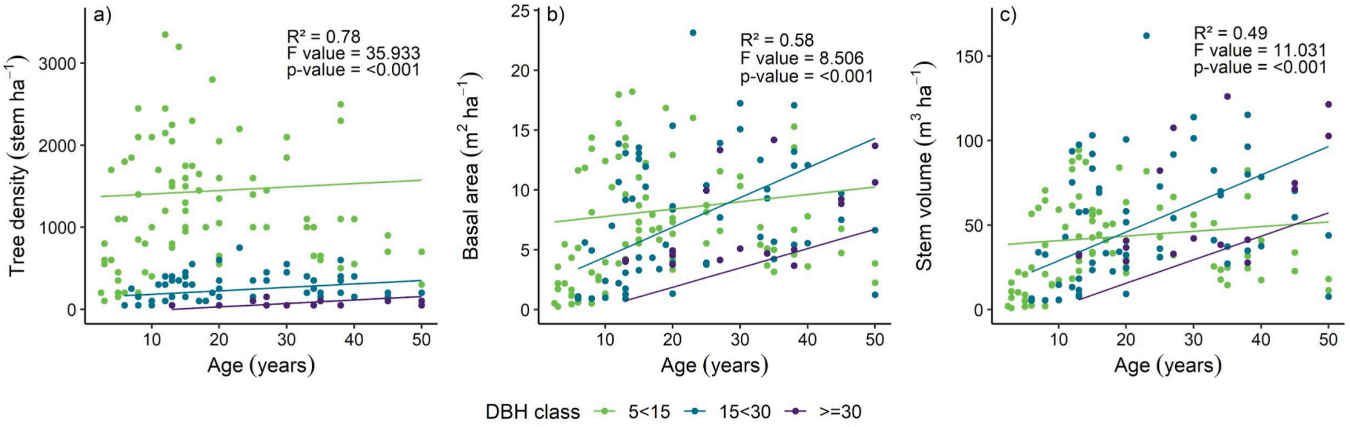

Fig. 3. Contribution of different-sized trees (dbh) to forest structure and volume in secondary forests 2–50 years old. Data include trees, palm trees and tree ferns. Each dot represents the total values for the respective dbh class in a single plot (overlapping may occur). R^2 is the variation explained by the full model (fixed + random), i.e., the conditional R^2 for linear mixed-effects models, and the other value (F value and p-value) is the summary of the model.

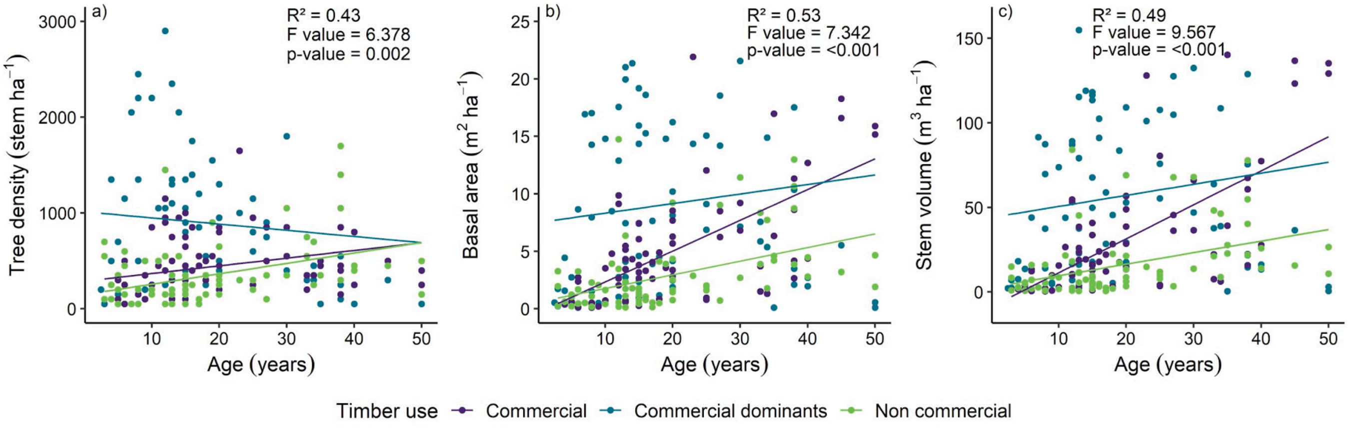

Fig. 4. Contribution of commercial and non-commercial species to forest structure and volume in secondary forests 2–50 years old. We followed Finegan (1996) who identified dominant species as those representing 50% of total IV. Each dot represents the total values for the respective category in a single plot (overlapping may occur). R^2 is the variation explained by the full model (fixed + random), i.e., the conditional R^2 for linear mixed-effects models, and the other value (F value and p-value) is the summary of the model.

