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**Florestas secundárias da Mata Atlântica: ecologia e manejo para produção de madeira**

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Daisy Christiane Zambiazi

**Florestas secundárias da Mata Atlântica: ecologia e manejo para produção de madeira**

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Daisy Christiane Zambiazi

**Florestas secundárias da Mata Atlântica: ecologia e manejo para produção de madeira**

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca  
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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi  
julgado adequado para obtenção do título de doutor em Agroecossistemas

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Para Maria (*in memoriam*) e Vitor

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## RESUMO

Exploração madeireira e expansão agrícola contribuem significativamente para a mudança e intensificação do uso da terra. Em todas as regiões tropicais, as perdas de floresta crescem e acarretam a diminuição da cobertura de florestas primárias. Em alguns casos, o impacto do desmatamento é compensado pela regeneração de novas florestas quando essas áreas não são convertidas para outros usos. Florestas secundárias estão se tornando a principal cobertura tropical diante da grande degradação e perda de florestas primárias. Elas apresentam um considerável volume de madeira de espécies comerciais, que podem contribuir significativamente para produzir renda e valorizar áreas regeneração em diferentes estágios sucessionais. Na Mata Atlântica, uma característica de grande parte dessas florestas é o volume significativo de madeira de espécies de crescimento rápido acumulado entre 30 e 40 anos de regeneração. Entretanto, esses ecossistemas ainda são muito pouco manejados para produção de madeira, em parte por conta da escassez de pesquisas sobre o tema. Nesta tese, busco compreender como a floresta secundária produz madeira de qualidade ao longo do processo de sucessão e os impactos da colheita dessa madeira na dinâmica da floresta. Foram analisados dois conjuntos de dados coletados de árvores com diâmetro a altura do peito (dap) acima de 5 cm. O primeiro é resultado do inventário de 82 parcelas em cronosequência de 2 a 50 anos, distribuídas em três trajetórias sucessionais: *Miconia cinnamomifolia*, *Miconia formosa* e *Tibouchina pulchra*. O objetivo da análise desses dados é compreender a produtividade de madeira em florestas secundárias em diferentes idades. Os resultados mostram que espécies arbóreas comerciais contribuem significativamente para o aumento da riqueza, área basal e volume comerciais das florestas regeneradas naturalmente e que estas representam 51% da diversidade de espécies de árvores. Entre as 12 espécies dominantes, 9 são espécies comerciais, que apresentam um volume comercial de até 155m<sup>3</sup>.ha<sup>-1</sup>. Árvores de espécies comerciais com mais de 30 cm de diâmetro produzem 126 m<sup>3</sup>.ha<sup>-1</sup> de volume comercial já aos 30 anos de sucessão. *Hieronyma alchorneoides*, *M. formosa* e *M. cinnamomifolia* são espécies dominantes de crescimento rápido e produzem 200 m<sup>3</sup>.ha<sup>-1</sup> de madeira de qualidade aos 40 anos de sucessão. Diversas outras espécies comerciais apresentam elevado estoque de madeira nessa idade da floresta. O segundo conjunto de dados representa uma floresta em estágio médio de sucessão, onde foram inventariadas 12 parcelas permanentes em 2009 e 15 parcelas permanentes em quatro ocasiões, com duas antes de uma colheita seletiva de árvores (2009 e 2014) e duas após a colheita (2014 e 2021). O objetivo da análise desses dados é compreender a dinâmica e o crescimento da floresta antes e após a intervenção silvicultural. Os resultados mostram que a floresta responde rapidamente à colheita de árvores com participação de espécies comerciais (45%) e com aumento da riqueza de espécies após a colheita. Entre as espécies dominantes (16 espécies), 11 são espécies comerciais, com destaque para *H. alchorneoides*, que atingiu 12% de valor de importância (IV) do ecossistema. Após a colheita, houve rápida recuperação da densidade de indivíduos, área basal e volume comercial para toda a floresta. A recuperação dessas variáveis foi mais lenta das espécies comerciais em relação à floresta como um todo. A sua taxa de recrutamento excedeu à taxa de mortalidade média da floresta, tanto antes quanto depois da colheita de árvores. A área basal remanescente da colheita foi determinante para as mudanças que ocorreram após a intervenção e influenciou a riqueza, a densidade de árvores e o volume comercial da floresta. A taxa de crescimento relativo (RGR) em diâmetro para toda a floresta teve um aumento significativo do período pré-colheita para o período pós-colheita. Para o conjunto de espécies comerciais, o padrão é o mesmo, porém com taxas médias menores em comparação à floresta como um todo. Por sua vez, o incremento médio periódico anual (PAI)

do volume comercial total foi de  $5,5 \text{ m}^3.\text{ano}^{-1}$  no período de crescimento antes da colheita e de  $4,4 \text{ m}^3.\text{ano}^{-1}$  após a colheita. A RGR mostrou relação inversa com a área basal para espécies comerciais, com maior taxa de crescimento em áreas com menor área basal após a colheita, enquanto o incremento foi impactado pela colheita. Os dados de árvores individuais de espécies comerciais cresceram com taxas maiores após a colheita, atingindo até  $3,06 \text{ cm.cm}^{-1}.\text{ano}^{-1}$ . As taxas médias foram de  $0,30 \text{ cm.cm}^{-1}.\text{ano}^{-1}$  antes da colheita e de  $0,33 \text{ cm.cm}^{-1}.\text{ano}^{-1}$  após a colheita. Entre as espécies dominantes (9 espécies), *H. alchorneoides*, *M. cinnamomifolia* e *Virola bicuhyba* apresentaram o maior incremento após a colheita. Os resultados obtidos nesta tese mostram que florestas secundárias são geralmente dominadas por espécies comerciais e produtoras de madeira de qualidade, mostrando um rápido aumento de estoque de madeira nos estágios iniciais de sucessão. A resposta rápida da floresta ao impacto da colheita seletiva de árvores pode ser observada principalmente nos dados de crescimento de árvores individuais e nas taxas de recrutamento de novas árvores. O período de sete anos de avaliação da floresta após a colheita foi insuficiente para a recomposição da densidade, área basal e volume comercial nos níveis verificados antes da colheita. Entretanto, os resultados deste estudo indicam que a colheita comercial de madeira acelera a dinâmica da floresta e reforça a perspectiva do seu uso para a produção sustentável de madeira de espécies dominantes, enquanto contribui para a conservação de grande diversidade de espécies.

**Palavras-chave:** sucessão, produtividade de madeira, colheita de árvores, espécies comerciais

## ABSTRACT

Logging and agriculture expansion contribute significantly to land use change and intensification. In all tropical regions, deforestation loss increases, reducing the coverage of primary forests cover decrease. In some cases, the impact of deforestation is offset by the regeneration of new forests when these areas are not converted to other uses. Secondary forests are becoming the main tropical coverage in the face of large-scale degradation and loss of primary forests. These forests can hold a considerable volume of timber of commercial species, which can contribute significantly to produce income and enhance the value of regenerating areas in different successional stages. In the Atlantic Forest, an important characteristic of most of these forests is the significant volume of timber from fast-growing species accumulated between 30 and 40 years of regeneration. However, these ecosystems are still rarely managed for timber production, partly because of the lack of research to support management decisions. In this thesis, I seek to understand how the secondary forest produces quality wood throughout the succession process and the impacts of a selective tree logging has on the forest dynamics. Two sets of data collected from trees with diameter at breast height (DBH) above 5 cm were analysed. The first is the result of an inventory of 82 plots in chronosequence from 2 to 50 years, distributed in three successional routes: *Miconia cinnamomifolia*, *Miconia formosa* and *Tibouchina pulchra*. The objective of the analysis of these data was to understand the timber productivity in secondary forests at different ages. The results show that commercial tree species a contribute significantly to the increase in richness, basal area and commercial volume of naturally regenerated forests and represent 51% of tree species diversity. Among the 12 dominant species, 9 are commercial species, which have a commercial volume of up to  $155\text{m}^3.\text{ha}^{-1}$ . Commercial trees over 30 cm in diameter produce  $126\text{ m}^3.\text{ha}^{-1}$  of commercial volume around 30 years of succession. *Hieronyma alchorneoides*, *M. formosa* and *M. cinnamomifolia* are dominant fast-growing species and produce  $200\text{ m}^3.\text{ha}^{-1}$  of quality timber by 40 years of succession. Several other commercial species show high timber stock at this forest age. The second dataset represents a forest in mid-successional stage, where 12 permanent plots were inventoried in 2009 and 15 permanent plots were inventoried in 2014 and 2021, two before a selective tree logging (2009 and 2014) and two after tree logging (2014 and 2021). The aim of the analysis of these data was to understand the dynamics and growth of the forest before and after the intervention. The results show that the forest responds rapidly to tree harvesting with high participation of commercial species (45%) and with increased species richness after harvesting. Among the dominant species (16 species), 11 were commercial species, especially *H. alchorneoides*, which reached 12% of the total importance value (IV) of the ecosystem. After harvesting, there was rapid recovery of the density of individuals, basal area and commercial volume of the forest. Recovery of these variables was slower for commercial species than for the whole forest. The recruitment rate exceeded the mortality rate for the forest, both before and after tree harvesting. The basal area remaining from harvest was a major driver of the changes that occurred after the intervention and influenced the richness, tree density and commercial volume of the forest. The relative growth rate (RGR) in diameter for the whole forest had a significant increase from pre-harvest to post-harvest period. The pattern was observed for the set of commercial species, but with lower average rates compared to the whole forest. The average annual periodic increment (PAI) of the total commercial volume was  $5.5\text{ m}^3.\text{year}^{-1}$  in the growing period before harvest and  $4.4\text{ m}^3.\text{year}^{-1}$  after harvest. RGR showed negative relationship with basal area for commercial species, with higher growth rate in areas with lower basal area after harvest, while increment was strongly impacted by

harvest. Data from individual trees of commercial species revealed that these trees grew faster after harvest, reaching up to  $3.06 \text{ cm.cm}^{-1}.\text{year}^{-1}$ . The average rates were  $0.30 \text{ cm.cm}^{-1}.\text{year}^{-1}$  before harvest and  $0.33 \text{ cm.cm}^{-1}.\text{year}^{-1}$  after harvest. Among the dominant species (9 species), *H. alchorneoides*, *M. cinnamomifolia* and *Virola bicuhyba* showed the highest increments after harvest. The results reported in this thesis show that secondary forests are dominated by commercial and quality timber-producing species, with a rapid increase in timber stock at early successional stages. The rapid forest response to the selective tree logging can be observed mainly in the increment of individual trees and in the recruitment rates of new trees. The regrowth of the forest during the seven-year period after harvest was insufficient for the forest to restore density, basal area, and commercial volume to pre-harvest levels. However, the results of this study indicate that commercial timber harvesting accelerates forest dynamics and reinforce the prospect of its use for sustainable timber production of dominant species, while contributing to the conservation of a significant species diversity.

**Keyword:** succession, timber productivity, tree harvesting, commercial species

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# **1 CAPÍTULO 1**

## **1.1 INTRODUÇÃO GERAL**

### **1.1.1 DESMATAMENTO E FLORESTAS SECUNDÁRIAS**

A demanda global por madeira, minérios e terras agrícolas impulsiona o desmatamento em áreas tropicais, o que leva a degradação, perda de biodiversidade e erosão de serviços ecossistêmicos (CLEARY; WAITS; FINEGAN, 2016; COCHARD, 2011; CURTIS et al., 2018; GHAZOUL et al., 2015). Desmatamento compreende a conversão de florestas para outros usos, independentemente se por indução humana ou não, incluindo áreas de florestas convertidas para agricultura ou criação de animais (FAO, 2023). Até 2020, a perda de florestas promoveu uma redução de 12% da cobertura florestal tropical, com o Brasil tendo a maior perda com 1.7 milhões de hectares de floresta (GLOBAL FOREST WATCH, 2022). A cobertura florestal já está abaixo do limite crítico de 30% da paisagem necessária para a conservação da biodiversidade em muitas regiões tropicais (BANKS-LEITE et al., 2014). Juntamente com o desmatamento, a degradação e a conversão para outros usos são os principais impulsionadores da perda de florestas tropicais (JAKOVAC et al., 2016; KARTAWINATA et al., 2001; PUTZ; REDFORD, 2010).

Em regiões das florestas tropicais, é crescente a redução da extensão de florestas primárias (PAIN et al., 2021), ao mesmo tempo que há a regeneração de florestas muito jovens com menor biomassa e biodiversidade (ROSA et al., 2021). A exploração madeireira e a expansão agrícola contribuíram significativamente para a mudança e intensificação do uso da terra (CHAZDON, 2016; PUETTMANN; COATES; MESSIER, 2009; WHALLEY, 1994). Do total global de florestas perdidas, 27% podem ser atribuídas à perda permanente para a mudança do uso da terra para a produção agrícola e pastagens, o que impede o crescimento da floresta (CURTIS et al., 2018). Como consequência, temos paisagens empobrecidas com áreas em regeneração com diferentes tipos, formas e graus de perturbação (ARROYO-RODRÍGUEZ et al., 2017; BARLOW et al., 2007; JOLY; METZGER; TABARELLI, 2014; RIBEIRO et al., 2009; SIMINSKI et al., 2021). Sem atingir estágios mais avançados de regeneração, as florestas estão sendo perdidas em um tempo muito curto sendo novamente usadas para fins agrícolas. Estima-se que há em torno de 250 a 300 milhões de hectares globais consideradas áreas agrícolas (HEINIMANN et al., 2013). Segundo essa estimativa, muitas das paisagens não são áreas agrícolas, mas sim, florestas secundárias em diferentes estágios de crescimento.

Floresta secundária regenera espontaneamente após o desmatamento da floresta original (CHAZDON, 2016) e também compreendem o crescimento da regeneração natural depois de uma área ter sido abandonada após agricultura ou criação de animais (JAKOVAC, 2015). Em áreas que são utilizadas durante um período e depois abandonadas, a floresta volta a crescer. Após ser abandonada, a floresta em regeneração inicia um processo contínuo de sucessão da vegetação (DELANG; LI, 2013; PADOCH; PINEDO-VASQUEZ, 2010). Alguns estudos em zonas tropicais apontam que o pousio favorece a recuperação dos níveis de nutrientes no solo, suficientes para outro ciclo de cultivo. Alguns estudos relatam que há aumento do estoque e a disponibilidade de nutrientes no solo, o que favorece o uso recorrente do solo (KOTTO-SAME et al., 1997; LINTEMANI et al., 2020). Outros estudos relatam que o estoque total de minerais no solo pode diminuir durante os ciclos subsequentes de pousio e cultivo (JUO; MANU, 1996), um problema que pode se agravar com períodos de pousio mais curtos. Sob circunstâncias adversas, a paisagem torna-se dominada por florestas mais jovens (JAKOVAC et al., 2017), com baixa disponibilidade de madeira e, após a supressão, a madeira exploração é destinada para lenha e para produção de carvão vegetal.

A permanência da floresta com ciclos de pousio mais longos, geram florestas com maior biodiversidade, biomassa, capacidade de fixação de carbono, estoque de nutrientes no solo e com potencial para suprimento de madeira. Ao longo do processo de sucessão, em florestas regeneradas naturalmente ocorrem mudanças na composição florística e estrutura (BROWN; LUGO, 1990; CIFOR, 1998), influenciadas pelos distúrbios, naturais ou humanos, sofridos anteriormente (BARNES et al., 1998; BREUGEL, 2007; CHAZDON, 2014; CHOKKALINGAM; JONG, 2001; FRELICH, 2002). Distúrbios são decisivos em processos de seleção de espécies em certas comunidades, além de influenciar os padrões de sua distribuição espacial e temporal, o que afeta a dinâmica natural do ecossistema (BEEBY, 1994). Os processos naturais de regeneração da floresta secundária refletem em mudanças na riqueza e composição de espécies, tamanho e estrutura das populações, e propriedades dos ecossistemas (BARNES et al., 1998; BREUGEL, 2007; BROWN; LUGO, 1990; CHAZDON, 2012, 2014; GUARIGUATA; OSTERTAG, 2001; HARTSHORN, 1980; LOHBECK et al., 2014; PEÑA-CLAROS, 2003; SIMINSKI; FANTINI, 2004).

Diferenças na composição florística no início da sucessão podem resultar de variações no banco de sementes, na composição da vegetação do entorno e mesmo nos padrões climáticos anuais (CHAZDON et al., 2007). A sucessão pode levar a múltiplos pontos finais e até mesmo a uma falta de estabilidade dos estágios sucessionais, permanecendo em constante mudança

(CHAZDON et al., 2007; DELANG; LI, 2013; EGLER, 1954; FINEGAN, 1984). Durante o uso, áreas cultivadas recebem sementes espécies e raízes permanecem vivas no solo, e a lavoura ou o pastoreio da terra age para quebrar e dispersar os propágulos e iniciar o processo de sua germinação no solo (EGLER, 1954). Na fase inicial da sucessão, ervas daninhas, gramíneas, arbustos pequenos ou dormentes e espécies arbóreas estarão presentes no local. A mudança é gradual e à medida que cada grupo deixa a sucessão, um novo grupo de espécies, presente desde o início da sucessão, assume o domínio do local. Geralmente, estudos sobre a dinâmica das florestas secundárias mostram que riqueza e diversidade de espécies aumentam com o tempo de pousio, assim como a área basal e a biomassa acima do solo (DELANG; LI, 2013). Entretanto, as florestas secundárias nas regiões neotropicais têm alto nível de dissimilaridade (JAKOVAC et al., 2022). Mesmo na paisagem podem ser observadas diferenças na estrutura e na diversidade entre áreas de floresta em pousio (CHAZDON, 2008).

O uso da terra, a quantidade de ciclos de uso e a intensidade de uso do solo podem determinar a rota sucessional e a diversidade da floresta secundária em regeneração (JAKOVAC et al., 2016). Mas, além dos distúrbios que determinam a trajetória sucessional e a diversidade, a dinâmica sucessional de uma floresta pode ser alterada por fatores abióticos, bióticos e antrópicos (CAPERS et al., 2005; CHAZDON, 2008, 2012, 2014; DELANG; LI, 2013; FINEGAN, 1984, 1992; GUARIGUATA; OSTERTAG, 2001; MASSOCA et al., 2012; MESQUITA, 2000; PEÑA-CLAROS et al., 2008; VAN BREUGEL et al., 2013), e outros diferentes processos podem interferir na determinação da estrutura da comunidade e diversidade de espécies. Em estudos realizados na Amazônia brasileira, foi possível verificar que a intensidade do uso da terra anterior à regeneração determina a composição das espécies na floresta secundária (JAKOVAC et al., 2016). Com o aumento da intensidade do uso do solo no sistema de agricultura de corte e queima, a redução da qualidade do solo estabelece filtros que favorecem espécies com potencial de rebrota e que podem se desenvolver com baixa disponibilidade de nutrientes. Os autores concluíram que, devido a filtros locais, a diversidade alfa e beta da vegetação regenerante diminui, tornando as comunidades sucessionais em estágio inicial semelhantes umas às outras.

Espécies arbóreas podem ser desenvolver através de sementes ou rebrota, passando por vários filtros até se estabelecer como indivíduos adultos ou serem excluídas do processo de sucessão (CHAZDON, 2016; EGLER, 1954; WHITMORE, 1990). A dominância de espécies arbóreas pode ser assegurada pela abundância de regenerantes e pode facilitar a compreensão

da dinâmica, estruturação e composição da comunidade arbórea (FINEGAN, 1984). Conforme o processo avança, ocorre o enriquecimento gradual de espécies e aumenta a complexidade estrutural da floresta (CHAZDON, 2012). Inicialmente, a área é dominada por espécies pioneiras de rápido crescimento e alta capacidade de dispersão (WHITMORE, 1998). Com o tempo, a abundância de espécies arbóreas pioneiras diminui, dando espaço para espécies arbóreas secundárias, tanto iniciais quanto tardias. Com o avanço do processo sucessional, outras espécies serão substituídas por espécies de estágios avançados que estarão presentes na floresta madura (BREUGEL et al., 2013).

Nesse processo de sucessão, as espécies madeireiras estarão presentes já nos estágios iniciais da regeneração florestal. Nas primeiras fases do processo, as espécies madeireiras de crescimento rápido podem colonizar áreas abandonadas e o crescimento rápido pode aumentar a produtividade da madeira já nos primeiros anos de pousio (BROWN; LUGO, 1984; GUARIGUATA; OSTERTAG, 2001). Outras espécies, que podem estar presentes desde o início da sucessão, podem suprimir essas espécies com taxa de crescimento inicial relativamente alta durante a fase de exclusão (OLIVER, 1981).

### 1.1.2 PRODUTIVIDADE DE MADEIRA EM FLORESTAS SECUNDÁRIAS

Considerando suas particularidades, as florestas secundárias podem ser fontes de madeira tropical. Essas florestas são consideradas alternativas essenciais para estoque de carbono, restauração e proteção da biodiversidade (CAPELESSO et al., 2021; HEINRICH et al., 2021; MATOS et al., 2020). A dominância de espécies de crescimento rápido, pode favorecer o manejo econômico dessas florestas para o fornecimento de madeira. Estudos como o de Brown e Lugo (1990) apontam que florestas secundárias acumulam espécies madeireiras em taxas relativamente altas em curto período de tempo, porém, períodos de pousio mais curtos não resultam em formações florestais com área basal suficiente para extração de madeira. Para atingir boa produtividade de madeira, seriam necessários períodos de pousio mais longos, com florestas que poderiam fornecer madeira através da colheita seletiva por longos períodos. A presença de espécies de rápido crescimento pode proporcionar às florestas secundárias alta produtividade de madeira no estágio médio de sucessão (FANTINI; SIMINSKI, 2016) e garantir madeira de boa qualidade. As espécies madeireiras podem se estabelecer rapidamente nos estágios iniciais de sucessão e o crescimento rápido pode promover a produção de madeira já nos primeiros 30-40 anos de pousio (BROWN; LUGO, 1984; GUARIGUATA; OSTERTAG, 2001), principalmente por meio de espécies pioneiras de longa vida e espécies

secundárias iniciais. A exploração da madeira proveniente de florestas secundárias poderia abastecer o mercado local de madeira, enquanto o manejo da floresta para a sua produção pode acelerar a taxa de crescimento de espécies tardias. Ainda é necessário aprofundar estudos sobre produtividade de madeira em florestas secundárias para entender como a riqueza de espécies comerciais madeireiras contribui para o aumento da área basal e volume de madeira ao longo do processo de sucessão. Com a identificação e seleção de espécies madeireiras comerciais, as fases de sucessão podem ser utilizadas como mecanismos para o sucesso do manejo florestal, para garantir o incremento e a produtividade de madeira nos anos seguintes. Espécies do sub-bosque que demandam luz dominam o comércio de madeira e podem regenerar após a colheita seletiva de árvores (FREDERICKSEN; PUTZ, 2003; PUTZ et al., 2012).

Áreas com alta produtividade de madeira promovem o uso madeireiro para diferentes fins e garantem ao produtor rural um aumento na renda familiar (FANTINI; SIMINSKI, 2016). Em diferentes regiões tropicais, propriedades rurais são tipicamente cobertas com várias áreas em pousio em diferentes estágios e fatores sucessionais, formando um mosaico de fragmentos de floresta secundária, com características semelhantes entre propriedade (CHAZDON, 2014; FANTINI; SIMINSKI, 2016; FRELICH, 2002).

Espécies comerciais madeireiras características de florestas secundárias têm boa aceitação no mercado, mas são escassos estudos sobre produtividade e rendimento de madeira. Na Costa Rica, o valor da madeira de espécies da floresta secundária cresceu à medida que o suprimento de madeira de florestas primárias se tornou escasso, mas o seu aproveitamento demanda adaptar técnicas silviculturais para aumentar o estoque de madeira em pequenas propriedades que retêm manchas de florestas (GUARIGUATA, 1999a). Este cenário não é diferente em florestas secundárias em outras regiões neotropicais, já que a pressão sobre florestas primárias vem aumentando significativamente e medidas legais terão que ser adotadas para frear a exploração desordenada e abastecer o mercado madeireiro.

#### **1.1.3 USO DA FLORESTA SECUNDÁRIA COMO FLORESTAS PRODUTIVAS E PARA CONSERVAÇÃO PERMANENTE**

A restauração de áreas e florestas degradadas é uma ferramenta que pode ser usada para gerar florestas produtivas através de restauração ativa que consiste no plantio, enriquecimento por meio do plantio de mudas de espécies florestais de interesse ecológico e econômico, e manejo da regeneração natural. Entretanto, muitas florestas iniciam o processo de restauração passiva através da regeneração natural com baixo custo ao proprietário, após o uso na

agricultura ou pastagens (ZAHAWI; REID; HOLL, 2014). A presença de espécies arbóreas comerciais em florestas secundárias torna-se um atrativo para a restauração em propriedades rurais, aumentando a biodiversidade e a cobertura florestal na paisagem. Estudos recentes mostraram que as florestas secundárias sem manejo já mostram um bom volume de madeira comercial em estágios iniciais de sucessão (ZAMBIAZI et al., 2021). Estudos que avaliaram as práticas de manejo da regeneração mostraram que espécies madeireiras têm crescimento superior e maior oferta de madeira com qualidade superior (VENTUROLI; FRANCO; FAGG, 2015), maximizando a produtividade de madeira. Nesse contexto, uma abordagem inovadora é gerenciar a floresta secundária como um sistema de uso da terra capaz de proporcionar produção de madeira de valor comercial, além de benefícios indiretos (serviços ecossistêmicos). Conhecer a floresta secundária de um ponto de vista de produção baseado na diversidade, dinâmica, produtividade e rendimento das espécies madeireiras comerciais pode apoiar essa abordagem.

Desenvolver e aplicar técnicas silviculturais e manejo de recursos florestais é o desafio para a conservação de áreas florestais, com as florestas tropicais tendo o papel específico de conservar a biodiversidade e fornecer produtos madeireiros sustentáveis (FREDERICKSEN, 1998). Entender como a produtividade e a produção de madeira ocorrem durante a sucessão pode permitir medidas para acelerar o crescimento de indivíduos de espécies comerciais de madeira para gerar uma floresta de alto rendimento. As espécies de rápido crescimento com alta produtividade de madeira podem ser dominantes nas florestas secundárias, com o manejo dessas espécies sendo atrativo para pequenos produtores rurais (FANTINI; GAIO, 2015; FANTINI; SIMINSKI, 2016). A seleção de árvores ao longo do ciclo pode diminuir a competição, reduzir o desenvolvimento de galhos laterais e promover o crescimento apical, favorecendo o rápido crescimento de árvores selecionadas no final da colheita (MAYHEW; NEWTON, 1998). Entretanto, é importante garantir a seleção de árvores com boa forma. Um regime com alta densidade de estocagem que otimize a maximização da produtividade pode revelar a sustentabilidade do modelo de manejo (MAYHEW; NEWTON, 1998).