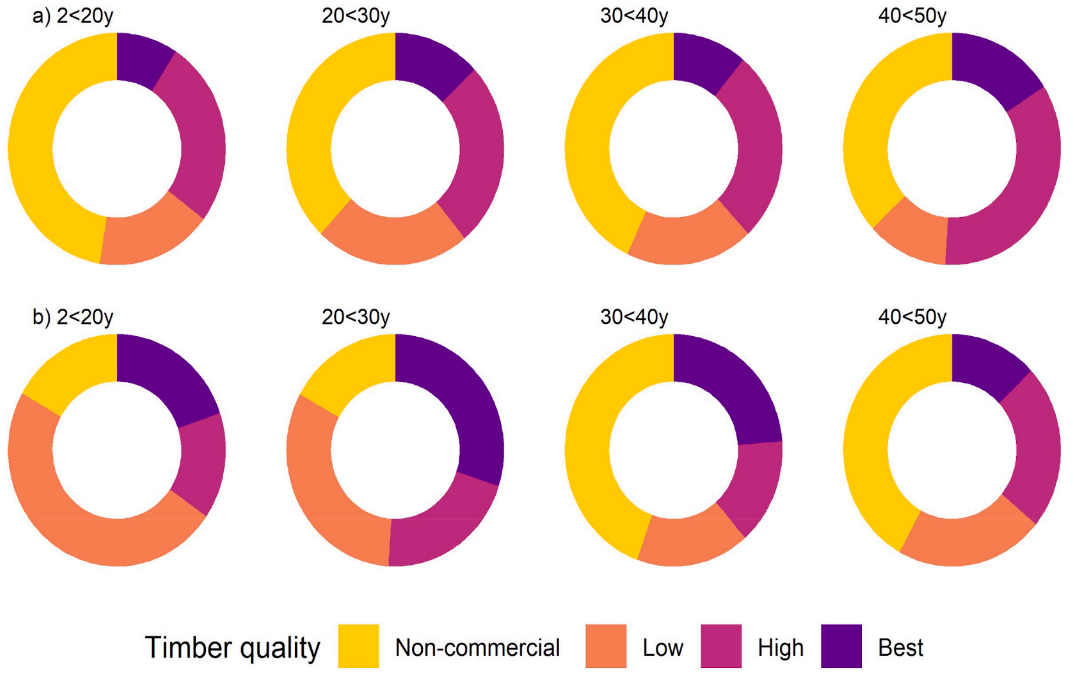

Fig. 5. Proportion of number of species (a) and number of individuals (b) by timber quality category (low, high, best, and non-commercial) and by age class in secondary forests from 2 to 50 years old.

timber quality highlights a large number of species in the commercial category (low, high and best) with a proportion higher than 50% (Fig. 5a). Even in young forests, up to 20 years of age, 53% of the richness is composed by commercial species. The occurrence of species that produce commercial timber increases with successional age, reaching 63% in forests between 40 and 50 years. At this age, high- and best-quality timber species represent 51% of species richness. Nevertheless, the proportion of individuals of commercial species reduced over time (Fig. 5b).

Among commercial species, low-quality timber species showed a decrease in tree density along the chronosequence, mostly after 35 years. Species of high- and best-quality timber showed a more stable pattern over time (Fig. 6a). The basal area increased with forest age with similar trends for the high- and best-quality timber species (Fig. 6b). Stem volume increased along the chronosequence, mainly resulting from the contribution of high- and best-quality timber species (Fig. 6c).

For tree species classified by timber quality (low, high and best), we found 17 best-quality timber species (Table A.2). Among them, 12 species presented trees with dbh over 15 cm, including *Aspidosperma parvifolium*, *Cabralea canjerana*, *Cupania vernalis*, *H. alchorneoides*, *M. cabucu*, *M. cinnamomifolia*, *Nectandra lanceolata*, *Nectandra leucothyrsus*, *Nectandra megapotamica*, *Nectandra oppositifolia*, *Ocotea pulchella* and *Vitex megapotamica*. The trees in this category can reach over 40 cm in diameter (Table A.2). Other best-quality timber species were found in smaller size classes in secondary forests, such as *Cedrela fissilis*, *Jacaranda micrantha* and *Ocotea catharinensis*. The largest group (53 species) is represented by species with high-quality timber (Table A.2). Among them, 21 species presented trees with a diameter over 15 cm. However, only six species presented trees with diameter ≥ 30 cm, e.g., *Cryptocarya moschata*, *Hirtella hebeclada*, *Nectandra membranacea*, *Piptadenia gonoacantha*, *Pisonia ambigua* and *Sloanea guianensis*. Among the 33 low-quality timber species, 13 (39%) presented trees exceeding 15 cm in diameter, including *Aegiphila integrifolia*, *Annona neosericea*, *Annona sylvatica*, *G. opposita*, *Maprounea guianensis*, *Myrcia eugeniopsioides*,

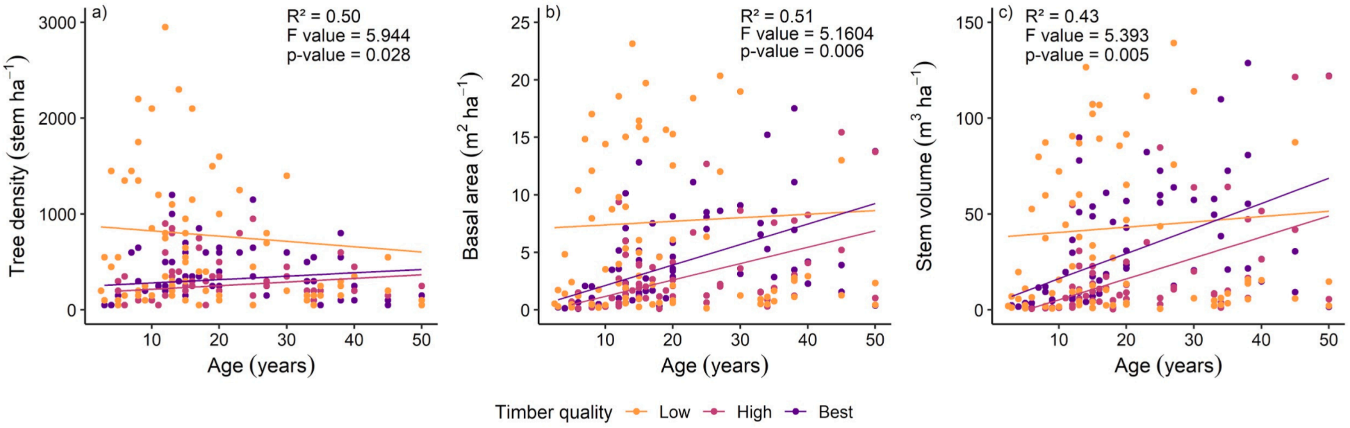

Fig. 6. Contribution of trees (commercial species) from different categories of timber quality to forest structure and timber volume in secondary forests 2 to 50 years old. Each dot represents the total values for the respective category in a single plot (overlapping may occur). R^2 is the variation explained by the full model (fixed + random), i.e., the conditional R^2 for linear mixed-effects models, and the other value (F value and p-value) is the summary of the model.

M. coriacea, *Myrsine umbellata*, *Piptocarpha angustifolia*, *Tapirira guianensis*, *T. pulchra*, *Virola bicuhyba* and *Zanthoxylum rhoifolium*. However, only three of these trees had high importance value and had dbh ≥ 30 cm: *T. pulchra*, *G. opposita* and *P. angustifolia* (Table A.2, A.3).

Commercial species that produced trees with dbh ≥ 15 cm correspond to 23% of the total species richness in the secondary forests. These commercial species follow different patterns of volume distributions between 20 and 50 years of succession (Fig. 7). Our results showed that fast-growing species may be being replaced by species of advanced successional stages and do not have trees with dbh ≥ 15 cm. Among these fast-growing species is *T. pulchra* (low-quality), which showed the largest stem volumes for trees with dbh ≥ 15 cm in the early secondary forests (<30 years of age), but in more advanced forests it did not show trees above 15 cm dbh (Fig. 7c). Dominant commercial species with fast-growing and short-lived species, such as *H. alchorneoides*, *M. cabucu* and *M. cinnamomifolia*, also produce timber in the first 40 years of succession and can be replaced by advanced secondary and climax species (Fig. 7a).