#### 1.1.4 MANEJO EM FLORESTAS SECUNDÁRIAS NEOTROPICAIAS

As florestas secundárias neotropicais são florestas que voltaram a crescer após um distúrbio, como desmatamento ou extração de madeira (DE JONG et al., 2001; GUARIGUATA; OSTERTAG, 2001; POORTER et al., 2016). O manejo sustentável e regenerativo pressupõe que a floresta seja manejada repetidamente em ciclos pré-determinados

(SEBBENN et al., 2008). Entretanto, a floresta secundária responde de diferentes maneiras ao corte seletivo. Com isso, o manejo pode ser direcionado a estágios intermediários e tardios de sucessão, onde há a presença de um grupo desejável de espécies ou grupos dominantes (ITTO, 2002). Mas, o sucesso dessa estratégia ainda demanda estudos científicos visando compreender o crescimento da floresta e os reflexos sobre produtividade e produção de madeira de espécies comerciais espacialmente e ao longo do tempo. O manejo de florestas secundárias tropicais envolve práticas destinadas a promover a regeneração e restauração de áreas degradadas ou desmatadas visando a formação de um ecossistema florestal diversificado (DUPUY; MAÎTRE; AMSALLEM, 1999; HOLL, 2012; ITTO, 2002; PAIN et al., 2021). Isso pode incluir atividades como o plantio de espécies arbóreas nativas, o controle de espécies invasoras e a implementação de métodos sustentáveis de colheita de produtos florestais. O objetivo final do manejo é proporcionar benefícios econômicos, tais como renda proveniente de produtos florestais madeireiros e não-madeireiros e créditos de carbono.

Soluções sustentáveis podem ser adotadas antes da colheita de árvores (BÖRJESON; ANGO, 2021; DAVID et al., 2019; PAIN et al., 2021; PIOTTO, 2008). Três estratégias podem ser implementadas para a melhoria da produtividade de madeira na floresta secundária: primeiro, é fundamental compreender bem o ecossistema que será manejado; segundo, definir claramente quais os objetivos do manejo; e terceiro, identificar quaisquer barreiras que possam impedir ou dificultar a regeneração de espécies comerciais, o crescimento de árvores remanescentes e a reposição do estoque de madeira. Ter uma visão clara do tipo de floresta que se deseja obter após o manejo e quais padrões se pode esperar ajuda a tomar decisões mais acertadas durante o processo de extração de madeira. Geralmente, a meta é ter uma floresta com produtividade de madeira comercial em ciclos futuros, diversidade de espécies e crescimento em diâmetro. Para aumentar a produtividade de madeira das florestas secundárias antes mesmo da primeira colheita de árvores, é possível realizar algumas práticas silviculturais, tais como refinamento e liberação (GUARIGUATA, 1999b; PUETTMANN; COATES; MESSIER, 2009). No refinamento, são eliminadas árvores indesejadas e se promove o crescimento de árvores de espécies de interesse madeireiro; já na liberação, eliminam-se as árvores que se desenvolveram mal para reduzir a competição entre árvores por recursos.

### 1.1.5 EFEITOS PÓS-COLHEITA DE ÁRVORES

Florestas secundárias têm alto potencial de restauração da biodiversidade com a presença de espécies com elevada dominância. Essas espécies, também de uso madeireiro,

apresentam alto incremento e podem favorecer a recuperação pós-distúrbio do volume colhido. Após a colheita seletiva de árvores, as florestas secundárias crescem a partir das árvores remanescentes, regenerantes do sub-bosque e de quaisquer fontes de sementes locais ou vindas da paisagem circundante. A taxa de crescimento e composição dessas florestas dependem de vários fatores, tais como a composição inicial das espécies arbóreas, o grau de perturbação, a disponibilidade de luz e nutrientes, e a presença de vegetação competitora. Existe a expectativa de que após a colheita de árvores haja uma aceleração da taxa de crescimento da floresta. O que ocorre é que após o distúrbio, diferentes cenários podem ser configurados em resposta à intensidade da redução da área basal da floresta. Os distúrbios causados pela colheita favorecem o aumento da densidade de espécies pioneiras e tolerantes à sombra imediatamente após a intervenção (SCHWARTZ et al., 2014), o que leva a uma alta taxa de recrutamento e aumento da densidade de árvores. No entanto, ocorrem também altas taxas de mortalidade. O rápido acúmulo de biomassa florestal secundária em curtos períodos de tempo (BRITTO et al., 2022; BROWN; LUGO, 1984; MUKUL; HERBOHN, 2016; POORTER et al., 2016; ROZENDAAL; CHAZDON, 2015) favorece a recuperação da área basal e do volume. Ainda assim, a redução de área basal pode se refletir em dois padrões de desenvolvimento florestal, que também podem ser devidos à riqueza de espécies e composição florística: o crescimento dos indivíduos já presentes na floresta e a colonização dos espaços por espécies de crescimento rápido.

Há um aumento na riqueza de espécies com o corte seletivo (BAWA; SEIDLER, 1998; BERRY et al., 2010; PUTZ et al., 2012; PUTZ; REDFORD, 2000) e espécies de crescimento rápido recuperam o ambiente após a perturbação (WIENER, 2010). Quando os distúrbios são frequentes, espera-se uma alta diversidade de espécies, com a presença de espécies de estágios sucessionais anteriores e futuros (TER STEEGER, 2003). Mas também é comum que árvores de espécies produtoras de madeira sejam favorecidas (SCHWARTZ; FALKOWSKI; PEÑA-CLAROS, 2017). Luz e espaço mudam na floresta. Portanto, mudanças na estrutura da floresta após a colheita acontecem mais rapidamente (KUULUVAINEN, 2009; LINDENMAYER; MARGULES; BOTKIN, 2000; PARROTTA; FRANCIS; KNOWLES, 2002) e as árvores remanescentes podem crescer mais rapidamente em condição de menor competição (BREUGEL et al., 2012; ROZENDAAL et al., 2020). Assim, a disposição espacial de uma árvore e seus vizinhos influenciará e será influenciada pelo ambiente de crescimento (ASHTON; KELTY, 2018) e a estrutura florestal determinará a competição entre as árvores e seus recursos (PRETZSCH, 2009). Enquanto algumas florestas recuperam rapidamente a estrutura do dossel e diminuem a intensidade da luz abaixo do dossel (LIKOSKI; VIBRANS;

DA SILVA, 2022), outras florestas secundárias podem mostrar evidência de corte seletivo no dossel e na estrutura, e densidade de árvores da floresta (VILLELA et al., 2006). Espécies indesejáveis também podem ser favorecidas em áreas com alta redução da área basal, o que pode inibir o crescimento de árvores de interesse madeireiro remanescentes. Por outro lado, árvores remanescentes sofreriam menos danos em áreas com altas intensidades de corte (LIKOSKI; VIBRANS; DA SILVA, 2022).

#### 1.1.6 MATA ATLÂNTICA E FLORESTAS EM REGENERAÇÃO

Florestas secundárias cobrem cerca de 28% do território da América Latina (ROZENDAAL et al., 2019), com alguns biomas altamente degradados, como a Mata Atlântica. Atualmente, esse bioma tem 28% (32Mha) de seu território coberto por florestas nativas (REZENDE et al., 2018), com 4,41Mha de florestas em regeneração em diferentes estágios sucessionais (PIFFER et al., 2022). No sul do Brasil, onde a Mata Atlântica é dominante e considerada um *hotspot* de restauração (NANNI et al., 2019), além de ser um *hotspot* de biodiversidade (SCARANO; CEOTTO, 2015), a madeira produzida provém de florestas secundárias presentes em pequenas e médias propriedades rurais cuja tradição de uso do solo é agricultura e pastagem (FANTINI et al., 2017; FANTINI; SIMINSKI, 2016). Desde o início do século XX até os anos 1990, a exploração madeireira e o extrativismo foram intensos em áreas de floresta primária, o que levou a redução drástica dessas florestas a um percentual de 12% da cobertura original (RIBEIRO et al., 2009). Com a redução da oferta de madeira de alto valor proveniente de florestas primárias, as restrições legais impostas pelo Decreto 750 de 1993 e pela Lei da Mata Atlântica nº 11.428 de 2006 (BRASIL, 1993; 2006) tornaram a extração de madeira ilegal. Como resultado, a produção passou a ser direcionada para espécies então consideradas de menor valor. Entretanto, ao mesmo tempo em que as restrições legais buscavam garantir florestas remanescentes na paisagem e a preservação da biodiversidade, a conversão para outros usos da terra não foi estancada (FANTINI e SIMINSKI, 2016; FANTINI et al., 2017). Nos últimos 35 anos (1985-2019), apenas dois terços das florestas secundárias persistiram na Mata Atlântica, enquanto 1,37Mha de florestas nativas regeneradas voltaram a ser desmatadas após quatro e oito anos do início do processo de regeneração natural (PIFFER et al., 2022).

O desmatamento precoce de áreas em regeneração impede o avanço da sucessão e diminui a presença de florestas em diferentes estágios sucessionais na paisagem. O manejo florestal é uma alternativa para aumentar a cobertura florestal e a persistência da floresta em

diferentes estágios de sucessão em áreas de restauração passiva. Além dos benefícios em termos de biodiversidade e estoque de carbono, a produtividade da madeira nas florestas secundárias pode favorecer a restauração e a persistência dessas florestas, com a atratividade econômica para os proprietários de terras (PAIN et al., 2021). Árvores com bom volume de madeira podem ser encontradas em florestas secundárias a partir de 30 anos em florestas restauradas passivamente, sem intervenção. A diversidade de espécies de árvores com a alta proporção de espécies comerciais de rápido crescimento contribui para a produtividade da madeira comercial. Entretanto, as técnicas de manejo e práticas silviculturais adotadas nos estágios iniciais da sucessão podem acelerar o crescimento das árvores produtoras de madeira, proporcionando ciclos de corte mais curto.

Em estudos realizados com cronomossequências na Floresta Ombrófila Densa de Santa Catarina, foi possível observar que áreas de floresta secundária com idade entre 20 e 50 anos têm árvores de valor comercial prontas para corte e uso em serrarias como *Miconia cabucu*, *Miconia cinnamomifolia* e *Hieronyma alchorneoides* (ZAMBIAZI, 2017). Como esses resultados foram obtidos em florestas sem qualquer manejo, é possível que se possa aumentar as taxas de crescimento com intervenções silviculturais.

Este estudo visa destacar que florestas secundárias apresentam espécies comerciais com potencial para produção de madeira. Ocorre um aumento da produtividade ao longo do processo sucessional e essas florestas têm uma resposta rápida aos distúrbios gerados por uma colheita seletiva de árvores. A presença de uma proporção significativa de espécies comerciais é uma contribuição importante para a análise de como essas espécies podem produzir madeira de qualidade em poucos anos na floresta em regeneração e, assim, contribuir para a colheita seletiva de árvores no estágio médio de sucessão. Os distúrbios causados pela colheita seletiva de árvores foram utilizados para analisar como a floresta e as espécies comerciais respondem às mudanças na riqueza, estrutura, demografia e crescimento. Os resultados deste estudo podem ajudar a consolidar o potencial madeireiro de florestas secundárias em regiões tropicais e apoiar sistemas de manejo que contribuem para a restauração, manutenção e expansão de áreas de floresta na paisagem. Além disso, esses buscam melhorar a visão sobre florestas secundárias, que muitas vezes são vistas como degradadas e não como importante componente na ecologia de florestas tropicais.

Em resumo, a demanda global por recursos naturais, como madeira, minérios e terras agrícolas, tem impulsionado o desmatamento em áreas tropicais, resultando em graves

consequências ambientais, incluindo a degradação dos ecossistemas, a perda de biodiversidade e a redução dos serviços ecossistêmicos. O desmatamento, juntamente com a degradação e a conversão de florestas para outros usos, é responsável pela diminuição da cobertura florestal tropical, que já está abaixo do limite crítico para a conservação da biodiversidade em muitas regiões tropicais. Em regiões de florestas tropicais, a perda florestal tem levado à redução das florestas primárias, sendo compensada pela regeneração de florestas secundárias com menor biomassa e biodiversidade. A exploração madeireira e a expansão agrícola têm desempenhado um papel significativo na mudança e intensificação do uso da terra, com 27% das florestas perdidas globalmente sendo atribuídas à conversão para produção agrícola e pastagens.

A sucessão florestal secundária desempenha um papel crucial na regeneração das florestas, com diferentes estágios de pousio resultando em mudanças na composição e estrutura das comunidades de espécies. Ciclos mais longos de pousio favorecem florestas com maior biodiversidade, biomassa, capacidade de fixação de carbono e estoque de nutrientes no solo. No entanto, a intensidade e a duração do uso da terra, juntamente com fatores abióticos, bióticos e antrópicos, podem influenciar a trajetória sucessional e a diversidade das florestas secundárias em regeneração.

As florestas secundárias podem ser fontes importantes de madeira tropical, com espécies de crescimento rápido favorecendo sua produtividade. A presença dessas espécies nos estágios iniciais de sucessão e seu rápido crescimento possibilitam a obtenção de madeira de boa qualidade em períodos relativamente curtos de pousio. No entanto, períodos de pousio mais longos ou a transformação permanente das florestas secundárias podem ser necessários para garantir uma área basal adequada para a extração sustentável de madeira.

Em conclusão, o manejo adequado das florestas secundárias, considerando a dinâmica sucessional, a diversidade de espécies e os impactos humanos, é fundamental para promover a conservação da biodiversidade, a restauração de ecossistemas e o suprimento sustentável de recursos naturais. É crucial adotar políticas e práticas que incentivem a proteção das florestas tropicais, o uso responsável da terra e a valorização das florestas secundárias como importantes fontes de madeira e serviços ecossistêmicos. Somente por meio de esforços integrados de conservação e manejo sustentável será possível enfrentar os desafios do desmatamento e garantir um futuro sustentável para as florestas tropicais.

## 1.2 ÁREAS DE ESTUDO

Neste estudo, foram avaliadas florestas secundárias da Mata Atlântica com diferentes idades, localizadas no estado de Santa Catarina. Foram analisados dois conjuntos de dados que fazem parte de um banco de dados de pesquisas desenvolvidas pelo Laboratório de Ecologia e Manejo de Ecossistemas Florestais da UFSC, coordenado pelo Prof. Alfredo Celso Fantini. O primeiro conjunto de dados (Capítulo 2) são referentes a três cronomossequências (*pathway*) com 82 parcelas no total, distribuídas de acordo com a espécie dominante de maior frequência: *Miconia cinnamomifolia*, *Miconia formosa* e *Tibouchina pulchra* (Figura 1.1). As parcelas desse conjunto de dados foram alocadas em propriedades rurais na Floresta Ombrófila Densa de Santa Catarina em áreas com florestas em regeneração. Foram selecionadas áreas com estágios sucessionais identificáveis em diferentes idades por meio de características das fitofisionomias e informações do histórico de uso dos agricultores. Historicamente, as áreas são utilizadas no sistema de agricultura de pousio.

O segundo conjunto de dados (Capítulos 3 e 4) consiste em parcelas permanentes em uma floresta secundária em estágio médio de sucessão. São 12 parcelas permanentes inventariadas em 2009 e 15 parcelas permanentes inventariadas em 2014 e 2021. Após o inventário de 2014, a floresta foi submetida a uma colheita seletiva de árvores e novamente inventariada. Após sete anos da colheita de árvores, em 2021, a floresta foi novamente inventariada. Portanto, essa floresta foi inventariada antes da colheita (2009 e 2014) e após a colheita (2014 e 2021; Figura 1.2). Esta área de floresta está inserida em uma propriedade rural de 42 hectares que foi abandonada após o uso para agricultura de roça e criação de animais (BRITTO et al., 2017) em 1978, na qual o proprietário tem uma pequena serraria onde a madeira foi processada. O projeto desenvolvido nesta área é único na Mata Atlântica, sendo um projeto piloto de manejo florestal em áreas de florestas secundárias. O projeto tem convênio e autorização de colheita seletiva de árvores pelo Instituto do Meio Ambiente de Santa Catarina (IMA/SC). A colheita seletiva de árvores foi baseada na longevidade e senescência das árvores em estágio médio e avançado de sucessão, a fim de aproveitar a produtividade de madeira dessas árvores.

Figura 1.1 Mapa da cobertura original e dos remanescentes da Mata Atlântica no Brasil (esquerda), indicando o tipo florestal no Estado de Santa Catarina. A localização das parcelas por trajetória sucesional (1. *Miconia cinnamomifolia*; 2. *Miconia formosa*; 3. *Tibouchina pulchra*) é fornecida em detalhes no mapa. Fonte: <http://mapas.sosma.org.br/> (SOS Mata Atlântica, 2020); Mapa com domínio da Mata Atlântica com base na Lei Federal nº 11.428/2006 (BRASIL, 2006); Fitogeografias do Klein (SAR, 2005).

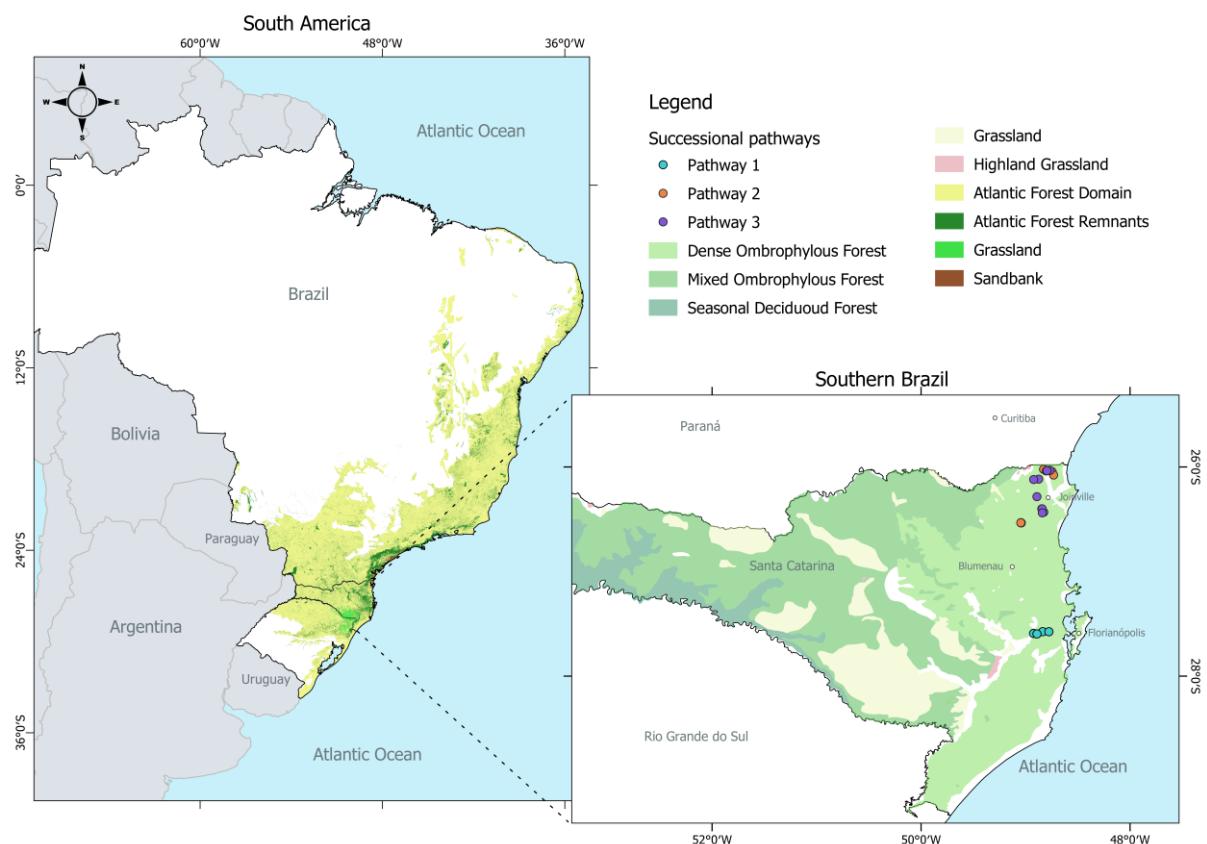
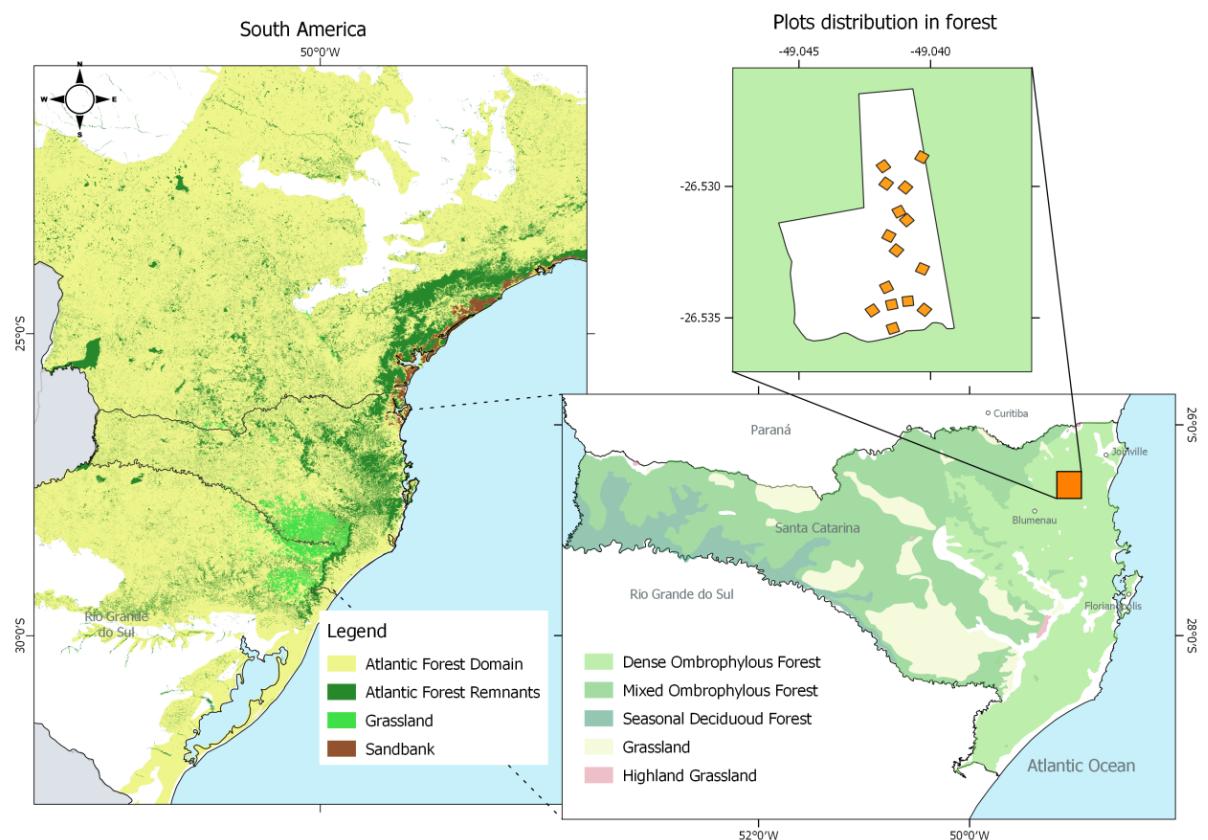


Figura 1.2 Distribuição das parcelas permanentes em uma floresta secundária com colheita seletiva de árvores na Mata Atlântica, sul do Brasil. Mapa da cobertura original e dos remanescentes da Mata Atlântica no Brasil (esquerda), indicando o tipo florestal no Estado de Santa Catarina. Fonte: <http://mapas.sosma.org.br/> (SOS Mata Atlântica, 2020); Mapa com domínio da Mata Atlântica com base na Lei Federal nº 11.428/2006 (BRASIL, 2006); Fitogeográficas do Klein (SAR, 2005).



### **1.3 APRESENTAÇÃO DA TESE E OBJETIVOS DO ESTUDO**

Este estudo tem como objetivo geral compreender a produtividade de madeira em florestas secundárias em diferentes idades e a dinâmica da diversidade, estrutura e crescimento e produtividade de madeira em uma floresta manejada para a produção de madeira por meio da colheita seletiva de árvores. Esta tese é composta por cinco capítulos, incluindo introdução geral (Capítulo 1), três capítulos de pesquisa (Capítulo 2 e 4), e uma discussão geral (Capítulo 5). Os capítulos de pesquisa buscam atingir o objetivo geral e propõem questões de pesquisa conectadas com a análise da riqueza, diversidade, estrutura, demografia, crescimento e produtividade de madeira de espécies comerciais em florestas secundárias, a partir de uma perspectiva sucessional e de manejo.

No Capítulo 2, eu investigo se a diversidade de espécies de florestas secundárias contribui para a produtividade de madeira em florestas com diferentes idades (de pousio), para o uso em serraria e aumento do volume de madeira. O cruzamento com análises ecológicas permitirá investigar quais espécies são as maiores responsáveis pela produtividade de madeira, como essas espécies contribuem para a dinâmica florestal secundária e se são espécies de alta qualidade de madeira, respondendo às seguintes questões: 1) florestas secundárias possuem diversidade e volume de madeira de espécies comerciais que tornam o seu manejo atraente?; 2) como o volume das espécies comerciais muda ao longo da sucessão em comparação com as espécies não comerciais?; e 3) quando as árvores de espécies comerciais atingem um tamanho de corte durante o processo de sucessão?

As mudanças na diversidade e estrutura da floresta secundária antes e depois da colheita de árvores em função da área basal e da intensidade da colheita estarão presentes nos Capítulos 3 e 4. No Capítulo 3, analiso os efeitos da área basal e da intensidade de redução de área basal na diversidade, aumento da densidade, área basal e volume comercial, além do recrutamento de espécies comerciais com as seguintes questões: 1) como a floresta secundária responde à colheita de árvores em um curto espaço de tempo?; 2) como a área basal e a intensidade da colheita impactam a dinâmica da floresta após uma colheita de madeira?; e 3) como as espécies de interesse comercial respondem à colheita de árvores em comparação com a floresta como um todo?

No Capítulo 4, analiso o efeito pré- e pós-colheita sobre o crescimento e o incremento em uma floresta secundária. A hipótese é que a floresta responde rapidamente ao corte de

árvore com aceleração do crescimento e aumento do volume comercial em relação à área basal inicial e pós-colheita. As questões de pesquisa que embasam este capítulo são: 1) a colheita favorece o crescimento das árvores de espécies comerciais?; 2) como a exploração afeta o crescimento das árvores em relação à área basal inicial e remanescente da floresta e ao diâmetro das árvores?; e 3) quais grupos ecológicos de espécies e árvores de quais classes de diâmetro se beneficiam da colheita das árvores?

Na discussão geral (Capítulo 5), é apresentada a dinâmica da produtividade de madeira ao longo do processo de sucessão e o impacto da extração sobre a floresta e a produtividade de madeira de espécies típicas da floresta secundária. São relacionados os principais resultados e conclusões dos outros capítulos com o objetivo geral da tese, além de serem discutidas implicações silviculturais, perspectivas e viabilidade do manejo de espécies comerciais em florestas secundárias. Por fim, é discutido como os resultados da tese podem contribuir para o conhecimento atual sobre conservação e manejo da floresta secundária.

## **2 CAPÍTULO 2**

### **2.1 Timber stock recovery in a chronosequence of secondary forests in Southern Brazil: adding value to restored landscapes**

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Special Issue *Active restoration of timber production and other ecosystem services in secondary and degraded forests*

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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 to 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 (10x20 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  $155 \text{ m}^3.\text{ha}^{-1}$ . Trees of commercial species with  $\geq 15 \text{ cm}$  in diameter are first observed after 20 years of succession, while trees  $\geq 30 \text{ cm}$  are found at 30 years of succession and produce  $126 \text{ m}^3.\text{ha}^{-1}$  of stem volume. We highlight *Hyeronima alchorneoides*<sup>1</sup>, *Miconia cabucu*<sup>2</sup> and *Miconia cinnamomifolia*, as fast-growing dominant species that produce timber quality  $\geq 20 \text{ cm}$  in diameter after 20 years of succession, with volume reaching  $200 \text{ m}^3.\text{ha}^{-1}$  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.

**Keywords:** commercial tree species, timber quality, fast-growing, dominant species, wood-producing species

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<sup>1</sup> *Hieronyma alchorneoides* é o nome aceito, sendo *Hyeronima alchorneoides* a variante. Porém, na publicação deste artigo em 2021, *Hyeronima alchorneoides* ainda era o nome aceito. Fonte: Flora e Funga do Brasil (<http://floradobrasil.jbrj.gov.br/>).

<sup>2</sup> *Miconia formosa* é o nome aceito, sendo *Miconia cabucu* sinonímia botânica. Porém, na publicação deste artigo em 2021, *Miconia formosa* ainda era o nome aceito. Fonte: Flora e Funga do Brasil (<http://floradobrasil.jbrj.gov.br/>).

## 2.2 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; ONYEKWELU, 2011; BARRANCE; SCHRECKENBERG; GORDON, 2009; COOMES; BURT, 2001; GUARIGUATA, 1999a; MOSER et al., 2015). Secondary forests also provide ecosystem services, such as soil conservation, nutrient cycling, carbon sequestration and storage, and biodiversity conservation (CHAZDON, 2014; CHAZDON et al., 2009; MATOS et al., 2020; MUKUL; HERBOHN, 2016; SILVA JUNIOR 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 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 JUNIOR 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., 2016a). 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 over-logged forests (CERULLO; EDWARDS, 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, 1999a; MESQUITA, 2000). 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; 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; BELTRAME; KARAM, 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; COOMES; MILTNER, 2017; FANTINI et al., 2017; LIEBSCH; MARQUES; GOLDENBERG, 2008; LINTEMANI et al., 2020; PIOTTO et al., 2009; RIBEIRO FILHO et al., 2015; SIMINSKI et al., 2011; WOOD; RHEMTULLA; COOMES, 2017). Other studies have focused on the natural regeneration of secondary forests as a strategy to restore forest ecosystems (BRANCALION et al., 2019; CHAZDON; BRANCALION, 2019; CHAZDON; 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, 2019; FANTINI et al., 2019; OLIVEIRA et al., 2018; PIAZZA et al., 2017; 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; FINEGAN, 1992; GUARIGUATA, 1999a; MESQUITA, 2000). 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.

## 2.3 METHODOLOGY

### 2.3.1 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., 2013). 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; 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 (10x20 m), totaling 16,400 m<sup>2</sup> of sampling area (Table 2.1). 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* (Figure 2.1). In each plot, we measured all living trees, palms, and tree ferns with diameter at the breast height (dbh) ≥ 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).

Figure 2.1 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 nº 11.428/2006 (BRASIL, 2006); Klein's phytogeographic (SAR, 2005).

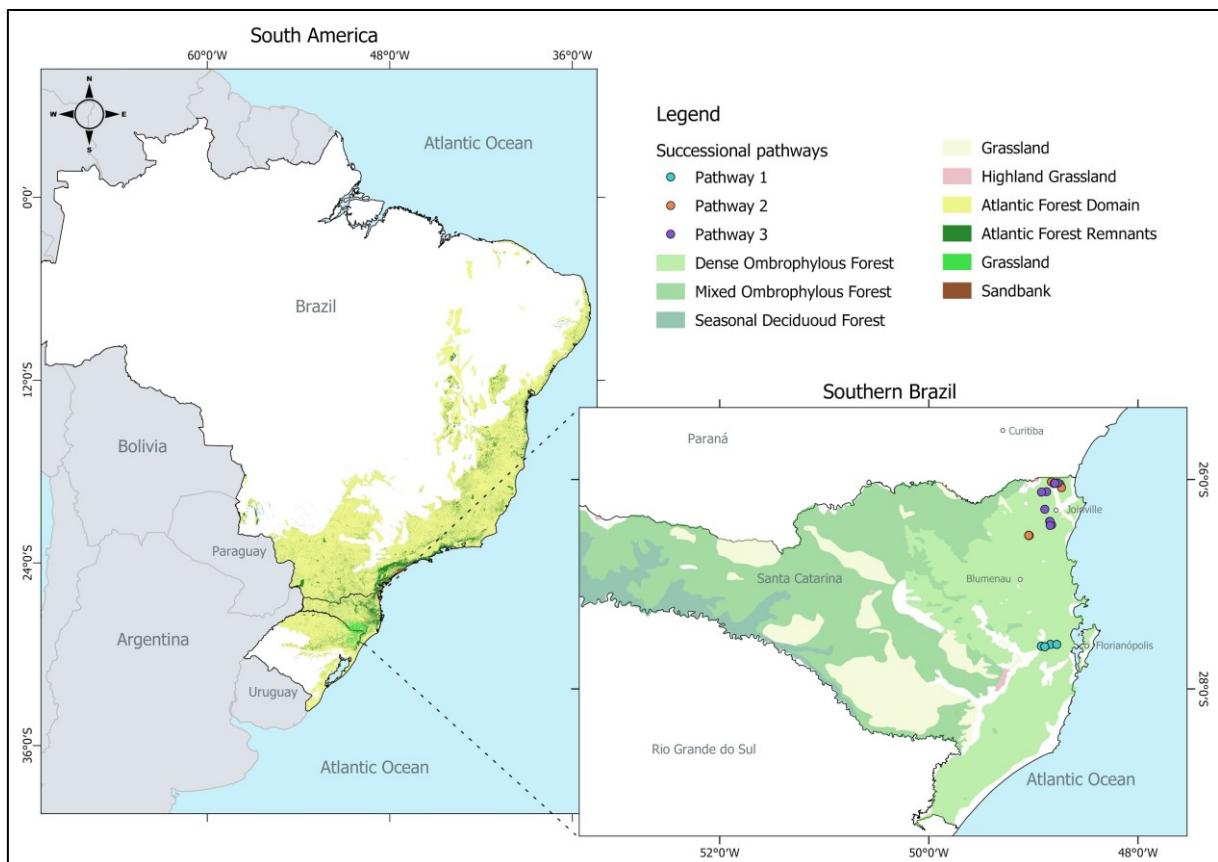


Table 2.1. Structure, volume, richness and species diversity in 82 plots of 200 m<sup>2</sup> in secondary forests of Dense Ombrophilous Forest in the Atlantic Forest, Brazil.

Parameter	Minimum	Maximum	Average	Stand. Dev.
Age (years)	2	50	--	--
DBH max	6.4	52.0	21.7	± 9.9
Density (stem.ha <sup>-1</sup> )	100	3550	1455	± 835
Basal area (m <sup>2</sup> .ha <sup>-1</sup> )	0.3	39.2	14.1	± 9.7
Tree volume (m <sup>3</sup> .ha <sup>-1</sup> )	0.7	265.5	99.7	± 77.6
Stem volume (m <sup>3</sup> .ha <sup>-1</sup> )	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	--	--

Species with potential timber use were classified into timber quality classes. To classify them, we used information from the literature (CARVALHO, 2006, 2010; CORADIN; SIMINSKI; REIS, 2011; REITZ; KLEIN; REIS, 1978; SCHUCH; SIMINSKI; FANTINI, 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 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<sup>-3</sup>. HQT species produce wood with medium durability and easy workability. This wood is used as beams, box board, joist wood, moulding, 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<sup>-3</sup>. 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<sup>-3</sup>. In most of our analyses, we also used the data on non-commercial species as these species may potentially be used for fuelwood.

### 2.3.2 DATA ANALYSES

For forest composition, we calculated species richness, Shannon's ( $H'$ ), and Simpson's (1-D) diversity for each plot (MÜELLER-DOMBOIS; 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., 2015), *BiodiversityR* (KINDT, 2020) and *fitoR* script (DALAGNOL et al., 2013) packages in RCore Team (R-CORETEAM; RCORE TEAM, 2019) and the Rstudio interface (RSTUDIO TEAM, 2019).

For forest structure, we calculated tree density (stems.ha<sup>-1</sup>), basal area (m<sup>2</sup>.ha<sup>-1</sup>), tree volume (m<sup>3</sup>.ha<sup>-1</sup>), and stem volume (m<sup>3</sup>.ha<sup>-1</sup>) for each plot. We used volumetric models adjusted for species of the Atlantic Forest (CORREIA; FANTINI; PIAZZA, 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<sup>3</sup>) 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; 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):  $y \sim 1 + (1|Pathway)$ . 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:  $y \sim Age + (1|Pathway)$ . For response variables analysed with categorical variable (dbh class, timber use and timber quality), we followed these structures: (i)  $y \sim Age + CVar + (1|Pathway)$  and (ii)  $y \sim Age + CVar + (1|Pathway/CVar)$ . 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 ( $\Delta AIC$ ) where we selected the model with the lowest  $\Delta AIC$ . The  $\Delta AIC$  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; 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).

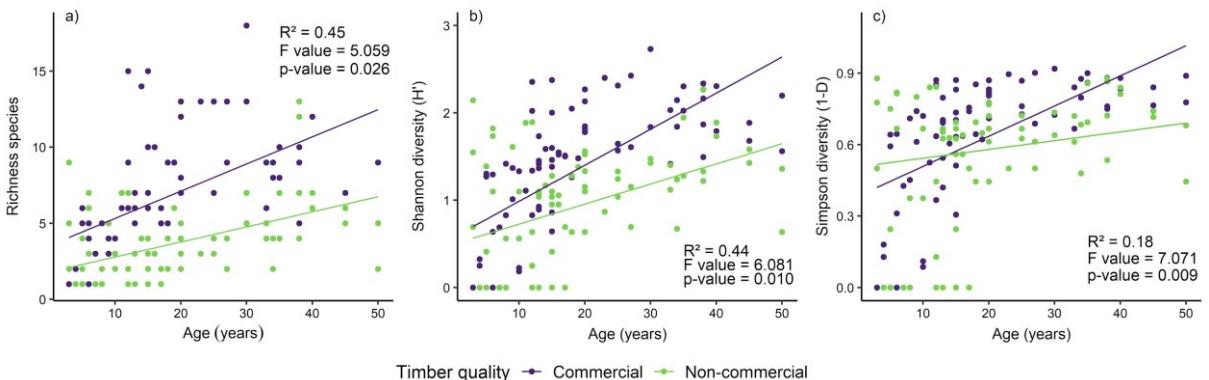
The analyses of linear mixed-effect models were performed with the *lme4* (BATES et al., 2019), *bbmle* (BOLKER, 2020), *lmerTest* (KUZNETSOVA; BROCKHOFF; CHRISTENSEN, 2017), *MuMIn* (BARTON, 2020) and *visreg* (BREHENY; BURCHETT, 2017) packages in RCore Team (R-CORETEAM; RCORE TEAM, 2019) and the Rstudio interface (RSTUDIO TEAM, 2019) (Appendix 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.

## 2.4 RESULTS

### 2.4.1 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, b, 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, A.3).

Figure 2.2 Richness species, as well as Shannon and Simpson diversity, of commercial and non-commercial species in secondary forests 2 to 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.

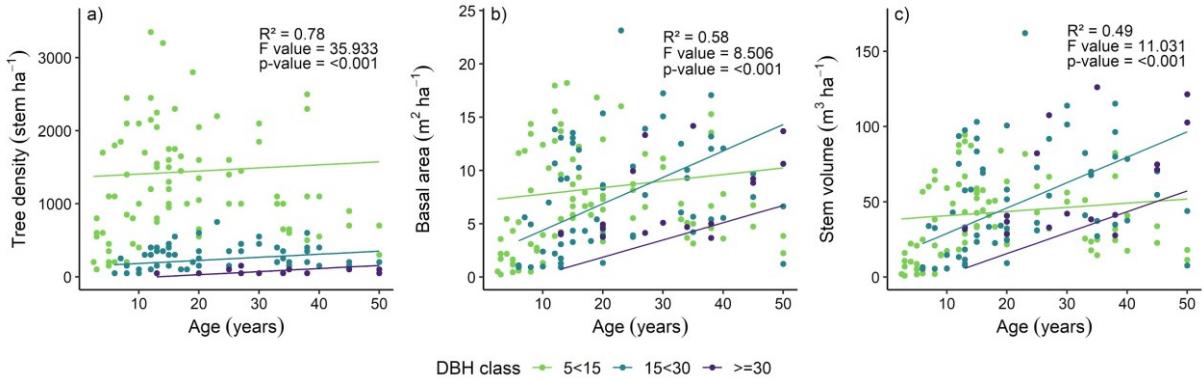


## 2.4.2 CHANGES IN FOREST STRUCTURE

Tree forest density ranged from 100 to 3,550 ind. $\text{ha}^{-1}$  through the chronosequence with an average of 1,455 ind. $\text{ha}^{-1}$  ( $\pm 835$  ind. $\text{ha}^{-1}$ ) (Figure 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  $\text{m}^2.\text{ha}^{-1}$ , with an average of 14.1  $\text{m}^2.\text{ha}^{-1}$  ( $\pm 9.7$   $\text{m}^2.\text{ha}^{-1}$ ) (Figure 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  $\text{m}^3.\text{ha}^{-1}$  (Figure A.1c). Stem volume followed the same trends as those of tree volume (Figure 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.

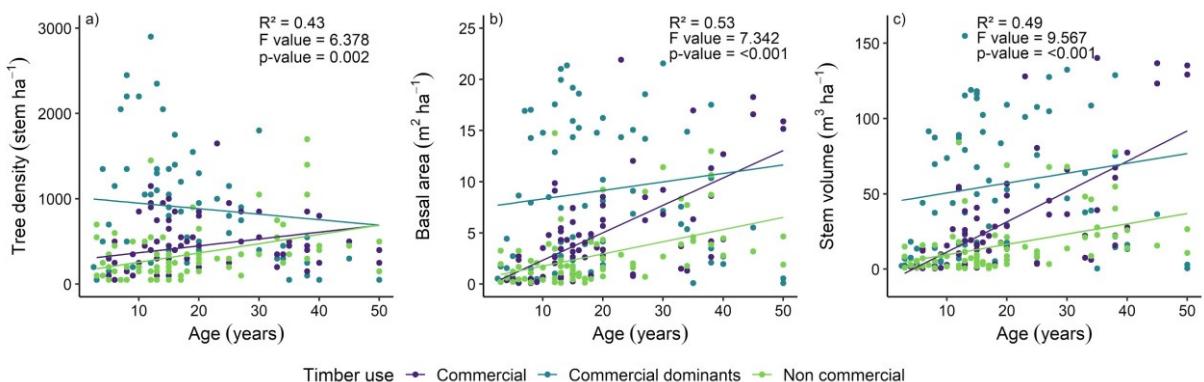
Small trees (dbh  $5 < 15$  cm) presented the highest density in young forests, but their number decreased with succession (Figure 2.3a). The mid-sized (dbh  $15 < 30$  cm) and largest trees (dbh  $\geq 30$  cm) appeared only after 5 and 13 years of succession, respectively. However, their contribution to the basal area increased fast (Figure 2.3b). The proportion of stem volume of the smaller trees remained stable throughout succession, while the volume of larger trees increased as the forests aged (Figure 2.3c). After 30 years of forest succession, the stem volume of trees  $\geq 30$  cm in diameter increased and reached 126  $\text{m}^3.\text{ha}^{-1}$ . The stem volume of small trees showed no correlation with forest age (Figure 2.3c), 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.

Figure 2.3 Contribution of different-sized trees (dbh) to forest structure and volume in secondary forests 2 to 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.



Commercial species showed higher density, basal area, and stem volume when compared to non-commercial species (Figure 2.4a, b, c). Among the 103 commercial species, 9 are considered dominant, which represents 75% of all dominant species (45% of the total IV) (Appendix 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  $140 \text{ m}^3 \cdot \text{ha}^{-1}$ , corresponding to 74% of the stem forest volume, while for dominant species, the stem volume was  $155 \text{ m}^3 \cdot \text{ha}^{-1}$  (Appendix Table A.3).

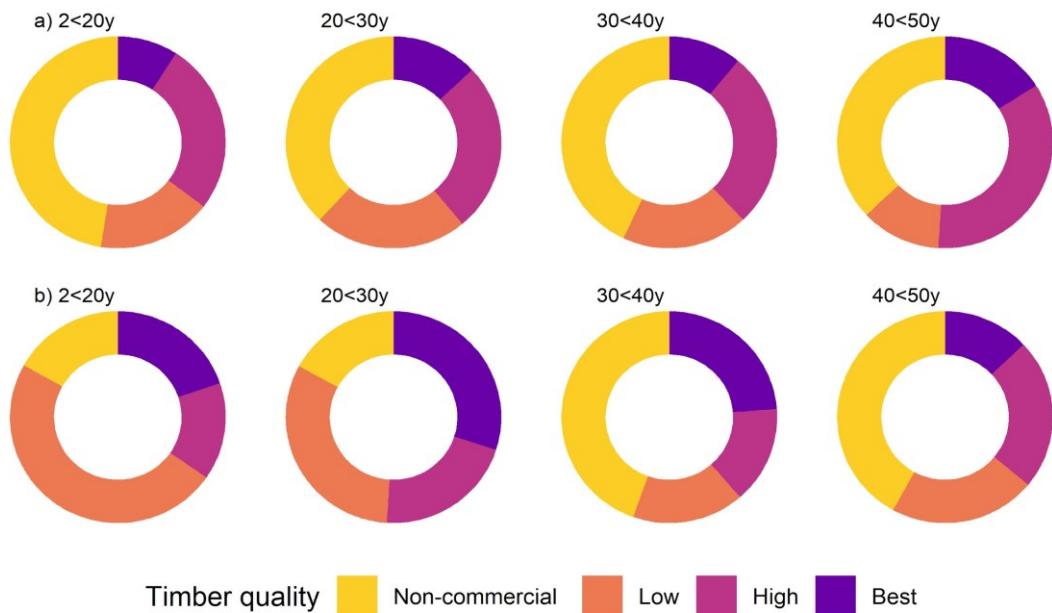
Figure 2.4 Contribution of commercial and non-commercial species to forest structure and volume in secondary forests 2 to 50 years old. We followed Finegan (1996) who identified dominant species as those representing 50% of total IV. Each dot represents the total values for the respective category in 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.



### 2.4.3 CHANGES IN VOLUME AND QUALITY OF TIMBER SPECIES

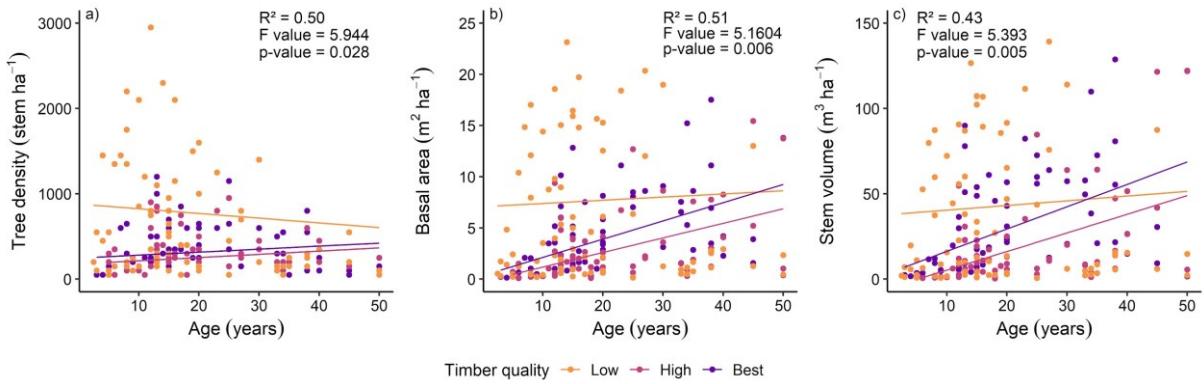
Overall, commercial species represented an important proportion of the forest tree diversity at all forest ages. The proportion of species by timber quality highlights a large number of species in the commercial category (low, high and best) with a proportion higher than 50% (Figure 2.5a). Even in young 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 (Figure 2.5b).

Figure 2.5 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.



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 (Figure 2.6a). The basal area increased with forest age with similar trends for the high- and best-quality timber species (Figure 2.6b). Stem volume increased along the chronosequence, mainly resulting from the contribution of high- and best-quality timber species (Figure 2.6c).

Figure 2.6 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.

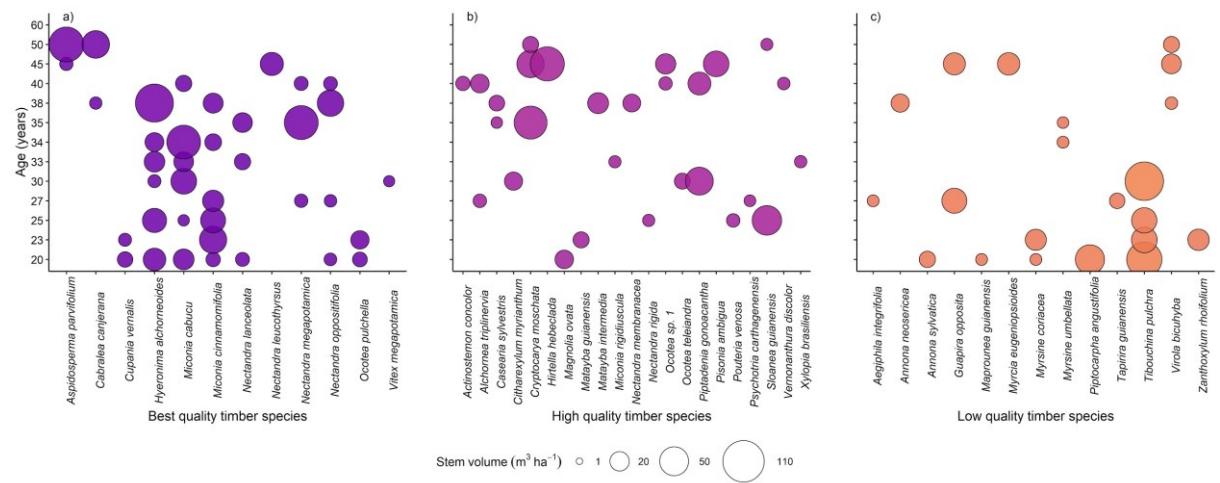


For tree species classified by timber quality (low, high and best), we found 17 best-quality timber species (Appendix Table A.2). Among them, 12 species presented trees with dbh over 15 cm, including *Aspidosperma parvifolium*, *Cabralea canjerana*, *Cupania vernalis*, *H. alchorneoides*, *M. cabucu*, *M. cinnamomifolia*, *Nectandra lanceolata*, *Nectandra leucothrysus*, *Nectandra megapotamica*, *Nectandra oppositifolia*, *Ocotea pulchella* and *Vitex megapotamica*. The trees in this category can reach over 40 cm in diameter (Appendix 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 (Appendix Table A.2). Among them, 21 species presented trees with a diameter over 15 cm. However, only six species presented trees with diameter  $\geq 30$  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 eugeniosioides*, *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  $\geq 30$  cm: *T. pulchra*, *G. opposita* and *P. angustifolia* (Appendix Table A.2, A.3).

Commercial species that produced trees with dbh  $\geq 15$  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 (Figure 2.7). Our results showed that fast-growing species may be being replaced by species of advanced successional

stages and do not have trees with dbh  $\geq 15$  cm. Among these fast-growing species is *T. pulchra* (low-quality), which showed the largest stem volumes for trees with dbh  $\geq 15$  cm in the early secondary forests (< 30 years of age), but in more advanced forests it did not show trees above 15 cm dbh (Figure 2.7c). 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 (Figure 2.7a).

Figure 2.7 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  $\geq 15$  cm). Each bubble represents the stem volume of a given species in a single plot.



## 2.5 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 (Figure 2.4) and productivity of high- and best-quality timber species (Figure 2.6). 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  $\geq 30$  cm and more than  $0.75\text{ m}^3$  of round wood.

### 2.5.1 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  $\geq 5$  cm (Figure 2.4), 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 (CHAZDON et al., 2007; PEÑA-CLAROS, 2003; PIOTTO et al., 2009; VAN BREUGEL; BONGERS; MARTINEZ-RARNOS, 2007). 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 (Figure 2.5a). 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  $\geq 30$  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 (Appendix 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 (Figure 2.4b, c). This rapid structural increase in the early stages has also been observed in other tropical forest studies (GUARIGUATA; OSTERTAG, 2001; PEÑA-CLAROS, 2003; POORTER et al., 2016; ROCHA; VIEIRA; SIMON, 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  $\geq$  15 cm in diameter increased in density, basal area and stem volume (Figure 2.3). 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  $245 \text{ m}^3.\text{ha}^{-1}$ . 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 forests, the timber volume reached  $444 \text{ m}^3.\text{ha}^{-1}$  with the presence of *Alchornea triplinervia*, *H. alchorneoides*, *Ocotea* spp. and *Nectandra* spp. (TABARELLI; 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; SIMINSKI, 2016). Remaining unharvested, as it is mandated by current regulations in the Atlantic Forest region, implies an opportunity cost to the landowner.

## 2.5.2 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 (Figure 2.6a). 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; VIEIRA; SIMON, 2016; RODRIGUES; MARTINS; DE BARROS, 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  $200 \text{ m}^3.\text{ha}^{-1}$  before 40 years of succession (Figure 2.7c). *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.

## 2.5.3 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., 2016b; CROUZEILLES et al., 2017, 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., 2021; 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, 1999a; HUTH; KAMMESHEIDT; KO, 2002; PIOTTO et al., 2020; ROZENDAAL; SOLIZ-GAMBOA; ZUIDEMA, 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; 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, 1999a; 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; GOLDENBERG; MARQUES, 2007; LIEBSCH; MARQUES; GOLDENBERG, 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; COATES; MESSIER, 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.