4. Discussion

In this study, we evaluated the effects of structure dynamics and diversity of secondary forest on commercial wood productivity in the Brazilian Atlantic Forest. We found a rapid increase in basal area and stem volume of commercial species already in the first 20 years of fallow age. Fallow time was determinant for the presence of commercial species (Fig. 4) and productivity of high- and best-quality timber species (Fig. 6). For commercial species, trees presented the ideal size and volume for harvesting in the mid-secondary forest with the largest individual trees reaching a diameter ≥ 30 cm and more than 0.75 m^3 of round wood.

4.1. Commercial timber species and volume in secondary forest

Commercial species show rapid recovery of richness, basal area and stem volume in naturally regenerating forests. Richness and diversity of commercial species were restored fast in regenerating secondary forests, following shifting cultivation, reaching high diversity values still in young-secondary forests. Wood-producing species, mostly non-pioneers, were present at the beginning of the regeneration process, as represented by trees with diameter ≥ 5 cm (Fig. 4), a successional pattern that fits the "initial floristic composition" model suggested by Egler (1954). The same pattern of succession was reported in other studies, in which different species, both pioneers and non-pioneer, initiate regeneration concurrently (van Breugel et al., 2007; Chazdon et al., 2007; Peña-Claros, 2003; Piotto et al., 2009). This pattern of richness and diversity of tree species found in our study is also reported to be common in secondary tropical forests (Siminski et al., 2021; Villa et al., 2018) given the high abundance of commercial species (Fig. 5a). Our results showed that the few dominant species of young-secondary forest are commercial. Some of these species are short-lived and tend to disappear as the succession process advances. Such is the case with *M. coriacea* (pioneer) and *T. pulchra* (non-pioneer), which are fast-growing trees and dominant as small trees, but produce low-quality timber.

Trees with a diameter ≥ 30 cm were present in forests as young as 13 years and became more common in mid-secondary forest. While tree density decreases as succession progresses, individual trees increase in diameter as forests increase in height, basal area and volume (Brown and Lugo, 1990). In our study, while the density of commercial dominant species decreased as succession progressed, the number of trees of commercial and non-commercial species increased. To explain, species that dominate the young-secondary forest are replaced by trees of species that will dominate the mid-secondary forest, gain volume, and eventually occupy the canopy to produce high-quality timber. Among the 12 most important species (50% of total IV), herein called the dominant species (following Finegan, 1996), nine are commercial species. Among them, we highlight *H. alchorneoides*, *M. cabucu* and *M. cinnamomifolia*, all best-quality timber species, with a combined IV of 16% of the total sampled area (Table A.2) but reaching higher dominance values in different single plots.

Fallow time was a determining factor that changed basal area and volume in the studied forests. Commercial species contributed to the rapid increase in basal area and volume with less marked growth in the mid-secondary forest (Fig. 4b, c). This rapid structural increase in the early stages has also been observed in other tropical forest studies (Guariguata and Ostertag, 2001; Peña-Claros, 2003; Poorter et al., 2016; Rocha et al., 2016; Rozendaal et al., 2019; Teixeira et al., 2020). Tree density increased rapidly at the beginning of the regeneration process, peaking at 14 years of fallow age. Trees ≥ 15 cm in diameter increased in density, basal area and stem volume (Fig. 3). This change in forest structure favours commercial species and timber productivity. At 25 years, it is already possible to have high timber productivity with a commercial volume of 245 m^3 ha^{-1}. At that age, we already see large trees *of C. vernalis*, *H. alchorneoides*, *M. cabucu*, *M. cinnamomifolia*, *N. lanceolata* and *N. oppositifolia*. In naturally regenerated secondary