## 2.6 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.

### **3 CAPÍTULO 3**

#### **3.1 The effect of the tree harvesting on secondary forest dynamics in the Brazilian Atlantic Forest**

##### **ABSTRACT**

Secondary forests can secure timber products and help to expand forest areas to promote biodiversity conservation. This study aimed to understand the impact of a timber harvest on tree diversity, structure, and demographic rates in a mid-succession secondary forest located at the Southern Brazilian Atlantic Forest. We inventoried 12 plots (40x40 m) in the year 2009 and 15 plots was inventoried in the years 2014 and 2021, resulting in two measurements before (2009-2014) and two after harvest (2014-2021). Our results showed that the forest responds rapidly to the intervention. For individuals larger than 5 cm in dbh, commercial species were prevalent in the composition of species (45%) and richness species increased over time before and after harvest. A group of a few species were dominant (16 species) and commercial species were the most representative among them (11 species), especially *H. alchorneoides*, which reached 12%. After harvest there was a rapid recovery in the density of individuals, a result of a high recruitment rate. The same occurred for basal area and commercial volume. Commercial species, however, recovered at lower rates in the first seven years after harvest. Both recruitment and mortality rates were affected by the basal area remaining from harvesting. The recruitment rate exceeded the mortality rate for the whole forest, both before and after harvest. However, for commercial species, the mortality rate exceeded the recruitment rate for individuals above 5 cm of diameter after harvest. The remaining basal area was a major determinant of the changes that occurred after harvest. Our results show that secondary forests respond rapidly to a selective tree logging and commercial species benefit from the disturbance generated. Richness, diversity, density, and commercial volume recover rapidly after disturbance and are influenced by basal area. Commercial species respond more slowly but benefit from the tree harvest and can replenish the timber stock. The predominance of fast-growing species favours the recovery of timber productivity.

**Keywords:** selective tree logging; timber products; forest structure; demographic rate

### **3.2 INTRODUCTION**

Secondary forests have been viewed as ecologically impoverished formations, with low or almost no potential to produce valuable quality timber with attractive productivity (BROWN et al., 2020; MERTZ et al., 2021). Much of this view is skewed by comparisons of these naturally regenerating forests, regenerated after land use or intense degradation, with the original mature forests (LENNOX et al., 2018; MERTZ et al., 2021; PAIN et al., 2021). However, in recent decades, secondary forests have been recognized as an important component of land cover in tropical areas (BASHAM et al., 2016; LETCHER; CHAZDON, 2009; MATOS et al., 2020). Proper management of secondary forest can reduce pressure on primary forests through their productive potential for timber and non-timber products (SEARS et al., 2021). Secondary forest are an integral part of the dynamic landscape (EMRICH; SEPP; POKORNY, 2000; NGO BIENG et al., 2021) with high biodiversity and timber productivity, they also make a significant contribution to carbon sequestration and other ecosystem services (CHAZDON et al., 2009, 2016; GILROY et al., 2014; MATOS et al., 2020).

The low priority of secondary forests on political agendas relating to global climate, forestry, and agriculture is reflected in their almost invisible presence in scientific research (ARNOLD et al., 2011; PAIN et al., 2021; TSCHARNTKE et al., 2012). However, scientific advances have brought secondary forest ecology and strategy to restore forest ecosystems to the fore, especially in the tropics. It is important to understand the impact of tree harvesting on timber productivity and the factors that influence it. Unlike mature forests where many commercial species occur with low tree density, secondary forests are dominated by a few species with a high density of individuals (LASKA, 1997). Some of these species are fast growing and produce quality timber and the focus of some research is just on dominant species of fast-growing that are responsible for timber productivity in mid-secondary forests (ZAMBIAZI et al., 2021). However, there is still little research that analyses the impact of logging in secondary forests.

In the global south, secondary forests predominantly exist on small and medium-sized farms, serving as vital resources for people's livelihoods (FANTINI; SIMINSKI, 2016; PAIN et al., 2021). These forests play a significant role in securing timber, expanding forest areas, and contributing to both productive endeavours and the conservation of biodiversity. Management practices in tropical areas provide benefits to smallholders. However, financial incentives for these forests to be conserved and remain in the landscape as productive forests

are lacking (PAIN et al., 2021). In addition, we need to understand how to manage the complexity of the forest landscape, which is a mosaic of secondary forests of different ages, types, and degrees of stability and instability.

The management of this complex dynamic system that are the secondary forests, requires a deeper look into the effects that the harvest of trees cause on floristic composition and forest structure. The complexity of secondary forests in form and type may determine the management system applied and the different responses that the forest will have to the degree of disturbance generated (FINEGAN, 1992; GUARIGUATA, 1999b; PUETTMANN; COATES; MESSIER, 2009; PUTZ, 1994; SIST; FERREIRA, 2007). Changes in species richness, density, basal area, timber volume, recruitment and mortality are ways of qualifying and quantifying these effects. To keep these forests productive, it is important to promote the maintenance and regeneration of timber-producing species.

Forests with trees of different ages and sizes are typically regenerated naturally, without any silvicultural intervention, giving rise to what is known as secondary forests. Selective logging will have different effects on the forest depending on the successional stage and intensity of logging. To understand how the forest responds to this disturbance, selective logging of trees of species characteristic of secondary forests and producers of commercial timber was carried out with different intensities in a secondary forest at mid-successional stage. At 40 years of age, this forest showed dominance of fast-growing species and trees of adequate size to be harvested and sectioned in sawmills. These characteristics of secondary forest are favourable to management and make these areas promising suppliers of timber. However, management techniques and silvicultural practices adopted in the early stages of succession can accelerate the growth of timber-producing trees and provide timber in less time and with shorter cutting cycles.

Our study aims to analyse the effect of tree harvesting on tree diversity, structure, and demographic rates in a mid-succession secondary forest. We asked (i) how do secondary forests respond to tree harvesting in a short time? (ii) how do reduced of basal area and harvesting intensity impact the dynamics of the forest after harvesting? (iii) How do commercial species respond to tree harvesting compared to the whole forest? In this study, we analysed a secondary forest during pre- and post-harvest periods at different harvesting intensity as measured by the basal area reduction. We expect that the forest responds rapidly to logging and that this response

is related to the post-logging basal area. We also expect that the forest will promote the recovery of the harvested timber volume in response to tree harvesting.

### 3.3 METHODOLOGY

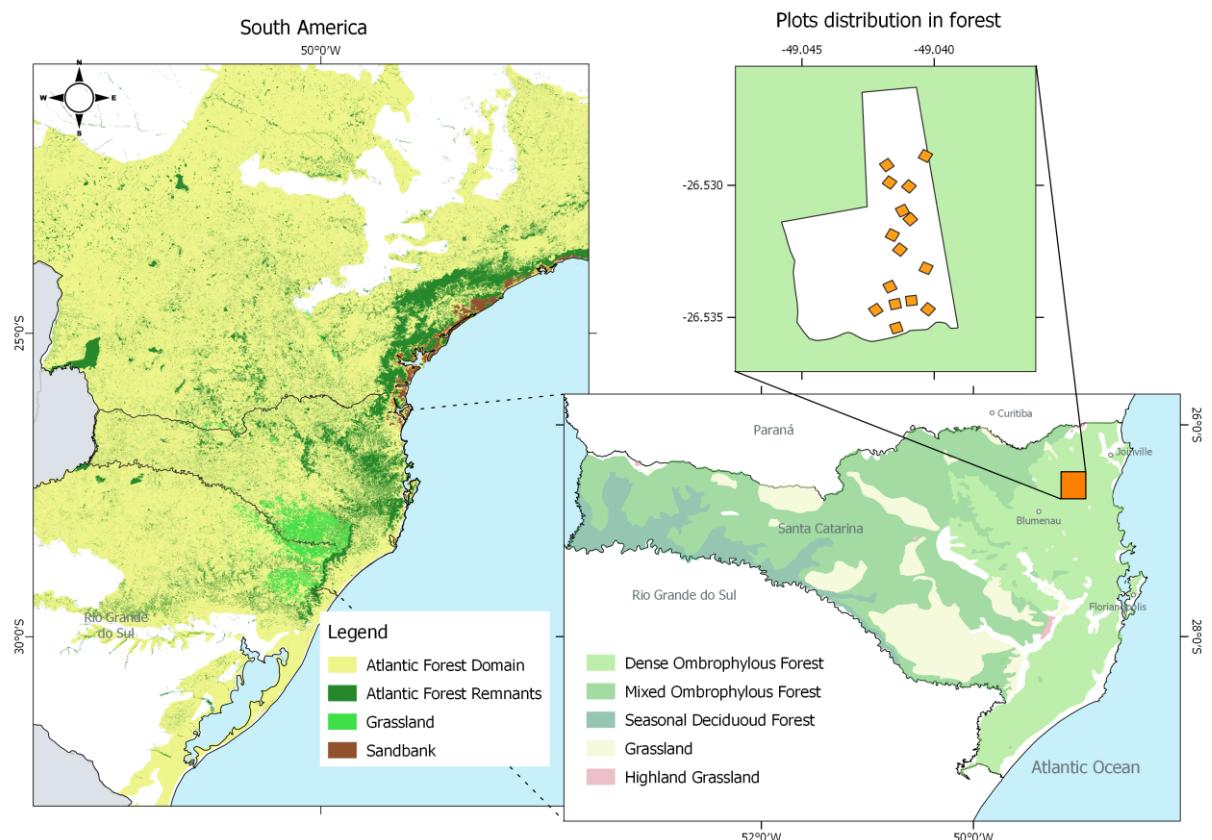
#### 3.3.1 STUDY AREA AND DATA

The study was conducted between 2009 and 2021 in a secondary forest located in the Southern Atlantic coast of Brazil ( $26^{\circ}32'01''S$  e  $49^{\circ}02'30''W$ ). Climate in the regions is humid subtropical with hot summers (Cfa), with an average temperature of  $20.7^{\circ}C$  and annual precipitation of 1,800 mm (Alvares et al., 2013). Elevation of the study site ranges from 600 m a.s.l. and slopes are mostly steep, up to 40% (ALVARES et al., 2013; MORELLATO; HADDAD, 2000). Soils are predominantly Red Yellow Podzolic (mainly Ultisols).

The region was originally covered by the Brazilian Atlantic Forest, (Dense Ombrophilous Forest - DOF), characteristically with an evergreen canopy and abundance of epiphytes and palm trees (GASPER et al., 2014; SIMINSKI et al., 2011; VIBRANS et al., 2013). Present day landscapes in the region are composed of a mosaic of secondary and mature forests, monocultures of *Eucalyptus* and *Pinus* species, agricultural fields, pastures and urban areas (VIBRANS et al., 2012). Secondary forests in the region regenerated mostly after the abandonment of crop fields cultivated under swidden-fallow agriculture (ZAMBIAZI et al., 2021). Dominant species include *Alchornea triplinervia*, *Alsophila setosa*, *Hieronyma alchorneoides*, *Annona neosericea*, *Cyathea phalerata*, *Euterpe edulis*, *Cabralea canjerana*, *Miconia cinnamomifolia*, among others (OLIVEIRA et al., 2022; VIBRANS et al., 2013).

The study site was set in 2009 when the forest had 41-year-old secondary forest. The study site is a 26-ha forest, but it is part of a large tract of forest land ( $> 5,000$  ha) that is mainly covered by successional forests. The forest here studied was enriched with seedlings of *Hieronyma alchorneoides*, *Miconia cinnamomifolia* and *Nectandra* spp. at the beginning of succession and weeded during the following five years. Permanent plots were installed, each of them with a total area of 60 x 60 m and a core area of 40 x 40 m used for data collection (Figure 3.1). 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 and HBR (Barbosa Rodrigues Herbarium). The species were classified according to the Angiosperm Phylogeny Website, version 14 (STEVENS, 2017), and Species 2000 & IT IS Catalogue of Life (ROSKOV et al., 2019) and Brazil Flora Group (2021).

Figure 3.1 Map of the original forest and remnants of the Brazilian Atlantic Forest in Brazil (left), indicating the forest types in Santa Catarina state. The location of the secondary forest inventoried is provided in the detailed map. Source: <http://mapas.sosma.org.br/> (SOS Mata Atlântica, 2020); Area under the jurisdiction of the Law n° 11.428/2006 (BRASIL, 2006); Klein's phytogeographic (SAR, 2005).



For this study, 12 plots were inventoried in the year 2009 and another three plots were added in 2014, with a total of 15 plots and with a total sampling area of 24,000 m<sup>2</sup>. After the second inventory (2014), the forest was harvested for timber production, the plots were updated in 2014 and reinvented in 2021. Tree selection aimed at combining the purposes of harvesting commercial species (for revenue) and non-commercial species (for stand improvement). The forest basal area reduction was randomly assigned to each plot to simulate different harvesting intensities, in addition to three unharvested plots, assigned as control plots.

### 3.3.2 DATA ANALYSIS

We analysed the structure and the dynamics of the forest before and after harvesting. The effect of harvesting was analysed on the basis of the remaining basal area of each plot after logging (m<sup>2</sup>.ha<sup>-1</sup>) as well as the harvesting intensity (the % of the initial basal area of each plot removed at harvest). We considered two periods of forest growth: (i) pre-harvest - from 2009 to 2014; and (ii) post-harvest - from 2014 to 2021. For forest structure, we calculated tree

density (stems.ha<sup>-1</sup>) and commercial volume (m<sup>3</sup>.ha<sup>-1</sup>) for each plot. We used volumetric models adjusted for species of the Atlantic Forest (CORREIA; FANTINI; PIAZZA, 2017; OLIVEIRA et al., 2018) to estimate stem volume (StemV) of each individual, including palm trees and tree ferns. StemV represents the commercial volume (m<sup>3</sup>) of the stem from the ground level to the commercial height (i.e., up to the point of the first stem fork) of the individual. For *Hieronyma alchorneoides*, a specific model (OLIVEIRA et al., 2018) was used because of the importance of this species for forest structure and management. Both models were developed in the same study site.

The dynamics of the forest was analysed by demographic rates. The recruitment rate ( $r$ ) was calculated by using the Sheil and May (1996) equation:

$$r = 1 - (1 - n_r/N_t)^{\frac{1}{t}};$$

where  $n_r$  is the number of recruited individuals,  $N_t$  is the number of stems present at the last measurement (in this case, 2014 pre-harvest and 2021 post-harvest), and  $t$  is the time interval between two measurements (2009-2014 and 2014-2021).

Mortality rate was calculated using the equation of Sheil, Burslem and Alder (2008):

$$m = 1 - (1 - (N_0 - m)/N_0)^{\frac{1}{t}};$$

where  $N_0$  is the number of stems at the beginning and  $m$  is the number of dead individuals. This mortality rate is derived from an exponential model of population decline and assumes a constant probability during the time interval  $t$ .

We calculated species richness, Shannon's (H'), and Simpson's (1-D) diversity (MÜLLER-DOMBOIS; ELLENBERG, 1974) of each plot for each inventory date, for the bulk of the whole forest as well as for the subset of commercial species. The importance value (IV) of each species, the sum of its relative density, relative dominance, and relative frequency, was also calculated. IV index was used to determine the group of dominant species, defined as the set of species with highest IV whose accumulated value was 50% of the total value (FINEGAN, 1996). Species richness, species diversity and IV metrics were estimated using the vegan (OKSANEN et al., 2015), *BiodiversityR* (KINDT; COE, 2005) and *fitoR* script (DALAGNOL et al., 2013) packages in RCore Team (RCORE TEAM, 2019) and the Rstudio interface (RSTUDIO TEAM, 2019).

We used linear mixed effect models for the analysis. The model for each response variable followed the structures: (i) basal area (BA) as fixed effect; and (ii) harvesting intensity (HarInt) and growth period (GrowP) as mixed effects. For each response variable, we first adjusted a model with fixed effect only for each response variable, using generalised least squares (GELMAN; HILL, 2007). When necessary, we transformed values that did not show normality using the Shapiro Wilk test, using square root transformation. Next, we fitted a model containing the three variables ( $X_i \sim BA + HarInt + GrowP$ ) with four combinations for mixed effects: (i)  $(1+HarInt|GrowP)$ ; (ii)  $(HarInt-1|GrowP)$ ; (iii)  $(1|GrowP/HarInt)$ ; and (iv)  $(1|GrowP)$ . The models were fitted with and without interaction among fixed effects. For model selection we used the backward stepwise selection with the model that contained all variables and removing the least significant variable one by one until the model with the significant variables. After these steps, we selected, among the models with significant variables, the best performance model for each response variable, the one with the lowest delta-Akaike Information Criterion ( $\Delta AIC$ ). The  $\Delta AIC$  is the result of the differences among the AIC of the models fitted for each variable (Appendix Table A.1). To explain the proportional of total variance on both fixed and random effects we used the  $R^2$  conditional for each model selected (Appendix Table A.1). After selecting the best model for each variable, the results were plotted with  $R^2$  and  $p$ -value.

The analyses of linear mixed-effect models were performed with the *lme4* (BATES et al., 2019), *bbmle* (BOLKER, 2020), *lmerTest* (KUZNETSOVA; BROCKHOFF; CHRISTENSEN, 2017) and *MuMIn* (BARTON, 2020) packages in RCore Team (R-CORETEAM; RCORE TEAM, 2019) and the RStudio interface (RSTUDIO TEAM, 2019). In the resulting plots, lines were fitted to each variable using the predictors of the chosen model, and the *ggplot2* (WICKHAM, 2009) and *cowplot* (WILKE, 2019) packages were used.

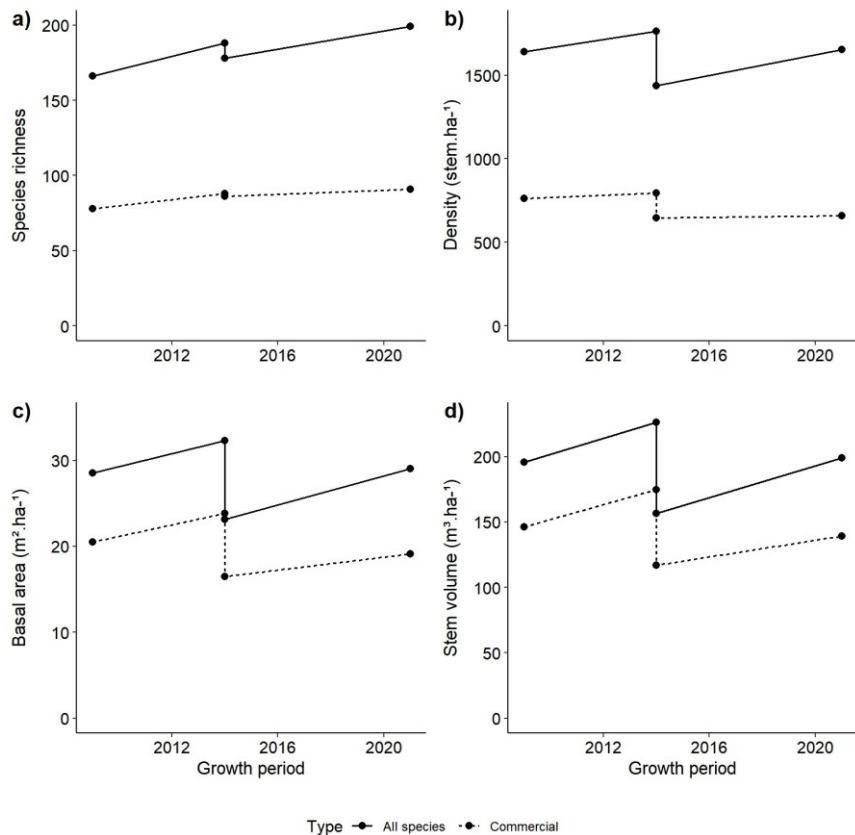
## 3.4 RESULTS

### 3.4.1 FOREST DYNAMICS BEFORE AND AFTER HARVEST

#### *Richness and floristic composition*

Along the 12 years of forest inventories, we measured a total of 6,095 trees, palms, and tree ferns, distributed among 220 species (Appendix Table A.2). Among all species, 99 (45%) presented commercial value, while 121 (55%) were non-commercial. Before harvesting, from 2009 to 2014, the average species richness increased from 166 to 188 species (Figure 3.2a). By 2014, the mean richness of commercial species per year (88 species) represented 47% of the total (Figure 3.2a). In that year, trees of 52 commercial species were harvested. The harvesting of trees removed 10 species (trees with dbh  $\geq$  5 cm), representing 5% of the forest richness, and seven years after harvest, another 10 species were not found in the plots inventoried. However, during the seven years of the post-harvest period, richness (whole forest) increased, from 178 to 199 species. Among the 21 entered species, 11 were classified as commercial species. The same pattern was observed for the commercial species richness: an increase from 86 to 91 species. During the post-harvest period, the number of new species of recruited trees varied from 2 to 20 species across plots, 1 to 10 new species considering only the commercial species. On the other hand, the floristic composition lost 20 species after the logging, 3 to 7 species per plot. Along the 12 years of the inventories, 55 entered species were observed while 22 species were no longer recorded.

Figure 3.2 Species richness, tree density ( $\text{stem} \cdot \text{ha}^{-1}$ ), basal area ( $\text{m}^2 \cdot \text{ha}^{-1}$ ) and commercial volume ( $\text{m}^3 \cdot \text{ha}^{-1}$ ) of a secondary forest in the Southern Atlantic Forest, Brazil, during a growth period before (5 years) and after (7 years) a tree harvesting, with highlights for commercial species. The vertical lines represent instantaneous decrease of the variables caused by a selective logging.



The secondary forest showed a small group of dominant species. During the period of 12 years, the species with highest importance value (IV) remained constant, even after the tree harvesting (Appendix Table 3.1). Among the 19 species with highest IV, 11 were commercial species: *Hieronyma alchorneoides*, *Miconia cinnamomifolia*, *Annona neosericea*, *Virola bicuhyba*, *Nectandra membranacea*, *Cabralea canjerana*, *Alchornea triplinervia*, *Cupania oblongifolia*, *Matayba intermedia*, *Casearia sylvestris* e *Guapira opposita* (Appendix Table 3.1). Together, these species accounted for 30% of the total IV in the periods pre- and 29% post-harvest. After logging, *G. opposita* appeared among those commercial species with the highest IV, reaching 1.8% of the total value (Appendix Table 3.1). For species non-commercial, *Euterpe edulis*, a palm tree that produces non-timber products, showed the highest IV in all inventories, reaching 11% of the total IV. *Cecropia glaziovii*, still an underused species in the region, showed a high IV (4% of the total IV), replacing species with lower IV such as *Casearia obliqua* and *C. sylvestris* 7 years after logging (Appendix Table 3.1). In the period after tree

logging, the abundance of *C. glaziovii* increased from 4 to 101 stems.ha<sup>-1</sup>. *E. edulis* became the species with highest IV in the forest, followed by *H. alchorneoides* (10%). The high dominance of *E. edulis* is a result of its abundance, from 219 to 343 stems.ha<sup>-1</sup>.

Table 3.1 Species with highest importance values (IV) between 2009 and 2021. The species listed within each forest type accumulate IV up to 50% (from a base of 100), C - commercial species.

Ecological group	Species	Importance Value (%) <sup>1</sup>			
		pre-harvest		post-harvest	
		2009	2014	Harvest point	7y
Pioneer	<i>Annona neosericea</i> (C)	2.70	2.89	3.00	2.61
	<i>Cecropia glaziovii</i>	--	--	--	4.13
Early secondary	<i>Hieronyma alchorneoides</i> (C)	12.15	11.02	11.41	9.75
	<i>Miconia cinnamomifolia</i> (C)	3.70	2.87	1.83	1.48
	<i>Bathysa australis</i>	2.78	2.46	2.72	2.28
	<i>Nectandra membranacea</i> (C)	2.06	2.05	--	--
	<i>Alchornea triplinervia</i> (C)	2.03	2.35	2.32	2.09
	<i>Casearia obliqua</i>	1.85	1.79	1.64	--
	<i>Cupania oblongifolia</i> (C)	1.81	1.74	1.82	1.72
	<i>Matayba intermedia</i> (C)	1.74	--	--	--
	<i>Casearia sylvestris</i> (C)	1.53	1.81	1.83	--
	<i>Guapira opposita</i> (C)	--	--	1.82	1.92
Late secondary	<i>Euterpe edulis</i>	5.24	6.49	7.24	10.70
	<i>Virola bicuhyba</i> (C)	2.48	2.24	2.02	2.19
	<i>Cabralea canjerana</i> (C)	2.05	2.54	2.83	2.61
Climax	<i>Cyathea</i> sp.	4.45	3.76	3.71	2.74
	<i>Psychotria nuda</i>	2.41	2.75	2.85	2.92
	<i>Allophylus petiolatus</i>	1.48	1.84	1.91	1.48
	<i>Psychotria suterela</i>	--	1.90	1.90	1.65
Sum of IV		50.46	50.50	50.76	50.27
Number of species		16	16	16	15

<sup>1</sup>The species ranking is defined as those species whose summed importance values, when ranked from the highest to lowest, contained 50% of the total for a given stand (Finegan, 1996).

### *Tree density and forest structural*

During the growth period before the harvesting, from 2009 to 2014, the average forest density increased from 1642 to 1765 trees per hectare (Figure 3.2b). In 5 years before harvest, 222 dead trees per hectare were recorded, while 395 trees were recruited. The density of commercial species in 2014 ( $796 \text{ trees.ha}^{-1}$ ) represented 45% of the entire forest (Figure 3.2b), varying across plots from 37% to 57%.

In 2014,  $328 \text{ trees.ha}^{-1}$  were harvested, on average, representing 19% of the forest density. A total of trees were harvested from the forest, belonging to 52 commercial species. *H. alchorneoides* was the species with the highest number of harvested trees ( $28 \text{ trees.ha}^{-1}$ , on average), followed by *M. cinnamomifolia* ( $14 \text{ trees.ha}^{-1}$ ). The post-harvest density of commercial species increased slowly during the following seven years ( $148 \text{ stems.ha}^{-1}$ ), while density of non-commercial species increased at a higher rate ( $457 \text{ trees.ha}^{-1}$ ). In this period, the mortality of trees was  $390 \text{ trees.ha}^{-1}$ , while  $605 \text{ new trees.ha}^{-1}$  were recruited.

During the 41 years of forest succession, commercial species increased  $0.50 \text{ m}^2.\text{ha}^{-1}$  per year, superior than the rate observed for non-commercial species ( $0.20 \text{ m}^2.\text{ha}^{-1}$  per year). In the five years before harvesting, the forest grew  $0.66 \text{ m}^2.\text{ha}^{-1}$  per year. Among the 10 species with the greatest increase in basal area, 9 were commercial species, notably *H. alchorneoides*, *A. triplinervia*, *A. neosericea*, *C. canjerana* and *C. fissilis*. During the pre-harvest period, the palm tree *Euterpe edulis* showed the highest basal area growth rate ( $0.58 \text{ m}^2.\text{ha}^{-1}$ ), followed by *Allophylus petiolulatus* ( $0.20 \text{ m}^2.\text{ha}^{-1}$ ). The harvesting in 2014 removed an average of  $9.2 \text{ m}^2.\text{ha}^{-1}$  of the forest basal area, equivalent to 28% of its original value (Figure 3.2c). The harvesting intensities across plots varied from 18 to 56% of the existing basal area in 2014. Out of the total basal area harvested ( $9.2 \text{ m}^2.\text{ha}^{-1}$ ), 79% were of commercial species; three of them were added up 48% of the logged basal area: *H. alchorneoides*, *M. cinnamomifolia* and *N. membranacea*.

During the post-harvest period, the basal area increased  $5.9 \text{ m}^2.\text{ha}^{-1}$  on average, with stocks at 2021 between from  $19.8 \text{ m}^2.\text{ha}^{-1}$  to  $41.5 \text{ m}^2.\text{ha}^{-1}$ , exceeding those observed in 2009 (from  $18.9 \text{ m}^2.\text{ha}^{-1}$  to  $36.7 \text{ m}^2.\text{ha}^{-1}$ ). Of the total basal area,  $7.3 \text{ m}^2.\text{ha}^{-1}$  was represented by commercial species, equivalent to 79% of the basal area removed. The reduction of basal area of commercial species ranged from  $3.9 \text{ m}^2.\text{ha}^{-1}$  to  $19.4 \text{ m}^2.\text{ha}^{-1}$ . The bulk of commercial species increased their basal area by  $2.6 \text{ m}^2$  per hectare after harvest, which represented only 36% of the total removed during the harvest. Although the recovery of basal area of commercial species was slow after the

harvesting, they represented 44% of the total regrowth in this period. Among the 88 commercial species present in the forest at the harvest time, 52 species had trees harvested.

#### *Commercial volume*

During the period before harvesting, from 2009 to 2014, the commercial volume in the forest increased from 195.8 to 226.4 m<sup>3</sup> per hectare (Figure 3.2d). In 41 years of fallow, the forest increased the commercial volume by 4.8 m<sup>3</sup>.ha<sup>-1</sup> per year, of which 3.6 m<sup>3</sup>.ha<sup>-1</sup> per year from commercial species. During the five years of measurements before harvesting, the increment of commercial species showed high values, reaching 5.6 m<sup>3</sup>.ha<sup>-1</sup> per year, on average. The nine commercial species with highest dominance had a volume increase ranging from 2 to 14 m<sup>3</sup>.ha<sup>-1</sup>. *H. alchorneoides* showed the highest commercial volume increment (14 m<sup>3</sup>.ha<sup>-1</sup>), exceeding the increment of all non-commercial species in the same period (12 m<sup>3</sup>.ha<sup>-1</sup>), and was followed by *A. triplinervia* with 4.5 m<sup>3</sup>.ha<sup>-1</sup>. During the five years of growth before harvest, commercial species had a total increment of commercial volume of 31 m<sup>3</sup>.ha<sup>-1</sup>.

Of the total volume observed in 2014, an average of 69.7 m<sup>3</sup>.ha<sup>-1</sup> were removed by the harvesting, 83% of which from commercial species (57.7 m<sup>3</sup>.ha<sup>-1</sup>). During the seven years of the growth period after the harvesting, the overall commercial volume of the forest increased 42.8 m<sup>3</sup>.ha<sup>-1</sup>, representing a recovery equivalent to 61% of the volume harvested. Commercial species increase by 22.4 m<sup>3</sup>.ha<sup>-1</sup> in this period. Of the forest growth, commercial species represent an increase of 32.1% in commercial volume. In the period of seven years, the average was 3.1 m<sup>3</sup>.ha<sup>-1</sup> per year. Non-commercial species, on the other hand, showed an annual increment rate 2.9 m<sup>3</sup>.ha<sup>-1</sup>. Among the 52 commercial species harvested, three species presented a high importance in the forest structure and stock of timber (48% of the basal area and commercial volume): *H. alchorneoides* (1.9 m<sup>2</sup>.ha<sup>-1</sup>; 15.3 m<sup>3</sup>.ha<sup>-1</sup>, respectively), *M. cinnamomifolia* (1.1 m<sup>2</sup>.ha<sup>-1</sup>; 8.6 m<sup>3</sup>.ha<sup>-1</sup>) and *N. membranacea* (0.5 m<sup>2</sup>.ha<sup>-1</sup>; 4.11 m<sup>3</sup>.ha<sup>-1</sup>).

#### 3.4.2 HARVESTING AS DRIVER OF FOREST DYNAMICS

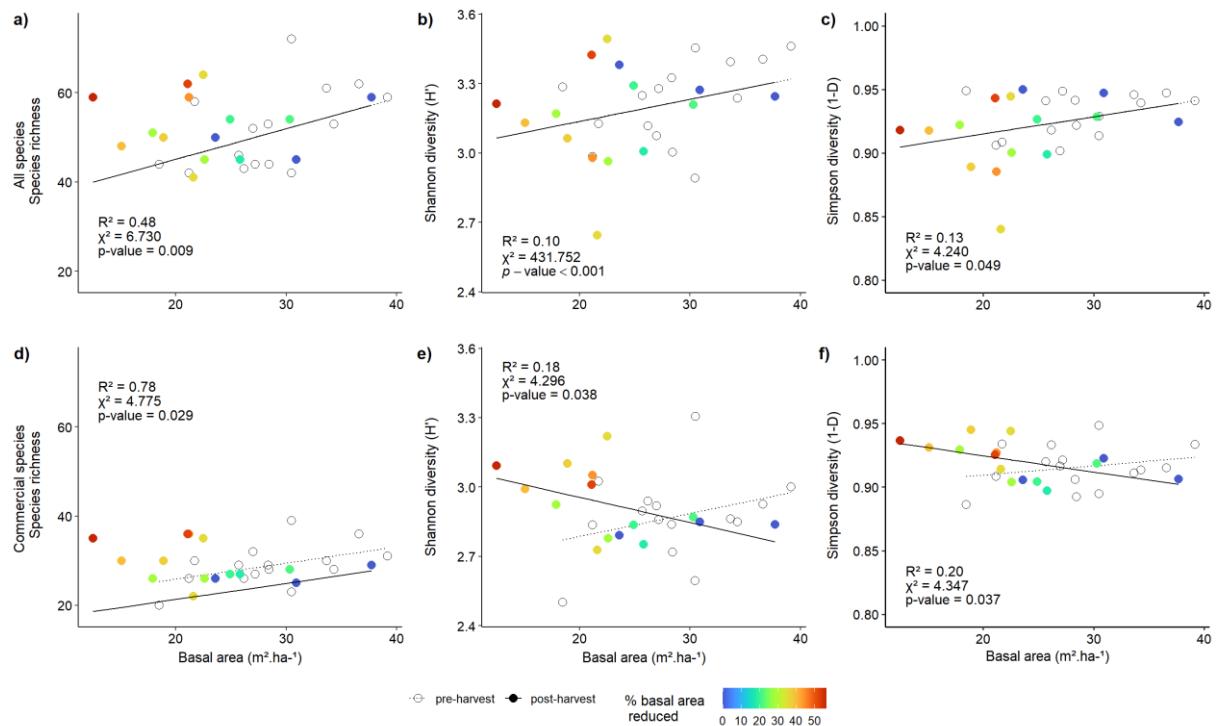
##### *Richness and diversity*

Species richness had a positive correlation with the forest basal area of both the bulk of the entire forest and the set of commercial species (Figure 3.3a, d). However, only commercial species showed significant differences between growth periods ( $\chi^2=4.775$ ,  $p=0.038$ ; Figure 3.3d). After the harvesting, richness of commercial species ranged from 22 to 37 per plot, with

an average of 28 species. Apparently, high harvesting intensity promoted an increase of richness of commercial species.

The basal area was also determinant for changes in the diversity of the forest, both for the forest as a whole and for the set of commercial species (Figure 3.3b, c, e, f). While for the bulk of whole forest diversity and basal area showed a positive correlation (Figure 3.3b, c), there was a negative correlation when only commercial species were considered (Figure 3.3e, f), both for Shannon and Simpson diversity. Harvesting intensity and growth periods had no influence on the diversity of both groups of species.

Figure 3.3 Species richness (a, d), Shannon (b, e) and Simpson (c, f) diversity of whole forest (trees, palm trees and tree ferns) and of commercial species as a function of pre-harvest (empty dots) and post-harvest (coloured dots) forest basal area. Each dot represents one plot. Dot colours scale represents the % of the initial basal area of each plot reduced by harvest.  $R^2$  is the variation explained by the full model (fixed + random) while  $p$ -value refers to the basal area of the model.



### Tree density

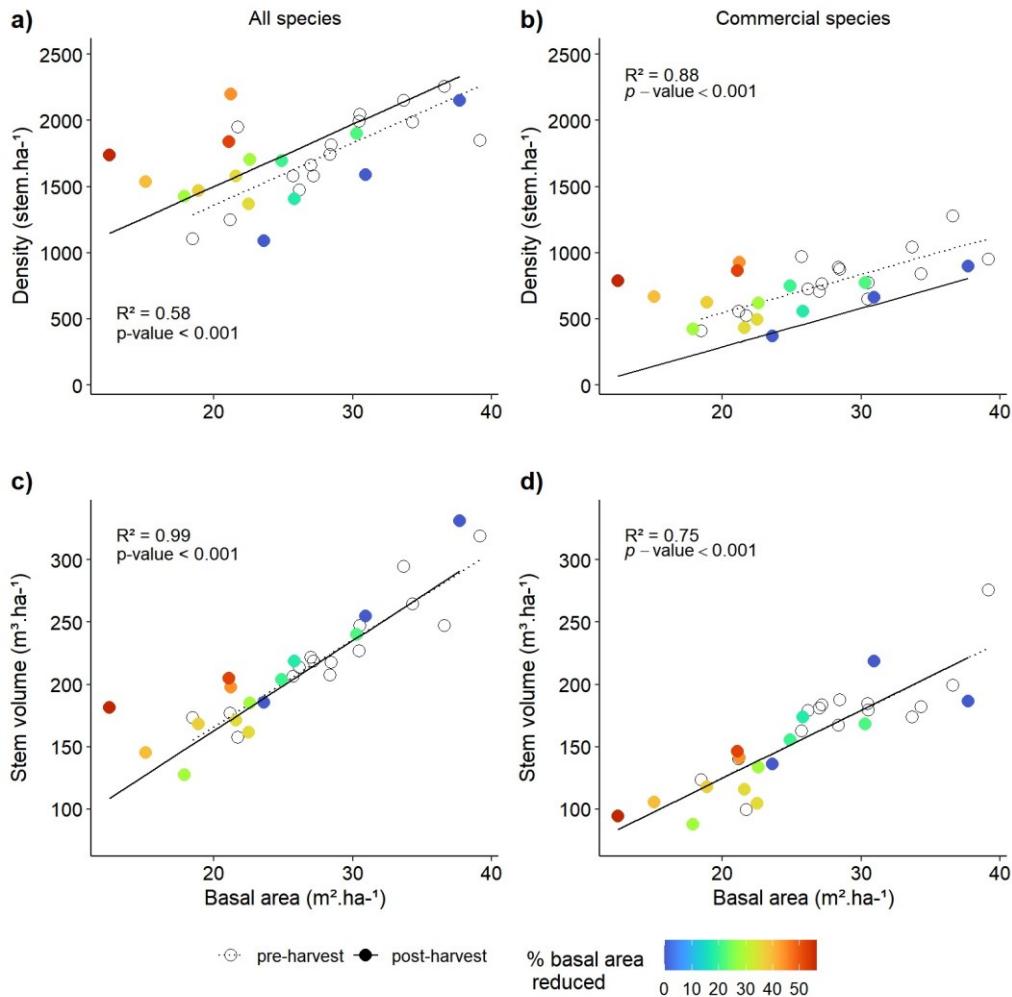
The initial and remaining forest basal area was determinant to forest tree density in both growth periods (Figure 3.4a, b). The relationship between density and basal area was positive for the forest and commercial species as well. For the bulk of the whole forest, harvesting intensity and basal area drove post-harvest changes, with significant differences between growth periods (Figure 3.4a; Appendix Table A.3). The significant difference in the relationship between density and basal area was determined by harvesting intensity and growth period, but

no interaction between variables. This way, the basal area determined the forest density after tree harvesting, for the whole forest. Some species showed changes in density pattern post-harvest. Among them, *E. edulis*, the species with the highest abundance in the forest, showed the greatest increase in the number of individuals during the period post-harvest: from 220 to 343 stem.ha<sup>-1</sup>. Other three species also increased their abundance after logging: *C. glaziovii* (from 4 to 101 stem.ha<sup>-1</sup>), *Schizolobium parahyba* (from 2 to 15 stem.ha<sup>-1</sup>) and *Trema micrantha* (from 4 to 15 stem.ha<sup>-1</sup>). For commercial species, the basal area determined the density of trees showing significant differences between growth periods ( $\chi^2=32.337$ ;  $p<0.001$ ; Figure 3.3b). The correlation was positive after the harvesting, and the relationship was higher within plots with highest harvesting intensities. The number of trees per hectare of commercial species such as *Hieronyma alchorneoides* and *Cabralea canjerana* remained among the highest after seven years of post-harvest growth, with 109 and 46 stem.ha<sup>-1</sup>, respectively.

#### *Commercial volume*

Commercial volume was affected by basal area for the bulk of whole forest and commercial species as well (Figure 3.4c, d). The basal area had a positive correlation with commercial volume for both groups of species. For the whole forest, the commercial volume was influenced by two interactions: (i) basal area and intensity ( $\chi^2=18.660$ ;  $p<0.001$ ); and (ii) basal area and growth period ( $\chi^2=10.012$ ;  $p=0.002$ ). The effect of basal area on commercial volume after harvest varied with the harvesting intensity (Figure 3.4c; Appendix Table A.3). For the commercial species, only the basal area influenced commercial volume, being determined the basal area resulted from harvesting (Figure 3.4d). After logging, forest commercial volume increased, reaching up to 100 m<sup>3</sup>.ha<sup>-1</sup> in 7y in the plot with the highest growth on volume, the same trend observed for commercial species (37 m<sup>3</sup>.ha<sup>-1</sup>) (Figure 3.4c, d).

Figure 3.4 Density (a, b) and commercial volume (c, d) of whole forest (trees, palm trees and tree ferns) (a, c) and commercial species (b, d) as a function of pre-harvest (empty dots and dotted lines) and post-harvest forest basal area. Each dot represents a single plot. Dot colours scale represents the % of the basal area of each plot reduced by harvest.  $R^2$  is the variation explained by the full model (fixed + random variables) while  $p$ -value refers to differences between pre- and post-harvest of the model.

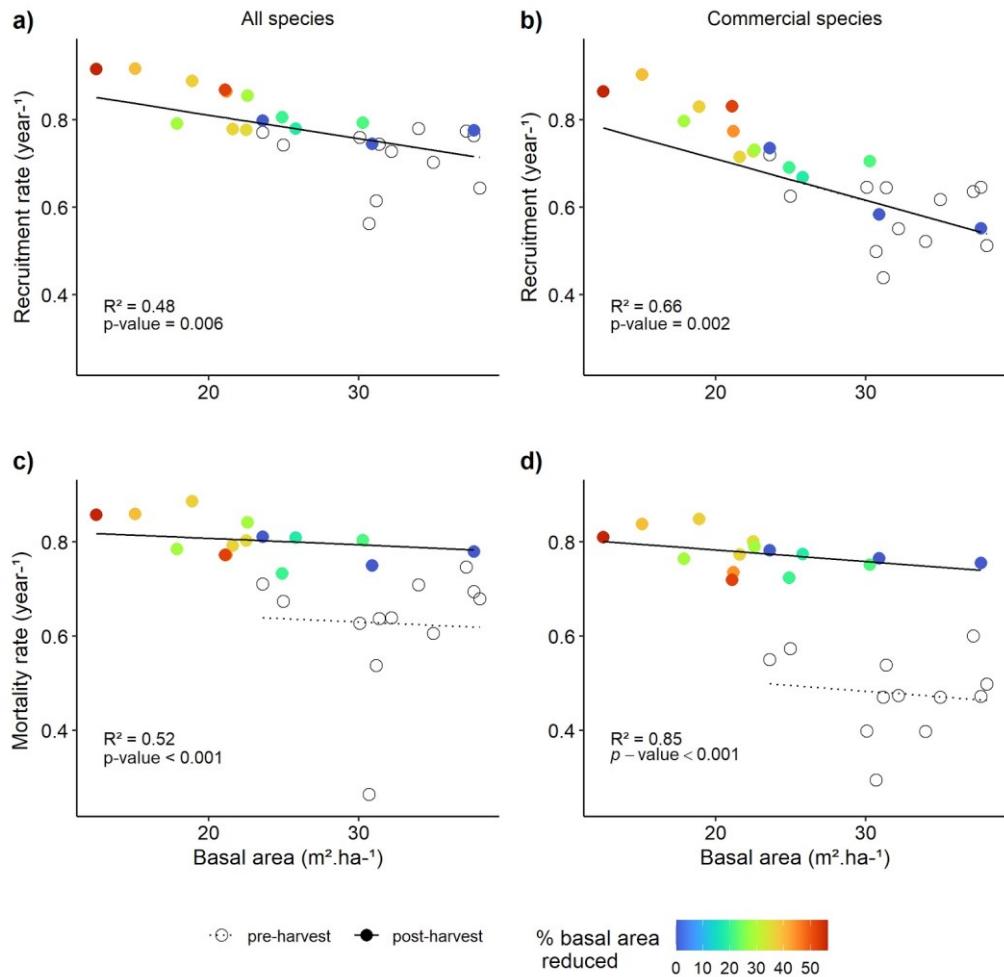


### Recruitment and mortality

Our results show that the forest basal area drives the recruitment and mortality of trees. The annual recruitment rate had a negative relationship with basal area, both for the whole forest and for the set of commercial species (Figure 3.5a, b). This relationship was observed for both growth periods, but it is more evident after harvesting. Harvesting reinforced that impact: the recruitment was higher during the period after logging for both groups. The harvesting intensity apparently impacted positively the recruitment rates, but only the basal area was significant (Appendix Table A.3). Basal area had a significant effect on recruitment of commercial species ( $\chi^2=12.602$ ,  $p<0.001$ ). Harvesting intensity and growing period influenced recruitment rate, but no significant effect for commercial species (Figure 3.5b). Among the commercial species, *S. parabyha* (10%), *G. opposita* (10%) and *Vernonanthura puberula* (9%)

showed the highest recruitment rates after logging. Two non-commercial species, *E. edulis* and *C. glaziovii*, also showed high recruitment rates (42 and 23%, respectively).

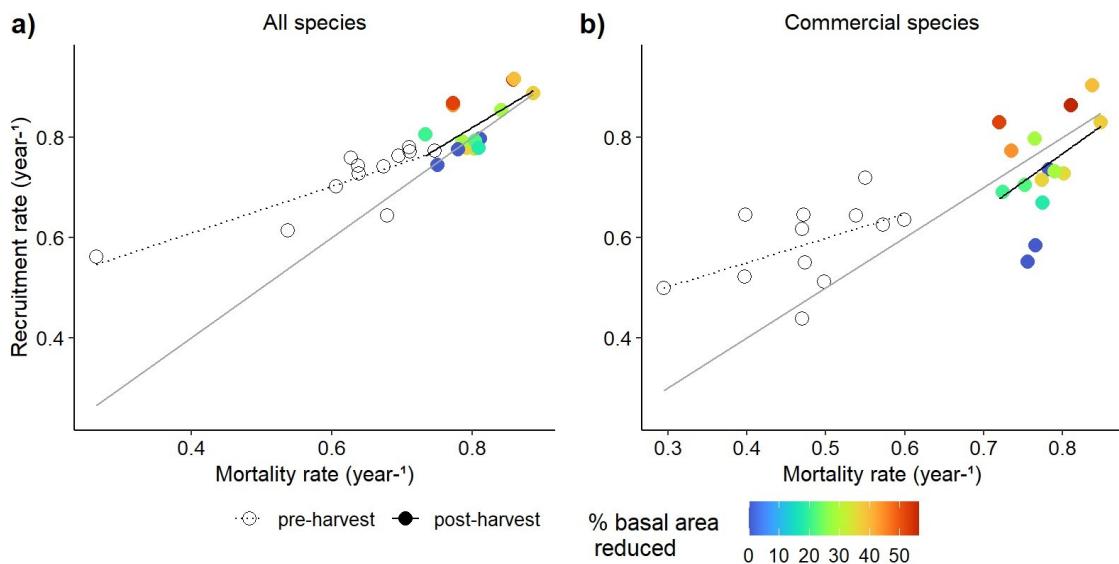
Figure 3.5 Recruitment (a, b) and mortality (c, d) of whole forest (trees, palm trees and tree ferns) (a, c) and commercial species (b, d) as a function of pre-harvest (empty dots) and post-harvest (coloured dots) forest basal area. Each dot represents a single plot. Dot colours scale represents the % of the basal area of each plot reduced by harvest.  $R^2$  is the variation explained by the full model (fixed + random) while  $\chi^2$  value and p-value refer to the basal area for recruitment and difference between pre- and post-harvest for mortality.



The impact of forest basal area on the annual mortality rates was more evident than on annual recruitment; the rates were significantly higher in the period after harvesting, for the whole forest as well for the commercial species (Figure 3.5c, d). There was also an apparent impact of harvesting intensity on mortality, but the relationship was not statistically significant. The commercial species with highest mortality were *H. alchorneoides* (12%), *C. canjerana* (8%) and *C. sylvestris* (6%). Among non-commercial species, *E. edulis* and *Cyathea* spp. showed the highest mortality rates (27% and 15%, respectively).

The relationship between recruitment and mortality rates was positive, and it was impacted by tree harvesting (Figure 3.6a, b). For the whole forest, during the period before harvesting the recruitment rate was higher than mortality, but figures became more similar after harvesting (Figure 3.6a). For commercial species, the higher rates of recruitment compared to mortality before harvesting is more evident (Figure 3.6b). For this group of species, in the post-harvesting period, the harvesting intensity showed a clearer correlation with recruitment versus mortality relationship; higher intensities seem to promote higher recruitment compared to mortality (Figure 3.6b). In this relationship, regarding the commercial species, the average annual mortality rate exceeded the annual recruitment rate after logging, 0.78 year<sup>-1</sup> and 0.74 year<sup>-1</sup> respectively (Figure 3.6b).

Figure 3.6 Relationship between recruitment and mortality rates of whole forest (trees, palm trees and tree ferns) (a) and of commercial species (b) of in the pre-harvest (empty dots and dashed line) and post-harvest (coloured dots and solid line) growth period. Grey solid line shows equality between variables. Dot colours scale represents the % of the basal area of each plot reduced by harvest.



### **3.5 DISCUSSION**

In this study, we used basal area as a variable to understand the impact of a selective tree logging on forest dynamics of a mid-secondary forest in the Brazilian Atlantic Forest, with focus on commercially valuable species. The results revealed that the forest rapidly responds to harvesting-induced disturbances for trees with a diameter at breast height (dbh) greater than 5 cm (Figure 3.3 and 3.4). Our findings also indicate an acceleration of forest dynamics, suggesting that selective harvesting can improve the forest to produce commercially valuable species.

#### *Effect of harvest on richness and diversity*

At the beginning of this study, after 41 years of regeneration, the forest accumulated 166 species, and 199 species twelve years later, by the time of our last inventory (Figure 3.2a). Considering that only woody individuals above 5 cm dbh were measured, this richness can be considered high for such a young second growth forest. Commercial species also showed an important increase of 13 species over the period. On the other hand, 22 species recorded in the first inventory were not found in the last one, at least in the inventoried plots, figures that resulted possibly from a combination of natural turnover and damage from the harvesting operations. Unlike other secondary forests where the presence of timber species is low (PIOTTO, 2007), our forests showed a high occurrence of timber species. Such results show the high potential of regional tropical secondary forests to restore and increase regional biodiversity, confirming other studies presented by Siminski et al. (2021) and Oliveira et al. (2022), as well studies reported for other tropical regions (CHAZDON, 2014; DENT; DEWALT; DENSLAW, 2013; GUARIGUATA; OSTERTAG, 2001; NORDEN et al., 2009; PEÑA-CLAROS, 2003; PEREIRA CABRAL GOMES et al., 2020; VILLA et al., 2018).

The selective harvesting of the studied forest also promoted an increase in species diversity. As diversity is a combination of the number of species and the evenness of the distribution of individuals across these species (JOST, 2010), it is possible that the harvesting of many dominant trees contributed to the higher diversity observed after the logging. A combination between the greater forest tree density following the harvesting and the disturbance in the environment, mainly the canopy opening, may also have played an important role in the increase of the diversity. This subject is yet to be further investigated. However, it is well known that the accumulation of species is a common trend in tropical secondary forests (OLIVEIRA

et al., 2022; ROZENDAAL et al., 2019; VILLA et al., 2018), and an increasing number of species over time is expected in a forest after a disturbance (BRITTO et al., 2022; LIKOSKI; VIBRANS; DA SILVA, 2022; PARROTTA; FRANCIS; KNOWLES, 2002). Frequent and intense disturbances drive environmental changes that will support species typical of both the previous and the future successional stages (TER STEEGE, 2003).

Regarding dominance, our results show that the same species that were dominant before harvesting remained prevalent after the intervention, with a high representation of commercial species. We observed a turnover among the dominant species during the pre-harvest period, but the total number of species remained the same (16 and 15 dominant species, Table 3.1). Late secondary species were the most benefited (11 species) by the changes in the forest structure promoted by the harvesting, followed by the early secondary and pioneer species. Among these species, *C. glaziovii* and *E. edulis* stood out. The climax species were mostly represented by different species of *Mollinedia* spp., subcanopy species classified as non-commercial timber. In other areas of the Atlantic Rainforest under selective logging, the harvesting altered the canopy structure and increased the relative abundance of early secondary species (VILLELA et al., 2006). Peña-Claros et al. (2008) related that pioneer species showed the high growth rate in response to intensive silviculture intervention.