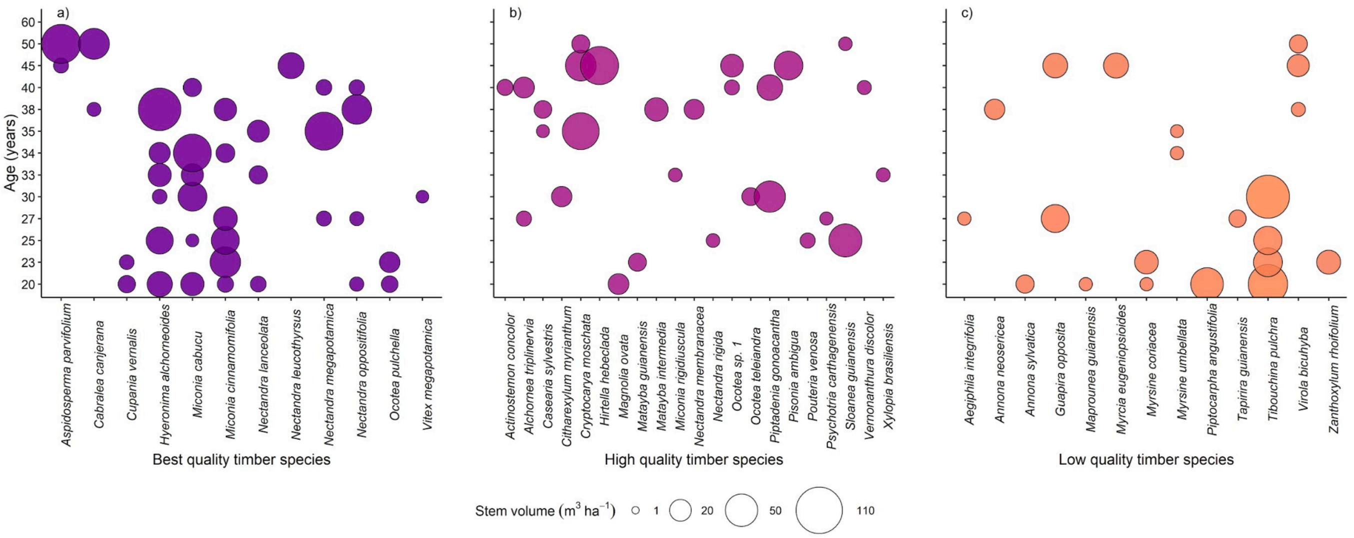

Fig. 7. Frequency and stem (commercial) volume of timber species with highest importance values in the secondary forests from 20 to 50 years old (only trees with dbh ≥ 15 cm). Each bubble represents the stem volume of a given species in a single plot.

forests, the timber volume reached 444 m^3 ha^{-1} with the presence of *Alchornea triplinervia*, *H. alchorneoides*, *Ocotea* spp. and *Nectandra* spp. (Tabarelli and Mantovani, 1999). In a 33-year-old secondary forest, no significant difference was noted for basal area or timber volume when comparing areas naturally regenerated and areas that were enriched with valuable wood-producing species (*H. alchorneoides*, *M. cinnamomifolia* and *Nectandra* spp.) (Fantini et al., 2019). However, the authors noted that the timber stock of these species was two times higher in the enriched forest area compared to their volume in the naturally regenerated area. Such results demonstrate the potential of secondary forest management to produce marketable wood in short rotations or cutting cycles. These dominant species form a high canopy of the secondary forest but mature as early as 30 to 50 years of age, and will be excluded from the successional process as the succession progresses (Fantini and Siminski, 2016). Remaining unharvested, as it is mandated by current regulations in the Atlantic Forest region, implies an opportunity cost to the land owner.

4.2. Timber quality of commercial species in secondary forest

Commercial species are an important component of tree diversity in all ages of the forest. The proportion of commercial species was higher than 50% along the chronosequence (Fig. 6a). Low-quality timber species performed better in the early stages of succession, while high-quality timber species had a higher share of the forest structure, starting from 30 years of succession. As succession progresses, species that produce timber outcompeted the other species, and high- and best-quality timber species together reach 51% of all commercial species between 40 and 50 years. Successional changes benefited the richness of commercial species throughout the succession, and, as a result, we observed an assortment of timber classes for different uses in different phases of forest regeneration.

In addition to the commercial species found in all forest age classes, our results show that seedlings or resprouts of wood-producing species are present at the very beginning of succession. Timber species invade an abandoned area at the very time of abandonment with the presence of small or dominant individuals (Rocha et al., 2016; Rodrigues et al., 2004). The proximity of open or degraded lands to mature and advanced successional forests increase the success of commercial species colonizing young-secondary forests. As the successional forest becomes more complex, tree density and timber volume of high- and best-quality timber species increases; best quality timber species can reach up to 200 m^3 ha^{-1} before 40 years of succession (Fig. 7c). *H. alchorneoides*, *M. cabucu* and *M. cinnamomifolia* are the main species in this category, quickly dominating secondary forests with trees over 20 cm in diameter in forests as young as 20 years. These results indicate the high potential of secondary forests to produce quality timber. However, the high stock of low-quality timber in forests between 20 and 30 years of succession is characteristic of unmanaged secondary forests. Both volume and quality of timber could be improved by tending the secondary forests from young ages.