A group of a few species showed high dominance in the studied forest, like *H. alchorneoides* and *M. cinnamomifolia*. For one hand, this result is, to some extent, a consequence of the silvicultural practices performed at the initial development of the forest (FANTINI et al., 2019). However, dominance of a few species is characteristic of secondary forests in the region, and these species represent common successional routes (DENT; DEWALT; DENSLAW, 2013; JOLY; METZGER; TABARELLI, 2014; PEREIRA CABRAL GOMES et al., 2020; ZAMBIAZI et al., 2021). The importance value (IV) of *H. alchorneoides* and *M. cinnamomifolia* decreased along the pre-harvest period, despite the low mortality of their trees. The increase in forest density, basal area and frequency of other species may explain this result. In fact, the IV of other seven species increased in the period, including the shade tolerant *A. petiolatus*, *C. canjerana*, *E. edulis*, *P. nuda*, and *P. suterela* (Table 3.1). Among these species, the impact of highly dominant understory species *P. nuda*, and *P. suterela* on timber productivity the other species that produce timber is yet to be studied but there is strong indication that silvicultural intervention may be necessary to support the growth of commercially desirable trees in a managed forest. Despite changes in dominance, *H.*

*alchorneoides* remained the species with the highest dominance and one of the species with highest potential for timber production. The occurrence of this species is continental in Latin America (MULER et al., 2014; SILVA et al., 2004; VENEKLAAS et al., 2005), its timber present high demand in the market (FANTINI; SIMINSKI, 2016) and it performs well in mixed plantations (CARNEVALE; MONTAGNINI, 2002; FONSECA G; ALICE G; MARIA REY B, 2009; MONTAGNINI; MENDELSONH, 1997). Among non-timber species, we confirmed the high importance of *E. edulis* for forest structure reported in other studies in the region, as well as its potential for economical management either to produce palm heart or açaí berries (FANTINI; GURIAS, 2007; GALETTI; FERNANDEZ, 1998; MULER et al., 2014).

#### *Effect of harvest on forest structure*

A tree harvesting leads to changes in forest structure and dynamics, and, in a short time, secondary forests may still show evidence of logging on the structure, abundance and canopy structure (VILLELA et al., 2006). However, in the studied forest, (LIKOSKI et al., 2021) showed that the forest canopy recovered quickly after harvesting. Still, it seems that the disturbance promoted a more diverse environment, benefiting a larger number of species. In our study, changes in the dynamics of the forest were evidenced by an increasing tree density, basal area, commercial volume, and species richness. The rapid recovery of tree density could have been facilitated by a high post-harvest rate of recruitment. Other studies have reported that disturbances produced in logged forests lead to a sharp rise in the density of both long-lived pioneer species and shade-tolerant species soon after the intervention (GAUI et al., 2019; SCHWARTZ et al., 2014). The forest basal area was positively correlated with forest density in the period before harvesting (Figure 3.4a). However, this relationship became weaker after the logging, possibly because the basal area was the only criteria to guide the choice of trees to be cut, disregarding the number of trees of each plot. The post-harvest changes in tree density were not related to the basal area present in the forest before harvesting, and also not related to the intensity of basal area reduction. This evidence reinforces the effect that the basal area resulting from harvesting has on the forest density. Therefore, the changes in forest density is largely determined by the forest basal area remaining after harvesting, a factor that determines the light incidence in the understorey (LIKOSKI; VIBRANS; DA SILVA, 2022; SILVA et al., 2017; WHITMORE, 1985). It is common for the density to increase after harvesting (BRITTO et al., 2022; DIONISIO et al., 2018; SILVA et al., 2017). It is known that opening the canopy favours the recruitment of fast-growing trees, but recruitment of undesirable species that will

compete directly with trees remaining from a harvest may occur. The combination of a variety of cutting intensities is a favourable factor for maintaining and increasing productivity from a variety of species in secondary forests. In this way, at landscape level we may have areas with low harvesting intensity where short cycles of harvesting could be performed (FREDERICKSEN; PUTZ, 2003), while in areas of high cutting intensity we would have the regeneration of light-demanding species and longer cycles (PUTZ et al., 2012).

During the pre-harvest period, basal area and commercial volume showed the same tendency of recovery. Commercial species made up the largest portion (74%) of the forest basal area due to their larger size (Figura 2c), particularly among fast-growing species. In another study (Chapter 2) that analysed a chronosequence in the Atlantic Forest high growth rates for fast-growing species were reported: an average increase of up to  $15.8 \text{ m}^2.\text{ha}^{-1}$  in 15-year-old secondary forests, which is equivalent to  $1.1 \text{ m}^2.\text{ha}^{-1}$  per year. The same study reported rates of up to  $25.8 \text{ m}^2.\text{ha}^{-1}$  for 45-years old secondary forests. The forest growth rate is expected to accelerate once conditions become favourable for commercial species. Our results show that the basal area played a crucial role in altering other components of the forest structure, especially the increase of commercial volume. Commercial species contributed significantly to the increase in commercial volume in the period before harvesting and in the control plots. Secondary forests present rapid increase of basal area in short periods (BROWN; LUGO, 1990; GUARIGUATA; OSTERTAG, 2001; PEÑA-CLAROS, 2003) and can resemble mature forest values (BROWN; LUGO, 1990; MUKUL; HERBOHN; FIRN, 2016), which implies in the commercial volume of the forest.

We found that basal area and commercial volume recovered fast after logging. For instance, 64% of the removed basal area regrew in the short period of seven years after harvesting, with a higher contribution of non-commercial pioneer and early secondary fast-growing species, replacing the role that commercial species had in the pre-harvest period. A significant portion (57%) of the recovery was due to trees with diameters between 10 to 30 cm (Chapter 4). Another part of the recovery was due to the recruitment and growth of smaller trees (dbh between 5 and 10 cm), as well as trees larger than 30 cm.

The increase in basal area and commercial volume may indicate that the forest has great potential to recover the timber stock after logging. Such capacity may be directly related to the interaction between the basal area resulting from logging and harvesting cutting intensity (BEDRIJ et al., 2022). Plots with largest basal areas may be in a better development site, or the

species composition benefits the timber productivity, with potential for the forest to replenish the timber stock, especially of commercial species. This means that the forest basal area before harvesting determines the commercial volume recovered after the forest is managed.

#### *Recruitment and mortality*

Recruitment of tree regeneration secured the sustained timber production in naturally managed tropical forests (PARIONA; FREDERICKSEN; LICONA, 2003). Demographic rates have changed after the tree harvesting: both recruitment and mortality increased. Before harvesting, the recruitment rate was higher than mortality rate for the trees inventoried (dbh above 5 cm). Although both rates were positively correlated, the higher recruitment rate was possibly a result of a continued recruitment of shade tolerant species, more competitive than light-demanding species in the lower light levels of the understory (OKUDA et al., 2003; VILLELA et al., 2006). A recruitment higher than mortality was also observed after harvesting, which seems consistent with the opening of the canopy of a harvested forest, which promotes the growth of young trees, including those belonging to subcanopy species. In another study carried out in the same forest, species with timber production potential show high regenerants density (PIAZZA et al., 2017). Our results indicated that *C. canjerana*, *C. oblongifolia*, *H. alchorneoides*, *N. membranacea*, *M. cabucu* and *V. bicuhyba* represented 40 % of the total 857 trees/ha of timber species. The high density of regenerants favours the recruitment of trees after a selective harvesting and the recovery of forest density. Possibly, in the plots harvested with lowest intensity, the residual forest favoured the growth of remaining individuals in the understory, which presented recruitment rates similar to those observed before the logging (Figure 3.5). Commercial species, however, presented mortality rates higher than recruitment after harvesting, which may explain why these species show slower recovery in density, basal area and commercial volume. Mortality may have also been augmented by damage caused by harvesting operations to remaining trees (BRITTO et al., 2022; LIKOSKI; VIBRANS; DA SILVA, 2022). Mortality was not affected by the forest basal area, but other unknown factors may have influenced the pre- and post-harvest rates. The increase in mortality rate was correlated to the increase in harvest intensity.

#### *Attractivity of the secondary forest for management*

Secondary forests have gained increasing attention in recent years as a potential source of timber and other forest products. Overall, the attractivity of secondary forests for management stems from their potential for both economic benefits and environmental services.

Some factors may boost the attractiveness of secondary forest for management, such as low establishment cost, shorter harvest rotations, and the presence of commercially viable species. Appropriated regeneration systems and silvicultural practices can provide a more favourable growing environment for fast growing species compared to primary forests. This can lead to higher productivity and fast growth, making secondary forests a desirable option for timber production. Some species may benefit from the silvicultural interventions, improving the forest quality and productivity. In some forests, however, the lack of diversity and the presence of invasive species may pose challenges to the forest owners to benefit from timber production. Effective management strategies, such as promoting the growth of a diverse range of native species and controlling invasive species, are then crucial to ensure and enhance the success and sustainability of the economic management of secondary forests.

Floristic composition is a key factor for successful management of secondary forests. Both in chapter 3 and 4 and in the Zambiazi et al. (2021), mid-successional forests can shelter approximately 50% of commercial species in areas of high diversity. A set of fast-growing species produce quality timber at this stage of secondary forest. However, few species are dominant at any time. So, differently from the management of mature forests, the focus of exploitation should be on a large number of relatively small trees from fast-growing species. A steady supply of timber should be achieved through repeated short rotation. However, our study suggests that the response of the secondary forest to selective logging varies depending on the extent of the reduction in the basal area. The challenge of managing a secondary forest is to maintain a certain species composition and structure over a long term and to ensure regeneration of the desired species. Effective management can target intermediate and late successional stages where desirable species or dominant groups are present (ITTO, 2002).

Forests in regeneration offer a valuable opportunity for the replenishment of harvested timber while also preserving and, in some cases, enhancing biodiversity, which makes them a crucial resource for sustainable forestry practices and the maintenance of healthy and diverse ecosystems. By effectively managing secondary forests, it is possible to achieve a balance between utilising their resources and preserving their ecological values, thereby ensuring their long-term viability. Additionally, the presence of a thriving secondary forest can provide numerous economic, social, and environmental benefits, making it a vital component of sustainable development and land use planning. The effective economic return may be the incentive factor for management initiatives in secondary forests. In the study region, multiple

timber products generated by low to best quality timber production have a guaranteed market and competitive price with timber from mature forests. Secondary timber is often considered a more sustainable alternative to primary timber, as it can be harvested from forests that have already regenerated, reducing pressure on primary forests and their unique ecosystems. These timbers are used in a variety of applications, including construction materials, furniture, paper, and bioenergy. In recent years, there has been growing demand for environmentally responsible products, leading to an increase in the market for secondary timber. Consumers are becoming more conscious of the environmental impact of the products they purchase and are seeking out alternatives that have a lower carbon footprint and are sourced from sustainable managed forests. As a result, the market for secondary timber is expected to continue growing in the future.

### 3.6 CONCLUSIONS

The selective logging of trees altered the dynamics of the investigated forest site. Change of the growth environment in a short period of time promoted the development of the forest, resulting in increase in the volume of species that produce quality timber. The timber productivity was high before harvest, from a variety of species but with few dominant wood-producing species, such as *H. alchorneoides* (its 10% dominance was responsible for the largest timber stock). The species richness increased after harvesting, with commercial species remaining among those of greatest dominance. Before the intervention, commercial species accounted for 72% of the basal area and 77% of the commercial volume, with no difference in growth after harvesting compared to non-commercial species. The basal area can be considered a driver of the changes that occurred after harvesting, affecting richness and diversity, density, and commercial volume of the whole forest. The harvest intensity determined the post-harvest forest density and commercial volume. *H. alchorneoides* and *C. canjerana* were the tree species mostly benefited by the canopy opening, while among non-timber species *E. edulis* and *C. glaziovii* stood up. In addition to the influence of basal area, cutting intensity was also determinant for changes in commercial volume after harvest. Areas with high cutting intensity resulted in low forest increments in the period analysed after logging because of the small number of residual trees. Recruitment and mortality were also impacted. Higher recruitment occurred in areas with lower basal area. For commercial species, recruitment exceeded mortality, with higher rates in areas of greater cutting intensity, favouring the presence of commercial species. Further studies on the impact of basal area reduction are still needed to clarify the contribution of the growth of individual trees that were already present in the understory, the increment of small diameter of residual trees in areas of lower harvesting intensity, and the fast-growing species in areas of greater reduction of basal area. These investigations will provide valuable insights into the long-term effects of basal area reduction and help inform sustainable management practices.

In summary, the selective cutting of trees in this study altered the forest dynamics, resulting in changes in species composition, density, and commercial volume. Understanding the effects of harvest intensity and basal area reduction is crucial for implementing sustainable forest management strategies that promote timber production while preserving biodiversity and ecosystem functions. Continued research and careful monitoring are necessary to ensure the long-term sustainability of timber extraction and the conservation of forest resources.

## **4 CAPÍTULO 4**

### **4.1 Impact of a selective harvesting on forest growth and trees increment in a tropical secondary forest**

#### **ABSTRACT**

Tropical mid-succession secondary forests can hold a significant volume of timber from dominant and fast-growing species. In this study, we investigated changes in the dynamics and timber productivity of commercial tree species in a secondary forest subjected to a selective logging, located in Santa Catarina state, Southern Brazil. We inventoried 12 plots (40x40 m) in the year 2009 and 15 plots was inventoried in the years 2014 and 2021, resulting in 2-time intervals: two measurements before (2009 and 2014) and two after the tree harvesting (2014 and 2021). Our results show that the relative growth rate (RGR) of the forest increased significantly from the pre-harvest to the post-harvest period. The commercial set of species showed the same pattern of increase, but the average of the rates was smaller compared to the whole forest. The average periodic annual increment (PAI) of total commercial volume was  $5.5 \text{ m}^3.\text{year}^{-1}$  in the growth period before harvesting and  $4.4 \text{ m}^3.\text{year}^{-1}$  after harvesting. RGR showed a negative relationship with the basal area for commercial species, with higher growth rate in areas with lower basal area remaining after tree logging. The increment of commercial volume was strongly impacted by harvesting: areas with lower basal area presented smaller growth rates in the period analysed. Trees classified as middle dbh (10-30 cm) had higher PAI, as well as high and best quality timber. Individual trees grew up to  $3.06 \text{ cm.cm}^{-1}.\text{year}^{-1}$ , with average growth rates of  $0.30 \text{ cm.cm}^{-1}.\text{year}^{-1}$  before and  $0.33 \text{ cm.cm}^{-1}.\text{year}^{-1}$  after harvesting. The highest growth rates were observed after harvesting, especially for trees belonging to the early and late secondary groups, and to best quality timber species. Among the trees of the nine dominant forest species, *H. alchorneoides*, *M. cinnamomifolia* and *V. bicuhyba* showed the greatest increment after harvesting. Our results indicate that secondary forests can respond rapidly to a selective tree logging and commercial species can benefit from the disturbance promoted to the forest. Remaining trees grow faster after harvesting and can replenish the timber stock. The dominance of fast-growing species suggests that silvicultural practices in mid-successional stages can increase timber productivity.

**Keywords:** timber productivity; selective trees logging; dominant species; forest structure

## 4.2 INTRODUCTION

The sustainable management of tropical forests has among its premises the presence of remaining young trees of commercial species after a harvesting, growing at rates that will replenish the harvested stock in a relatively short time (BEDRIJ et al., 2022; DE AVILA et al., 2017; PUTZ et al., 2008; SIST et al., 2021; WAGNER et al., 2006). It also requires an environment favourable for the recruitment of trees of commercial species and for the maintenance of the diversity of species. However, regarding the secondary forest the effects of selective logging are still poorly understood, especially its impact on basal area and commercial volume, and on diameter growth of remaining trees. Secondary forest grows naturally on lands which have been farmed or grazed and abandoned after use (AIDE et al., 1995; BROWN; LUGO, 1990; CHAZDON, 2014). They now represent more than half of the tropical forest coverage in the world (CHAZDON et al., 2009; FAO, 2020). Only in the recent decades secondary forests have started being recognized for their richness of tree species, dominance of fast-growing species and presence of commercial species of economic interest (BROWN; LUGO, 1990; FANTINI; SIMINSKI, 2016; OLIVEIRA et al., 2018, 2022; SCHUCH; SIMINSKI; FANTINI, 2008; ZAMBIAZI et al., 2021), characteristics that may make the management of these forests attractive.

During the logging operations, remaining trees may be directly damaged by the cutting and skidding of the trees selected for harvesting. The forest structure is also impacted by the felling intensity, changing light incidence, growth rate, survival, mortality and recruitment (DEARMOND et al., 2022; SILVA et al., 1995; STORCH; DORMANN; BAUHUS, 2018; SULLIVAN; SULLIVAN; LINDGREN, 2008). The effect of cutting intensity may be positive for relative growth rate (RGR) for forest, but negative for increment. Looking at the difference between these variables is justified. While RGR is dependent only on the growth in diameter of individual trees, volume growth depends on diameter growth, density and the size class distribution (JONKERS, 2011). The greater the intensity of harvesting, the lower the abundance of individuals in the largest diameter classes and the lower the growth in basal area and volume, especially of commercial species.

The known effects of harvesting on growth and increment are mostly related to mature forests. However, the few studies related to secondary forests show that the effects of tree harvesting on the dynamics of the forest resemble those observed in mature forests. In the Brazilian Atlantic Forest, the current legal framework prohibits the management of secondary

forests for timber production. This prohibition can be attributed, at least in part, to the relatively small remaining extent of remnant forests in this biome, accounting approximately 12% of its original cover. Such law was also based on an allegedly lack of knowledge on the feasibility of sustainable management of secondary forests. The few managed secondary forests in the region are the results of scientific research seeking results that demonstrate their potential timber production. Understanding how growth and increment respond to selective harvesting of trees is crucial to shed light on the sustainable use of regenerating forests, aiming to prevent further deforestation and to promote land restoration, biodiversity conservation, carbon stock and ecosystem services, as well as income generation for forest owners.

Our study aims to analyse the effect of different tree harvesting intensities on growth and increment in a mid-successional secondary forest. We asked: (i) does harvesting favour the growth of commercial tree species? (ii) how does logging impact tree growth in relation to after-harvest forest basal area and tree diameter? and (iii) which groups of trees and species benefit from a tree harvesting? To answer these questions, we analysed the dynamics of a managed secondary forest before and after a selective harvesting at different intensities of basal area removal. We expected that, after harvesting, the trees of commercial species would increase their growth rates and, consequently, the increment and recovery of the harvested volume of commercial timber.

## 4.3 METHODOLOGY

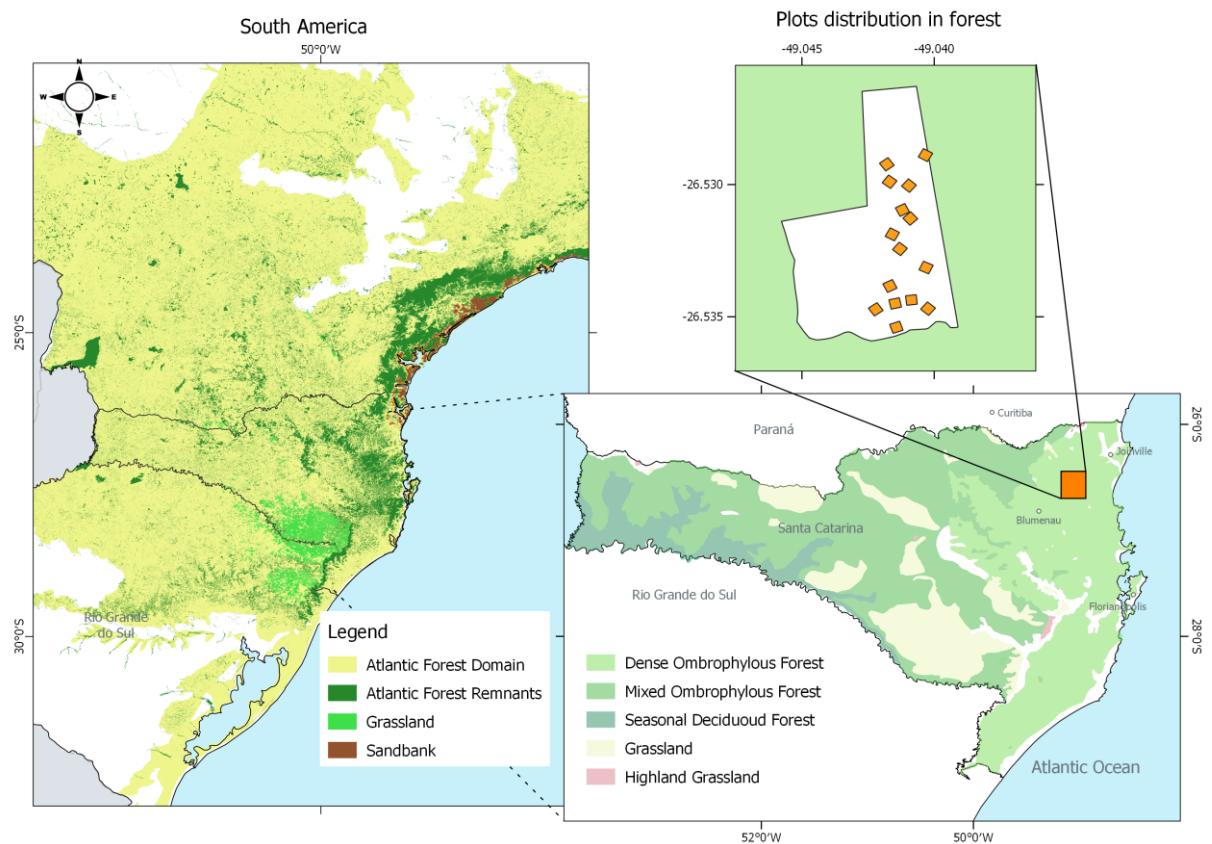
### 4.3.1 STUDY AREA AND DATA COLLECTION

The study was conducted between 2009 and 2021 in a secondary forest in Santa Catarina State, Southern Brazil ( $26^{\circ}32'01''S$  e  $49^{\circ}02'30''W$ ). The climate in the region is humid subtropical with hot summers (Cfa), with average temperature of  $20.7^{\circ}C$  and annual precipitation of 1,800 mm (ALVARES et al., 2013). The region was originally covered by the Brazilian Atlantic Forest, specifically the Dense Ombrophilous Forest (DOF), which characteristically presents an evergreen canopy, abundance of epiphytes and palm trees (GASPER et al., 2014; SIMINSKI et al., 2021; VIBRANS et al., 2013). DOF is also characterised by the dominance of species such as *Alchornea triplinervia*, *Alsophila setosa*, *Hieronyma alchorneoides*, *Annona neosericea*, *Cyathea phalerata*, *Euterpe edulis*, *Cabralea canjerana*, *Miconia cinnamomifolia*, and others (OLIVEIRA et al., 2022; VIBRANS et al., 2013). This region is covered with altitudes up to 500 and 600 m with medium elevations of <1000 m (ALVARES et al., 2013; MORELLATO; HADDAD, 2000). The characteristic soils of the region are Podzolic Red-Yellow Alicus Tb A Moderate, Gleissol Low Humic Dystrophic Ta and Tb, and Cambissol Distrofie Ta and Tb Gleic A Moderate (EMBRAPA, 2004). Landscapes in the region are formed by a mosaic of secondary and mature forests, monocultures of *Eucalyptus* and *Pinus* species, agricultural fields, pastures and urban areas (VIBRANS et al., 2012). In the region, the secondary forest regenerated mostly after the abandonment of crop fields cultivated under swidden-fallow agriculture (ZAMBIAZI et al., 2021).

For this study we used data from inventories carried out over twelve years in a secondary forest regenerating for 41 years until the beginning of this study. The landowners reported that the forest was previously used for swidden-fallow agriculture and pasture. The inventories were carried out at 4-time intervals, two measurements before (2009 and 2014) and two after tree harvesting (2014 and 2021). In 2009, 12 plots were inventoried, and another three plots were added in 2014, totaling 15 plots. After the second inventory (2014), the forest was harvested for timber production, the plots were updated in 2014 and reinvented in 2021. In each plot measured was 60x60m with a core area of 40 x 40 m, totalling 24,000 m<sup>2</sup> of sampling area (Figure 4.1) and ewe 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 (Federal University of Santa Catarina

- UFSC), Herbarium Roberto Miguel Klein (Regional University of Blumenau - FURB) and Barbosa Rodrigues Herbarium. The species were classified according to the Angiosperm Phylogeny Website, version 14 (STEVENS, 2017), and Species 2000 & IT IS Catalogue of Life (ROSKOV et al., 2019) and Brazil Flora Group (2021).

Figure 4.1 Map of the original and remaining Brazilian Atlantic Forest in Brazil (left), indicating the forest type in Santa Catarina State. Location of the inventoried plots in the detailed map. Source: <http://mapas.sosma.org.br/> (SOS Mata Atlântica, 2020); Area under the enforcement of the Law nº 11.428/2006 (BRASIL, 2006); Original Forest types according to Klein (SAR, 2005).



#### 4.3.2 THE HARVESTING

The plots were installed in 2009, and the selective tree logging occurred in 2014, after the second forest inventory. The selective harvesting consists in selected individual trees for harvesting based on economic considerations of stem size and/or quality (FREDERICKSEN, 1998). Basal area reduction was the criterion used to harvest selected trees. The intention was to simulate different harvesting intensities, resulting in basal area reduction from 18 to 56%. Three plots were not harvested and were used as controls. The trees selected for harvesting varied in diameter and species, seeking to improve the timber quality of the remaining trees in

the forest for the next cutting cycle. However, the immediate demand for revenue by the forest also guided the selection of trees for harvesting. Only trees with diameters above 20 cm were harvested. For this study, we considered two periods of forest growth in reference to harvest: (i) pre-harvest (from 2009 to 2014); and (ii) post-harvest (from 2014 to 2021).

#### 4.3.3 CATEGORIZATION OF TREES AND SPECIES

For single trees of commercial species, we used diameter at breast height (DBH, cm) to analyse the growth rate ( $\text{cm} \cdot \text{year}^{-1}$ ) relative to their initial diameter (at the beginning of the pre- and post-harvest periods). We measured 1,720 individual trees of commercial species considering both growth periods (some trees were harvested, while new trees were recruited). Among the 99 commercial species identified in the forest, 85 presented trees that were measured at least in two inventories. For such analyses, a small number of tree species that produce timber with high economic value was selected. We also studied the structural changes in the forest, by grouping the individuals into three dbh classes:  $5 < 15 \text{ cm}$ ,  $15 < 30 \text{ cm}$ , and  $\geq 30 \text{ cm}$ . Trees  $\geq 30 \text{ cm}$  dbh include most of the short-lived, fast-growing species with a harvestable size; trees between 15 and 30 cm dbh are those potentially harvestable in a short time; trees  $5 < 15 \text{ cm}$  in dbh will possibly be harvested in the mid-term). The species also were classified as commercial or non-commercial species. Commercial species are those having marketable timber that is useful for any purpose other than charcoal. Commercial species with potential timber use were further classified into timber quality classes following Zambiasi et al. (2021): (i) best quality timber; (ii) high quality timber; and (iii) low quality timber. The classification considered information on regional timber use and market price (Appendix Table A.1 and Table A.2). Data on use and market price of timber from some secondary species are difficult to obtain due to restricted management practices and the illegal market of such species. We also classified commercial species into ecological groups (pioneer, early secondary, late secondary, and climax; Appendix Table A.2), following the criteria proposed by Budowski (1965), and other sources (BARBOSA et al., 2017; CARVALHO, 2003, 2006, 2008, 2010; FERREIRA et al., 2013; KLAUBERG et al., 2011; MANTOVANI et al., 2005; MARTINS, 2005; SANTOS et al., 2004; SIMINSKI et al., 2021; VIBRANS et al., 2013).

A small group of commercial species with high economic and ecological value and dominants in secondary forests was selected to analyse the tree growth rate in diameter in relation to initial dbh. This species showed trees with at least two measures pre- and post-harvest: *Alchornea triplinervia*, *Cabralea canjerana*, *Cedrela fissilis*, *Cupania oblongifolia*,

*Hieronyma alchorneoides*, *Miconia cinnamomifolia*, *Miconia formosa*, *Nectandra membranacea* and *Virola bicuhyba*.

#### 4.3.4 DATA ANALYSIS

We analysed the forest growth before and after harvesting. To analyse the effect of harvesting we used the remaining basal area ( $\text{m}^2.\text{ha}^{-1}$ ) of each plot after logging as well as the harvesting intensity (the % of the initial basal area of each plot removed at harvest). We calculated basal area ( $\text{m}^2 \text{ ha}^{-1}$ ) and commercial volume ( $\text{m}^3 \text{ ha}^{-1}$ ) for each plot to both periods of forest growth. We used volumetric models adjusted for species of the Atlantic Forest (Correia et al., 2017; Oliveira et al., 2018) to estimate stem volume (StemV) of each individual, including palm trees and tree ferns. StemV represents the commercial volume ( $\text{m}^3$ ) of the stem from the ground level to the commercial height (i.e., up to the point of the first stem fork) of the individual. For *Hieronyma alchorneoides*, a specific model (Oliveira et al., 2018) was used because of the importance of this species for forest structure and management.

The effect of harvesting on forest growth per plot was measured as the relative growth rate (RGR) in diameter ( $\text{cm}.\text{cm}^{-1}.\text{year}^{-1}$ ) to analyse the growth per plot. This parameter was calculated as:

$$RGR = \ln(dbh_{t2}) - \ln(dbh_{t1}) / t2 - t1 ;$$

Where,  $dbh$  is the diameter measurement in different times, and  $t_1$  and  $t_2$  are the dates (years) when that the plots were measured. We also computed the periodic annual increment in basal area ( $\text{m}^2.\text{year}^{-1}$ ) and commercial volume ( $\text{m}^3.\text{year}^{-1}$ ).

The periodic annual increment (PAI) was calculated for both variables as:

$$PAI = \sum_{k=1}^{n_{jh}} (X_{t2} - X_{t1}) / t_2 - t_1 ;$$

Where,  $X$  is stem volume. The effect of harvesting was analysed for the entire forest, for commercial species, grouping the trees according to diameter class and timber quality.

#### 4.3.5 PLOT BASED ANALYSIS CONCERNING THE ENTIRE FOREST

We used linear mixed effect models (*lmem*), following the methodology of the Zambiazi et al. (2021), to analyse the effect of initial basal area ( $\text{m}^2.\text{ha}^{-1}$ ) on the relative growth rate (RGR) of diameter, as well as to analyse the periodic annual increment (PAI) of basal area and commercial volume for the whole forest and for the set of commercial species for that purpose, the initial basal area ( $\text{m}^2.\text{ha}^{-1}$ ) was included in the models. Harvesting intensity (%) was also included, as a random intercept, while the growth period was included as a random effect. Values that did not show normality by the Shapiro Wilk test were transformed to the square root of their original value. For each response variable, we established a linear model using a generalised least squares model (*gls*) without random intercept and random effect. The model was structured with fixed effects and random effects according to RCore Team (2021): (i)  $y \sim 1 + (1+\text{Intensity}|\text{GrowthPeriod})$ ; (ii)  $y \sim 1 + (\text{Intensity}-1|\text{GrowthPeriod})$ ; (iii)  $y \sim 1 + (1|\text{GrowthPeriod}/\text{Intensity})$ ; and (iv)  $y \sim 1 + (1|\text{GrowthPeriod})$ . The best model was then selected to test the effect of initial basal area on forest growth. After establishing the models, we selected the best one to test the effect of initial dbh on forest growth by using  $\Delta\text{AIC}$  (Appendix Table A.3 and Table A.5). The significance of the deviations was analysed using ANOVA with Chi-square statistics. When the growth period was not significant and decisive for the effect of basal area on the dependent variable, we chose to analyse the data by generalised linear models (*glm*). This was the case when individuals were categorised by dbh class and timber quality.

#### 4.3.6 SINGLE-TREES BASED ANALYSIS

The effect of initial dbh (cm) on dbh growth rate ( $\text{cm year}^{-1}$ ) of single-trees was analysed using generalised linear models (*glm*). Growth period was included in the models to compare the forest growth before and after harvesting. We transformed variables that did not show normality by the Shapiro Wilk test using the square root of their original values. For each response variable, we established a null model without a dependent variable:  $\text{GrowthRate} \sim 1$ . We established structures with fixed effects to: (i)  $\text{GrowthRate} \sim \text{InitialDBH}$ ; and (ii)  $\text{GrowthRate} \sim \text{InitialDBH} + \text{GrowthPeriod}$ . After establishing the models, we selected the best one to test the effect of initial dbh on forest growth using  $\Delta\text{AIC}$  (Appendix Table A.7). The significance of the deviations was analysed using ANOVA with Chi-square statistics.

The analyses of linear mixed-effect models and generalised linear models were performed with the *lme4* (BATES et al., 2019), *lmerTest* (KUZNETSOVA; BROCKHOFF;

CHRISTENSEN, 2017), *MuMIn* (BARTON, 2020) and *visreg* (BREHENY; BURCHETT, 2017) packages in RCore Team (R-CORETEAM; RCORE TEAM, 2019) and the Rstudio interface (RSTUDIO TEAM, 2019). We also used *bbmle* (BOLKER, 2020) package in linear mixed-effect models. For the plotted data, lines were fitted to each variable using the predictors of the chosen model, and the *ggplot2* (WICKHAM, 2009), *viridis* (GARNIER, 2018) and *cowplot* (WILKE, 2019) packages were used.

## 4.4 RESULTS

### 4.4.1 FOREST GROWTH

Our results refer to two consecutive growth periods of the forest: the five years before a selective tree logging was applied to the forest (pre-harvest period) and the seven years after the cutting (post-harvest period). We used the basal area of the forest at the beginning of each growth period to evaluate the impact of the forest harvesting on its dynamics and productivity. The basal area at the beginning of the study and the basal area remaining from the harvesting are here called the initial basal area of a given period.

The dbh relative growth rate of the whole forest increased significantly from the pre-harvest period to the period after harvesting (Figure 4.2a). The same pattern was observed for commercial species, although the plot averages were smaller compared to the whole forest (Figure 4.2d). After the harvesting, dbh growth of plots subjected to harvesting compared to control plots and the plots with logging (Figure 4.2a, d). The PAI in basal area and commercial volume, however, decreased significantly in the period after harvesting (Figure 4.2b, c, d, e). The average increment of commercial volume was  $5.5 \text{ m}^3.\text{year}^{-1}.\text{ha}^{-1}$  in the growth period before harvesting and  $4.4 \text{ m}^3.\text{year}^{-1}.\text{ha}^{-1}$  after the harvesting. However, after harvesting there was no difference between the increment of harvested and unharvested plots.

The relative growth rate in diameter showed a negative relationship with the basal area during the growth period before harvesting, and this relationship became more evident after harvesting, although the difference between the two periods was not significant (Figure 4.3a, b; Appendix Table A.4). The same results were found for the set of commercial species (Figure 4.3b; Appendix Table A.4). The harvesting intensity (the % of basal area reduction), on the other hand, did no significant impact, although the highest post-harvest growth was observed in plots that were subjected to harvesting intensities above 35%. The lowest growth rates were observed in plots without tree harvesting with values of  $0.007 \text{ cm.cm}^{-1}.\text{year}^{-1}$ .

Figure 4.2 Per plot relative growth rate in diameter (a, d), periodic annual increment per hectare of basal area (b, e) and commercial volume (c, f) of the whole forest (trees, palm trees and tree ferns) and of the set of commercial species in the two growth periods. For the post-harvest period, the dark and light grey colour represent control and harvested plots, respectively.

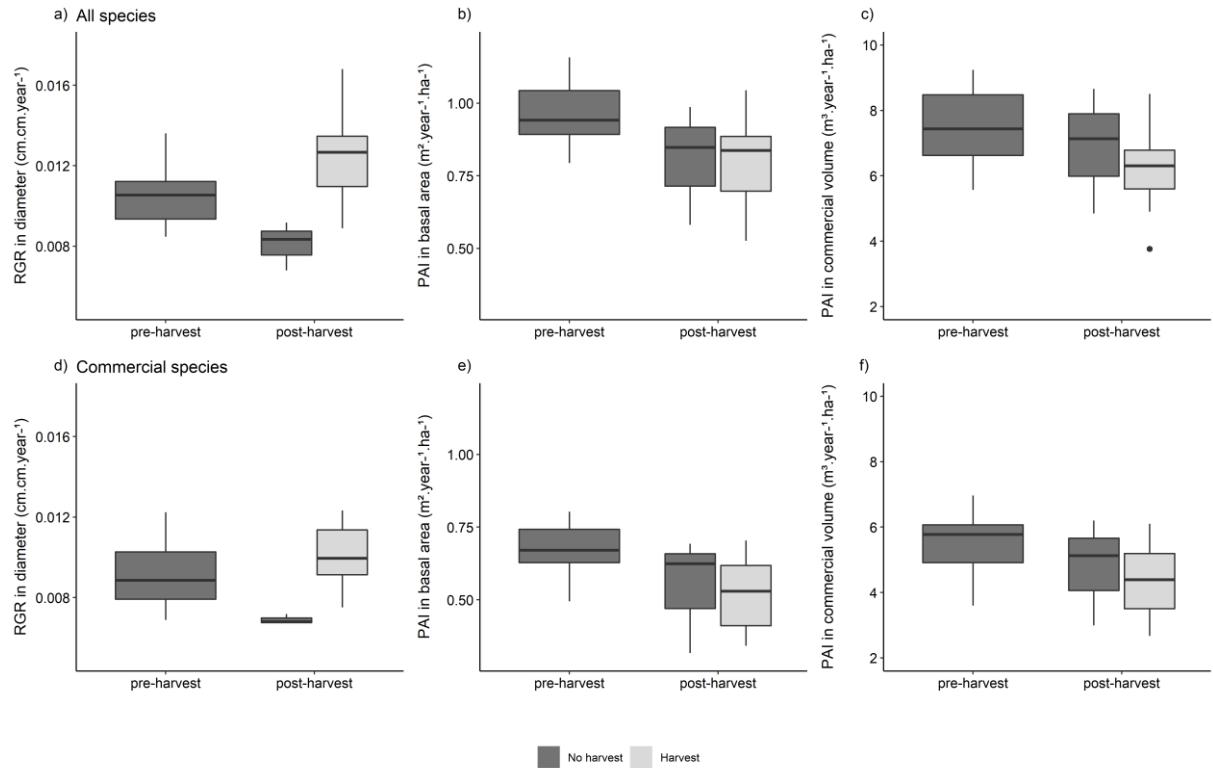
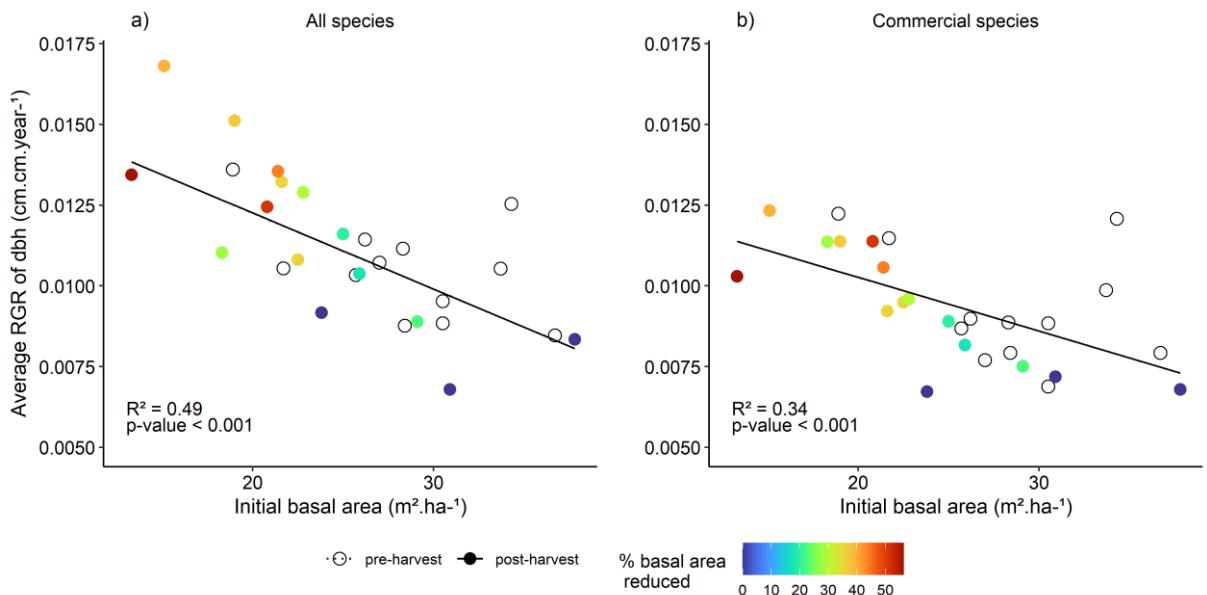
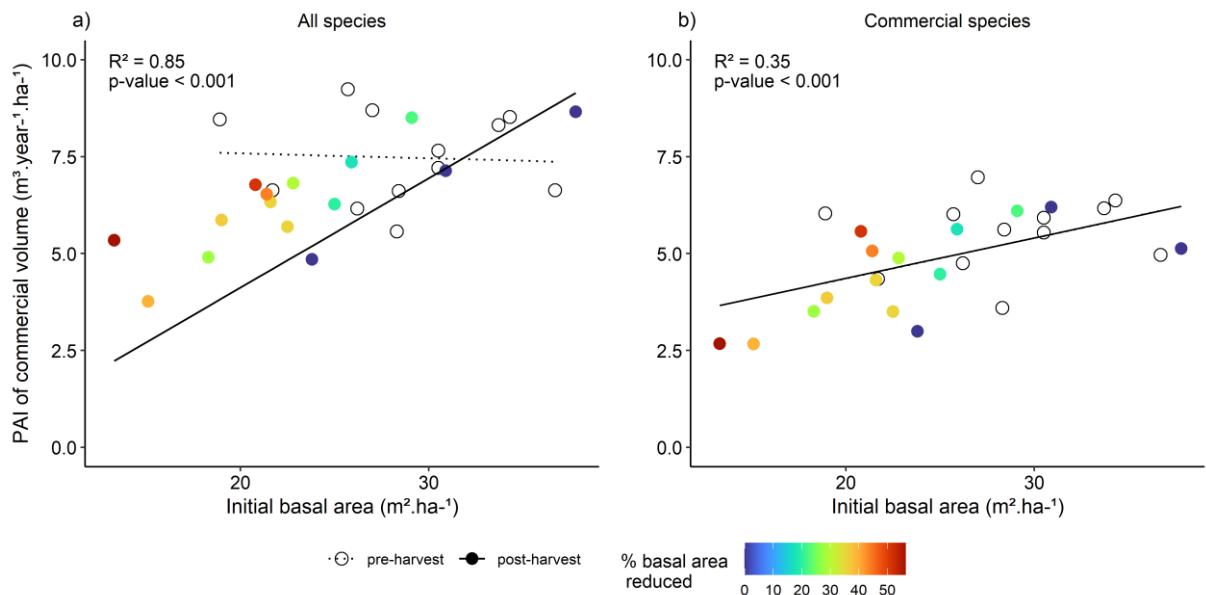


Figure 4.3 Relative diameter growth rate of the whole forest (a) and of the set of commercial species (b) as a function of the basal area at the beginning of the growth period. Each dot represents a single plot. Dot colour scale represents the % of the basal area of each plot that was reduced by the harvest.  $R^2$  is the variation explained by the full model while  $p$ -value refers to differences for the basal area of the model.



The PAI of the commercial volume of the forest before harvesting was not correlated with the forest basal area at the beginning of the measuring period (Figure 4.4a). On the other hand, the harvesting strongly impacted the increment of PAI of the commercial volume, which became negatively correlated with the initial forest basal area. The difference of increment between the two growth periods was significant ( $\chi^2 = 13.092$ ;  $p < 0.001$ ; Figure 4a; Appendix Table A.4). The intensity of harvesting, however, was not significantly correlated with the periodical increment of commercial volume, although there is an apparent trend of the intensity of harvesting being positively correlated to the initial basal area. Regarding the set of commercial species, the PAI of the volume presented a dynamic similar to the forest as a whole (Figure 4.4b). However, there was no statistical difference of increment before and after the harvesting.

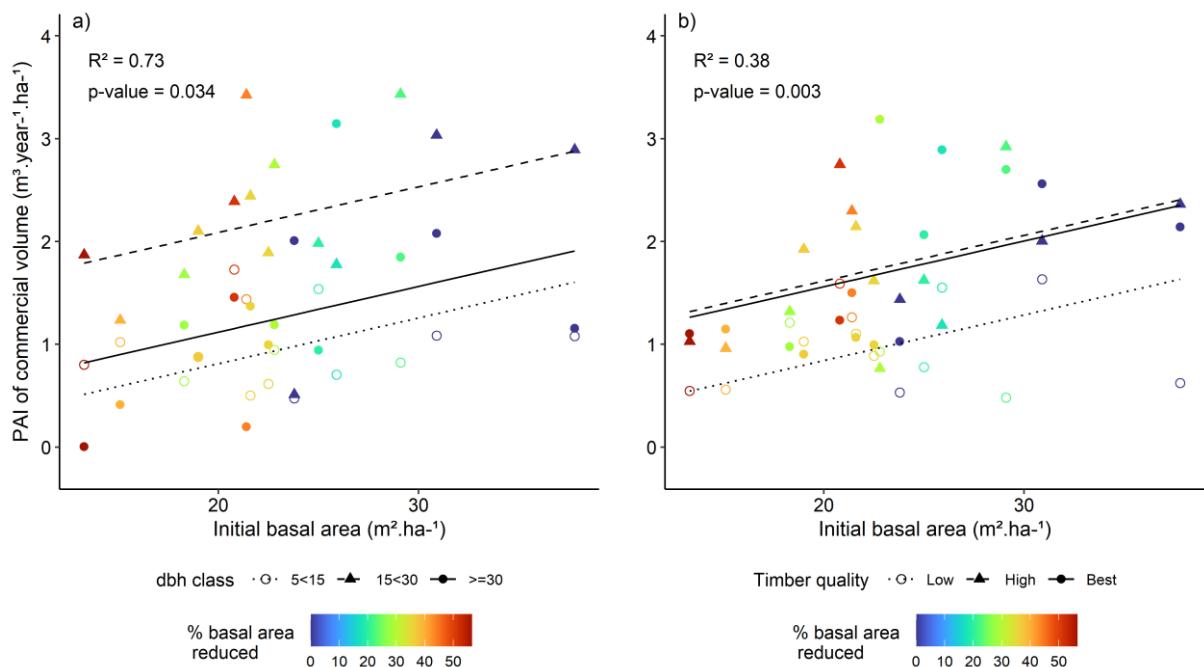
Figure 4.4 Periodic annual increment of commercial volume of the whole forest (trees, palm trees and tree ferns) (a) and the set of commercial species (b) as a function of pre-harvest (empty dots and dotted lines) and post-harvest forest basal area. Each dot represents a single plot. Dot colour scale represents the % of the initial basal area of each plot reduced by the harvesting.  $R^2$  is the variation explained by the full model (fixed + random variables) while  $p$ -value refers to differences for PAI and the basal area of the model.



For the set of commercial species, we also analysed whether the relationship between PAI of commercial volume and remaining basal area from the harvesting varied across tree dbh sizes (Figure 4.5; Appendix Table A.6). The average DBH trees ( $\text{dbh } 15 < 30 \text{ cm}$ ) showed the highest PAI and a positive relationship with the initial forest basal area ( $t\text{-value} = -3.166$ ;  $p\text{-value} = 0.003$ ; Figure 4.5a). The interaction between harvesting intensity and basal area was

determinant to increment of middle dbh class trees ( $t$ -value = 2.867;  $p$ -value = 0.007;  $t$ -value=3.300;  $p$ -value = 0.002). The PAI of smallest and biggest trees also showed significant positive interaction with harvesting intensity ( $t$ -value=2.389;  $p$ -value = 0.023; and  $t$ -value=2.216;  $p$ -value = 0.033, respectively). Commercial species were also categorised by timber quality (low, high and best). The PAI of commercial volume was higher for the high and best quality timber species, which show a positive but not significant relationship with basal area after harvesting (Figure 4.5b; Appendix Table A.6). Low quality timber species showed lower increment but showed a significant relationship with initial basal area ( $t$ -value=-3.339;  $p$ -value = 0.002).

Figure 4.5 Periodic annual increment of commercial volume of commercial species for dbh class (a) and timber quality (b) as a function of the forest basal area remaining from a selective logging. Each dot represents a single plot. Dot scale represents the % of the initial basal area of each plot reduced by harvest.  $R^2$  is the variation explained by the full model while  $p$ -value refers to differences for PAI and the initial basal area of the model.



#### 4.4.2 TREE INCREMENT

The DBH of measured trees ranged from 5 to 68 cm. Most trees (89%) grew less than 1 cm per year. However, some trees increased at rates up to 3.06 cm per year (Table 4.1). The average diameter growth rate of the set of commercial species was significantly higher in the period after harvesting of the forest (0.33 cm per year) compared to the period before harvesting

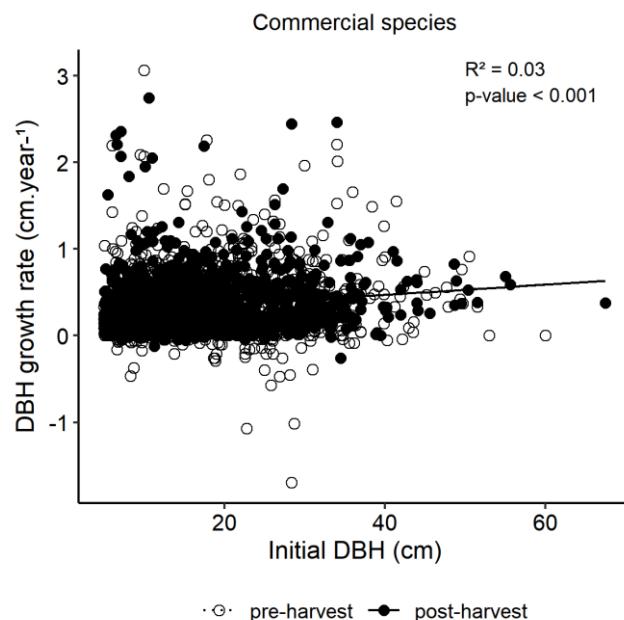
(0.30 cm per year) (Figure 4.6). Among the ten fastest periodical growth of individual trees of commercial species, six were recorded in the period after harvesting.

Table 4.1 Thirteen trees species with the greatest growth rate for both growth periods (pre- and post-harvest) in the studied forest, by ecological group and marketability.

Species	Ecological group	Growth rate (cm.year <sup>-1</sup> )
Commercial species		
<i>Schizolobium parahyba</i>	Pioneer	3.06
<i>Alchornea triplinervia</i>	Early secondary	2.75
<i>Hieronyma alchorneoides</i>	Early secondary	2.46
<i>Hieronyma alchorneoides</i>	Early secondary	2.45
<i>Annona neosericea</i>	Pioneer	2.35
<i>Cabralea canjerana</i>	Late secondary	2.31
<i>Cupania oblongifolia</i>	Early secondary	2.26
<i>Hieronyma alchorneoides</i>	Early secondary	2.21
<i>Cryptocarya</i> sp.	Climax	1.69
<i>Cryptocarya</i> sp.	Climax	1.51
Non-commercial		
<i>Ficus luschnathiana</i>	Late secondary	5.63
<i>Cecropia glaziovii</i>	Pioneer	2.98
<i>Cyathea</i> sp.	Climax	2.11

For all ecological groups, harvesting had no significant effect on tree growth rate of commercial species (Figure 4.7). On the other hand, significant differences were observed among groups (Appendix Table A.8). Most trees that presented the highest annual increase in DBH despite the growth periods evaluated were individuals from pioneer and early secondary species (Table 4.1). Before harvesting, trees of pioneer and early secondary groups presented the fastest growth rates (Figure 4.7). After harvesting, trees of early and late secondary species grew faster, especially trees from *A. triplinervia*, *H. alchorneoides*, *C. canjerana*, *P. gonoacantha* and *V. bicuhyba*, with values ranging from 2.75 to 2.07 cm.year<sup>-1</sup>.

Figure 4.6 Annual growth rate of individual trees of commercial species as a function of tree diameter (cm) at the beginning of pre-harvest period (empty circles and dashed line) and at the beginning of post-harvest period (dark circles and dark line).



Similar to the results regarding ecological groups, we found no significant difference of increments before and after harvesting for the trees grouped by timber quality (Figure 4.8). However, there was a significant difference ( $\chi^2 = 13.278$ ;  $p\text{-value} = 0.001$ ) among groups of timber quality in relation to initial dbh. The growth rate of the best quality timber species was higher before logging while the trees in the high- and low-quality timber category grew more after the forest logging. Among the trees that grew more within the best quality timber group we highlight *H. alchorneoides* and *C. canjerana*.

Figure 4.7 Growth rate in diameter of individual trees, by ecological groups, as a function of diameter (cm) at the beginning of pre-harvest period (empty circles and dashed lines) and at the beginning of post-harvest period (dark circles and dark lines).