4.3. Managing secondary forests for timber production and ecosystem services

While the need to restore degraded lands/forests is unquestioned, scaling up programs to achieve ambitious targets remains elusive because of several limiting factors, costs being an important one (Brancalion et al., 2016; Crouzeilles et al., 2017; Crouzeilles et al., 2020). Passive restoration through natural regeneration, after agriculture, has proved to be successful in some ways, suggesting economic efficiency as a factor that could incentivise management initiatives (César et al., 2020; Crouzeilles et al., 2020; Siminski et al., 2021). Nonetheless, even bringing the cost of investments to near zero may not even be sufficient to stimulate landowners to set aside parcels of their land for restoration, especially in the case of small farmers (Alarcon et al., 2017). Managing the regeneration of forests to produce commercial timber may be an alternative to make restoration attractive to all landowners. The forests we studied did not benefit from any management efforts, even though they presented a good volume of commercial timber to be exploited at ages as young as 30 years. Other studies have also shown that combining natural regeneration with forest tending has the potential to significantly increase the volume and quality of timber in secondary forests (Fantini et al., 2019; Guariguata, 1998; Kammesheidt, 2002; Piotto et al., 2020; Rozendaal et al., 2010; Swinfield et al., 2016).

The high diversity of species and the high proportion of fast-growing commercial species found in our study make the options of silvicultural systems and regeneration methods wide open, from clearcutting to individual tree selection. Clearcutting is already practiced by some farmers in the region (Siminski and Fantini, 2010). In the Plateau region of the State, for example, some farmers manage secondary forests to favour the fast-growing *Mimosa scabrella* in cycles of 25 years, leading to almost homogeneous forests harvested for diverse products along the development of the forest (Steenbock et al., 2011). In the DOF region, some swidden farmers allow desirable species to grow amidst crop plants, anticipating their development, with the aim of having harvestable-sized trees by the time a new clearing of the land is reached (Fantini et al., 2017). However, even though these regeneration methods improve the quality of the forests, clearcutting at the end of a fallow period is overall perceived as deforestation, negatively impacting the societal perception of such land use. An alternative is to use either single or group selection of trees assisted by silvicultural treatments (refinement and liberation thinning, pruning) along the forest development. This strategy is likely to have the greatest impact on forest productivity and quality, as even the sparse experience in the tropics has shown (Finegan, 1992; Guariguata, 1998; Mesquita, 2000; Piotto et al., 2020; Swinfield et al., 2016).

Secondary forests in the region are dominated by a few commercial species, along with several non-commercial species. Such combination of species is ideal for the application of silvicultural systems aiming to balance timber production and environmental conservation. That is, while harvesting is concentrated on the dominant commercial trees, a range of other species can be retained to maintain the forest structure and to produce ecosystem services, such as supporting the local fauna and carbon sequestration, as mentioned by Chazdon et al. (2016) and Naime et al. (2020).

The secondary forests we studied varied largely by their composition and structure, as reported in many other studies (Liebsch et al., 2007; 2008; Oliveira et al., 2019; Siminski et al., 2011; Vibrans et al., 2013), forming a mosaic of patches across the landscape. Accordingly, a regeneration method suitable for each forest patch should be applied, ranging from intensive intervention to maximize timber production to light management that will promote ecosystem complexity. Applied at varied scales, from individual trees to stand to landscape, well planned silvicultural systems can produce the best compromise among purposes (Puettmann et al., 2009). Forest plantations with native species and agroforestry systems should also be promoted to increase forest land use in the landscape matrix.

Beyond forest restoration, incentives like increasing economic value of regenerating forests may stimulate landowners to perpetuate restored forests instead of converting more land to non-forest uses. However, studies on regeneration methods and silvicultural treatments to improve timber quality and productivity in secondary forests are still scarce in the tropical world. Given the variability of secondary forests found in this and other studies, large-scale experimental studies should be performed in order to compare different silvicultural systems at various spatiotemporal scales.

5. Conclusion

In the Atlantic forests of Southern Brazil Secondary forests have a high diversity of timber species, and are characterized by timber volumes and trees suitable for harvest from 20 years of fallow age. Commercial species represent 45% of the dominant species, with species like *H. alchorneoides*, *M. cinnamomifolia* and *M. cabucu* being fast-growing species. Best-quality timber species have high density and dominance in these forests with tree size suitable for roundwood production. Given that the secondary forests studied presented a high diversity of species, it would be possible to harvest the dominant commercial trees and retain a range of other species. In this way, managed secondary forest can produce revenue for landowners, while maintaining adequate forest cover to produce other ecosystem services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119352.

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