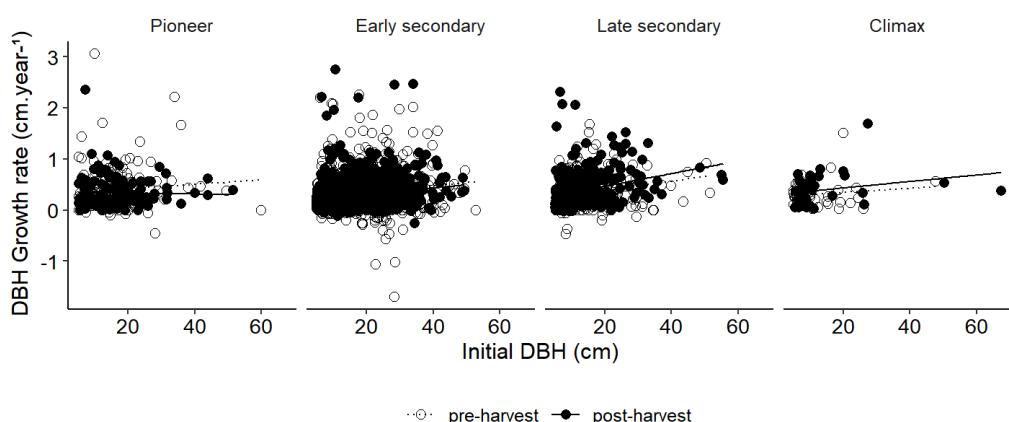
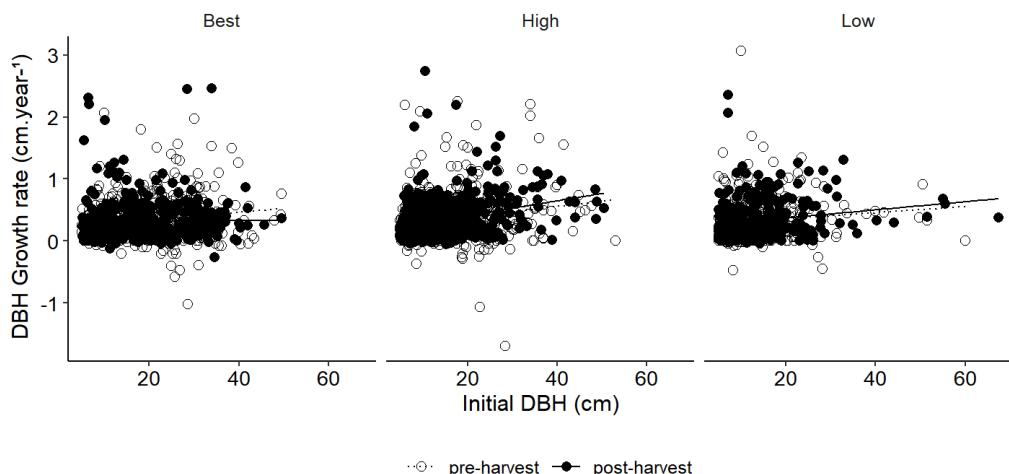
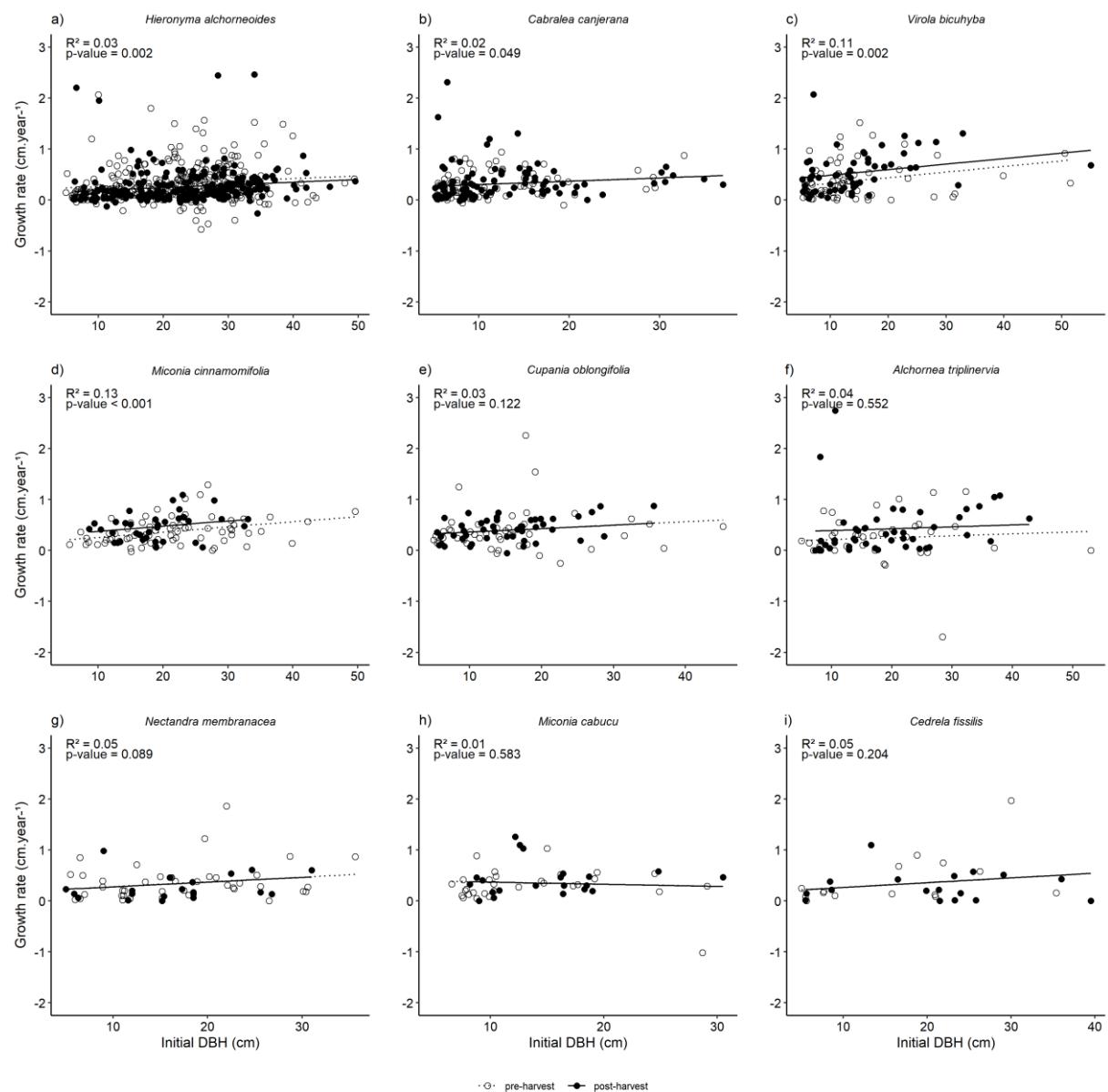


Figure 4.8 Growth rate of individual trees by timber quality as a function of diameter (cm) at the beginning of pre-harvest period (empty circles and dashed lines) and at the beginning of post-harvest period (dark circles and dark line).



Trees of nine commercially interesting timber species were selected to better analyse the diameter growth rate in both growth periods: *Alchornea triplinervia*, *Cabralea canjerana*, *Cedrela fissilis*, *Cupania oblongifolia*, *Hieronyma alchorneoides*, *Miconia cinnamomifolia*, *Miconia formosa*, *Nectandra membranacea* and *Virola bicuhyba*. A total of 704 were measured before and 587 after the forest harvesting, most of them *H. alchorneoides* (538 trees). During the twelve years of forest measurement, the trees of these species grew 0.32 cm per year, on average, while the forest growth was 0.29 cm per year. The highest growth was observed during the post-harvest period: 0.36 cm.year<sup>-1</sup>, on average, especially for *H. alchorneoides*, *M. cinnamomifolia* and *V. bicuhyba*, species that showed growth rate significantly higher after harvesting (Appendix Table A.9). Best average performances were from *V. bicuhyba* (0.53 cm per year), *M. cinnamomifolia* (0.47) and *M. cabucu* (0.42). Except for *M. cabucu*, all species showed a positive relationship between growth rate and the initial dbh in both periods (Figure 4.9).

Figure 4.9 Growth rate in dbh of individual trees of selected commercial species as a function of diameter at the beginning of pre-harvest period (empty circles and dashed line) and at the beginning of post-harvest period (dark circles and dark line).



## 4.5 DISCUSSION

In this study, we investigated the impact of tree harvesting on growth and increment of commercial species in a naturally regenerated secondary forest in the Brazilian Atlantic Forest. Results showed that commercial species had a higher rate of growth in diameter after harvest, but the recovery of basal area and commercial volume was slower in the period analysed. Harvesting altered the growth patterns of trees, causing increased growth, particularly in trees with diameters between 15 and 30 cm and belonging to early and late secondary species. Species such as *H. alchorneoides*, *M. cinnamomifolia* and *V. bicuhyba* showed significantly higher growth rates after harvest and individual trees displayed growth potential in managed forest.

### 4.5.1 GROWTH AND INCREMENT AFTER DISTURBANCE

In this study, we analysed the impact of tree harvesting on growth and production of commercial species in a secondary forest. We expected that the disturbance caused by tree harvesting would have a positive effect on the growth patterns of commercial species. The results showed that the relative growth rate in diameter had different responses to tree harvesting with regards to basal area and commercial volume. While the RGR in diameter was higher after harvest, the increment in basal area and volume was lower both for the whole forest and for the set of commercial species. In areas with selective tree logging, the RGR in diameter was significantly higher compared to pre-harvest values (Figure 4.2a). For commercial species, growth was high compared to pre-harvest values, but without significant difference (Figure 4.2d). In control areas, RGR was much lower compared to harvesting areas. Normally, with the advance of succession more mature trees become common and the forest tends to stability. As the forest matures and advances in succession, it tends to stabilise and growth slows down (GUARIGUATA; OSTERTAG, 2001). Disturbances in forest structure, however, can lead to accelerated growth of the remaining trees, and major disturbances may be necessary for some commercial species to benefit (FREDERICKSEN; PUTZ, 2003).

### 4.5.2 BASAL AREA REDUCTION IMPACTS ON GROWTH AND INCREMENT

The RGR in dbh of commercial species increased after harvesting, a probable consequence of basal area reduction. On average, trees grew more in areas where the basal area was smallest after harvesting. In areas where the intensity of harvesting was highest, the change in forest structure created a favourable environment for the growth of the remaining trees and

for the recruitment of new individuals. With the opening of the canopy, the relative growth rate of commercial species in the understory was improved due to increased light and reduced competition between individuals. These factors positively impacted the growth rate of commercial species. Research in managed forests has shown that the diameter growth rate of trees increases with cutting intensity after a harvest (FINEGAN; CAMACHO, 1999; PEÑA-CLAROS et al., 2008; SWINFIELD et al., 2016) and that high cutting intensities result in less damage to remaining trees (LIKOSKI; VIBRANS; DA SILVA, 2022), leading to increased growth of undamaged trees.

Although there was a high relative growth rate in diameter of individual trees in the harvested plots, the post-harvest annual increment of both volume and forest basal area was lower. The growth pattern changed after harvesting, as expected. Although the commercial volume of the forest increased by 21%, the seven years period was insufficient to restore the total commercial volume harvested. However, despite the limited increment in the seven-years period, the high growth in diameter of the remaining trees suggests that the forest may recover the harvested volume. The goal of sustainable forest management is to ensure that the forest can recover the harvested volume through sufficient increment of commercial species volume after harvesting (JONKERS, 2011). Before harvest, the forest had large trees that contributed greatly to the increment of both the whole forest and the commercial species. However, after harvest, small diameter trees were prevalent and contributed to the increment of forest basal area and volume, despite the increasing number (Chapter 3) and fast increment. Secondary forests under management recover the timber volume of commercial species slowly, which directly affects the volume increment (GOURLET-FLEURY et al., 2013).

#### 4.5.3 WHAT GROUP HAVE BEEN BENEFITED?

The cutting intensity had different effects on tree and species groups, as expected. When we looked at medium size trees (15 and 30 cm diameters), the increment was higher compared to the smallest and the largest trees. This result may suggest that remaining trees benefited from tree harvesting. As some commercial species grow more than others, growth in diameter favours faster recovery in volume and basal area, and middle trees may contribute to fast recovery in volume after harvest. Regarding the timber quality (low, high and best), high and best species showed higher increment of commercial volume compared to the low-quality timber species. In some cases, species with low commercial value or non-commercial value may have their growth stimulated by removal of large diameter trees and by a high cutting

intensity (VILLEGAS et al., 2009), especially fast-growing commercial species. Possibly, this lower growth may be due to the group of species of low timber quality have a lower density of individuals in the forest, a characteristic of these species with short longevity in the middle secondary stage.

#### 4.5.4 TREES OF COMMERCIAL SPECIES CAN BENEFIT FROM THE HARVEST

The high growth of individual trees demonstrated the potential of silvicultural treatments to increase timber productivity of managed forests. Increasing growth rates of commercial species trees can make secondary forest more attractive for selective logging. In the studied forest, trees of commercial species increased their growth rate after harvesting in comparison to the rates observed in the period before harvesting: the average growth of the residual trees increased by 79% in relation to the pre-harvest period. The trees of commercial species that grew above  $0.5 \text{ cm.year}^{-1}$  increased their mean growth rate from  $0.82 \text{ cm.year}^{-1}$  during the period before the logging to  $1.47 \text{ cm.year}^{-1}$  after harvesting. This set of trees represented 22 and 23 % of the total density of the forest in both growth periods, respectively. Such results line up with other studies showing that timber-producing species can benefit from disturbances caused by selective logging systems (SCHWARTZ; FALKOWSKI; PEÑA-CLAROS, 2017). Light and space are factors that drive the rapid changes in the growth pattern of residual trees and the recruitment of new ones following changes in forest structure caused by a harvesting (KUULUVAINEN, 2009; LINDENMAYER; MARGULES; BOTKIN, 2000; PARROTTA; FRANCIS; KNOWLES, 2002). New spatial arrangement among a tree and its neighbours influences the growth environment (ASHTON; KELTY, 2018). It is known that trees grow faster when they are not competing with others for forest resources (BREUGEL et al., 2012; PRETZSCH, 2009; ROZENDAAL et al., 2020) as well as the conditions for growth of smaller trees and the development of regeneration. Mid-sized trees can grow better in more favourable light conditions created by the canopy openings than in the shade of their neighbours. The increase in the growth rate of a proportion of trees affects the growth of its surroundings, either by altering the growth rate, recruiting shade-tolerant species or increasing the mortality rate of smaller individuals. In clearings opened up by harvesting, many light-demanding commercial species occur (SCHWARTZ; FALKOWSKI; PEÑA-CLAROS, 2017; SWAINE; HALL, 1983) that would benefit, with their trees having rapid growth in diameter and height (FINEGAN; CAMACHO; ZAMORA, 1999). However, undesired species may also be favoured by a high basal area reduction (DEARMOND et al., 2022; URLI et al., 2017).

Regarding the recruitment of new trees into open spaces created by the harvesting, both commercial and non-commercial trees can inhibit the growth of residual trees, especially after intense reduction of basal area. Trees of fast-growing species benefit more from canopy openings (WIENER, 2010). At the same time as the commercial trees grew, there was an increase in the density of non-commercial species with dbh above 5 cm (Chapter 3). Species such as *Cecropia glaziovii* and *Schizolobium parahyba* rapidly occupied the open spaces, while individuals from *Euterpe edulis* regenerated in the higher intensity of light in the forest understory. Our results show that *S. parahyba* is the commercial species that presented the highest dbh growth rate, while *C. glaziovii* and *E. edulis*, two non-commercial timber species, and are among the three fastest growing species seven years after harvest. In an area adjacent to that of this study, two years after a harvesting, *C. glaziovii* and *S. parahyba* were the main recruited species with dbh < 5 cm, while *Euterpe edulis* was the most recruited with dbh  $\geq$  5 cm (BRITTO et al., 2022).

The harvesting affected differently the ecological groups of commercial species. Trees of early to late secondary species, as well as low- and high-quality timber species seemed to have benefited from a better growing environment. Best quality timber species grew more during the pre-harvest period, but many of their trees were harvested, decreasing the individuals of the species in the forest. Remaining trees of early and late secondary species may have benefited from the large sunlight incidence, compared to trees of climax species. The decrease in basal area and the loss of remaining trees of climax species may suggest that harvesting removed senescent trees from the forest (LIKOSKI; VIBRANS; DA SILVA, 2022). Their results point out that low intensities can cause more damage to remaining trees, which leads to reduced growth and even mortality of trees of climax species. Competition may also have been determinant for the low growth rate of climax species. Competition among the remaining trees influence the structure of the forest, as well as the timber productivity of commercial species of interest in secondary forests. Generally, commercial species benefit from a tree harvesting, with remaining tree growth and increased recruitment. Such species may create patches of dominance within the forest in areas with greater canopy openings. In our study, these dominant species produce quality timber with good market acceptance and are classified as low, high and best quality timber. In unlogged mid- and advanced secondary forests of region of our study, commercial best quality timber species are dominant, produce high timber volume and with the advance of the successional process, tend to be replaced by other species (Zambiazi et al., 2021).

Diameter growth gives an idea of the horizontal occupation of the forest. In managed natural forests, each species may change its growth over time, according to changes in light incidence, spatiality, competition, as well as recruitment and mortality rates. Among the species that we analysed individual tree growth, *H. alchorneoides*, *M. cinnamomifolia* and *V. bicuhyba* showed changes in growth pattern after harvest and increased, while *A. triplinervia*, *C. canjerana*, *C. fissilis*, *C. oblongifolia*, *M. cabucu*, and *N. membranacea* maintained the growth pattern similar to that observed in the pre-harvest period. These nine species with individual trees growth analysis are among the most dominant in our study, both before and after tree harvest (Chapter 3).

#### 4.5.5 GROWTH AND INCREMENT OF TREES IN SECONDARY FORESTS

The selective harvesting applied to the studied forest focused on immediate economic aspect, largely disregarding a particular regeneration method. The landowner aimed trees of wood-producing species, dominant in the forest, with dbh above 20 centimetres. Nonetheless, the intervention was useful to understand the impact of a basal area reduction of the forest and some clues on further post-harvest management options, especially regarding cutting intensity. While remaining trees of commercial species showed a higher growth rate, cutting intensity is determinant for growth.

Our results suggest that remnant trees grow faster under lower competition in their surrounding. Silvicultural practices such as thinning would increase growth rates of remaining trees and promote the recruitment of commercial species regenerating in the understory. Increased growth rates accelerate the recovery of the timber stock, but there will be a trade-off between the harvesting intensity and the time required to replenish the harvested stock. In any case, however, selective harvesting seems to represent a better regeneration method as compared to clearcutting, largely used in the region, as it provides a combination of periodical timber production from a dominant species and conservation of a large diversity of species of unmature commercial and non-commercial. The maintenance of a forest covered landscape is also a clear advantage, helping to provide a series of environmental services. In such a threatened biome as the Brazilian Atlantic Forest, the sustainable production of timber may become a catalytic strategy to retain the still wide coverage of secondary forests.

#### **4.6 CONCLUSION**

Selective tree logging altered the structure, dynamics, and productivity of the studied forest. The basal area of the forest showed good correlation with the studied variables and could be used as a guide for interventions aimed at increasing the quality and productivity of the forest. The relative growth rate in diameter decreased in plots with highest basal areas after harvesting, while the increment in commercial volume increased. Trees between 15 and 30 centimeters in diameter and classified in the categories of high and best timber quality were those that responded best to canopy opening caused by harvesting. Seven years after harvesting, trees of commercial species had the highest growth ( $0.33 \text{ cm.cm}^{-1}.\text{year}^{-1}$ ) compared to pre-harvest values ( $0.30 \text{ cm.cm}^{-1}.\text{year}^{-1}$ ). These species represented 45 % of the total richness. Individual increment of most trees was less than 1.0 cm per year, but some trees of some species grew at rates up to 3.1 cm per year, suggesting that adequate forest management can improve forest productivity. However, in this study we did not distinguish the effect of species, tree dbh and the position of a tree in the forest on the individual increment, so further analysis is needed to understand the contribution of each of these factors to tree increment. The seven-year post-harvest growth period provided valuable insights into the impact of harvesting on post-intervention forest dynamics. Nonetheless, conducting longer-term inventories would be beneficial in assessing the replenishment of timber stock in the managed forest over an extended period.

## **5 CAPÍTULO 5**

### **5.1 DISCUSSÃO GERAL**

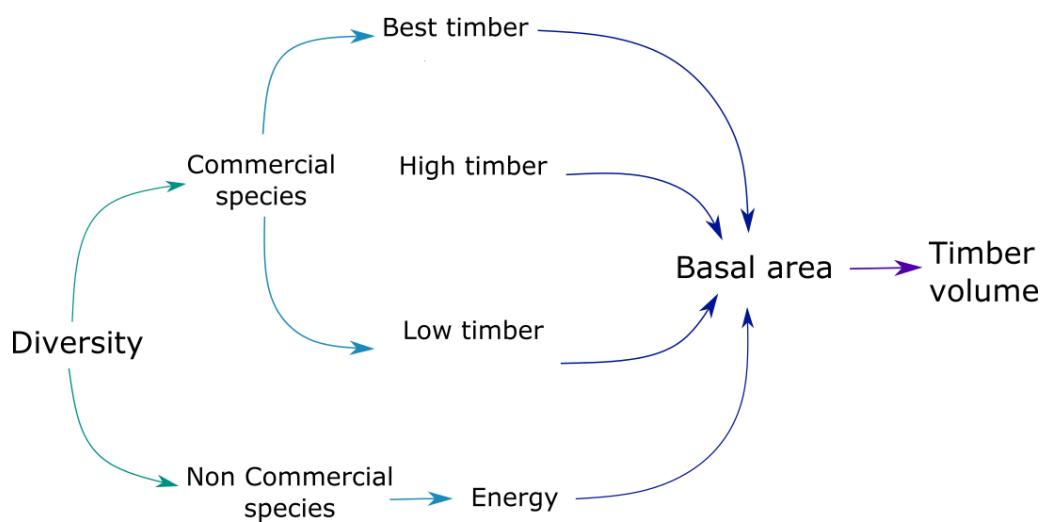
Florestas secundárias estão se tornando a principal cobertura tropical diante da grande degradação e perda de florestas primárias. Entretanto, ainda são vistas como ecossistemas de baixo potencial produtivo. Florestas secundárias apresentam um considerável volume de madeira de espécies comerciais, que poderiam contribuir significativamente para produzir renda e valorizar áreas cobertas com florestas nesses ecossistemas. Além de contribuir para a segurança da subsistência de pequenos proprietários, o manejo das florestas secundárias para serviços de provisão pode promover a conservação de grandes áreas de florestas degradadas e de áreas abandonadas pelo uso agrícola e pastagens.

Ainda são escassos os estudos que mostram o potencial das florestas secundárias para a produção de madeira de espécies comerciais. Principalmente, há escassez de estudo sobre manejo dessas florestas para múltiplos usos e para melhorar a qualidade e aumentar a produtividade de madeira, estratégia que pode tornar-se central para a conservação da cobertura florestal. O baixo custo de restabelecimento das florestas secundárias por meio da regeneração passiva (BRANCALION et al., 2016b; SIMINSKI et al., 2021; STRASSBURG et al., 2016) é um atrativo para pequenos e médios proprietários rurais. Mas, o foco em estratégias para promover o crescimento de espécies comerciais pode aumentar significativamente o valor econômico das florestas secundárias (PIOTTO, 2007).

O principal objetivo desta tese foi compreender o potencial produtivo de madeira em florestas secundárias e a dinâmica da diversidade, estrutura, crescimento e produtividade de madeira destas florestas quando manejadas para a produção de madeira por meio da colheita seletiva de árvores. O potencial de produção de madeira em florestas com até 50 anos de sucessão florestal foi avaliado no Capítulo 2. A diversidade de espécies é uma característica que torna essas florestas adequadas para o manejo (Figura 5.1), com destaque para a presença de regenerantes de espécies madeireiras desde o início do processo de sucessão. Além disso, o volume de madeira dessas espécies é superior ao das espécies não comerciais. Aos 30 anos de sucessão, as florestas secundárias da região deste estudo já possuem elevado valor de volume comercial de madeira e árvores com tamanho adequado à colheita. Essas árvores geralmente são de espécies de rápido crescimento e são dominantes nas florestas, e pertencem majoritariamente aos grupos de espécies pioneiras de vida longa e de espécies secundárias

iniciais. Nas regiões da Floresta Ombrófila Densa é muito comum a ocorrência de uma espécie com forte dominância na composição e estrutura de florestas secundárias, caracterizando fortemente uma rota sucessional. Na área deste estudo, destacamos três trajetórias sucessionais: 1. *Miconia cinnamomifolia*; 2. *Miconia formosa*; 3. *Tibouchina pulchra*. Todas essas espécies apresentaram boa produtividade de madeira. Porém, em florestas com dominância da *Tibouchina pulchra*, espécie que tem vida curta, a espécie está presente no processo sucesional por mais que 30 anos (Capítulo 2, Figura 7).

Figura 5.1. Participação da riqueza em espécies comerciais e não-comerciais e contribuição com área basal.



Os capítulos 3 e 4 desta tese concentraram resultados sobre o impacto da colheita seletiva de árvores na dinâmica de uma floresta secundária em estágio médio de sucessão. Verificamos que a colheita seletiva de madeira modificou a estrutura da floresta que, por sua vez, respondeu rapidamente ao distúrbio gerado. No período de sete anos que se seguiram à colheita, ocorreu um considerável aumento da riqueza de espécies, densidade de árvores, área basal e volume comercial para toda a floresta, embora espécies comerciais tenham apresentado recuperação relativamente mais lenta para área basal e volume comercial (Capítulo 3). O recrutamento de árvores com mais de 5 centímetros de diâmetro evidenciou a resiliência da floresta ao impacto gerado pela colheita de árvores; remanescentes apresentaram aceleração da taxa de crescimento (Capítulo 4), indicando potencial para recuperação do estoque de madeira para novo ciclo de colheita.

A composição de espécies nos primeiros anos de regeneração da floresta é determinante para o desenvolvimento da floresta. A presença de espécies comerciais produtoras de madeira e as mudanças na dominância das espécies são fatores que, de certa forma, permitem prever o comportamento dinâmico do ecossistema ao longo do processo de sucessão. A análise da dinâmica do conjunto de florestas da cronomossecuência utilizada neste estudo evidenciou as mudanças ocorridas na composição florística e na estrutura dos ecossistemas durante o processo sucessional. Entretanto, há que se destacar a presença de espécies comerciais já no início do processo sucessional, um aspecto extremamente relevante para as possibilidades de manejo econômico dessas florestas, mas ainda muito pouco abordado em estudos de florestas secundárias tropicais. A presença de espécies comerciais em florestas muito jovens implica que é possível realizar intervenções silviculturais já nos primeiros anos do processo de sucessão, promovendo o crescimento de árvores de espécies de maior valor comercial e com maior produtividade de madeira.

A regeneração de árvores de interesse comercial no manejo florestal para a produção de madeira já foi destacada como elemento central para a aplicação de sistemas silviculturais e métodos de regeneração adequado em florestas temperadas (PUETTMANN; COATES; MESSIER, 2009; SMITH, 1997). Para florestas secundárias não é diferente. A característica mais marcante de florestas secundárias da região é que essas são dominadas por espécies de rápido crescimento. Além da forte dominância, essas espécies compõem mais de 50% da riqueza de espécies, principalmente dos grupos das secundárias tardias e clímax. Outra característica importante revelada neste estudo, e que confirma relatos de outros autores sobre o tema (BRITTO et al., 2019; FANTINI et al., 2019; FANTINI; SIMINSKI, 2016), é que muitas das espécies dominantes apresentam boa qualidade de madeira e bom tamanho para produção de toras para serraria.

Algumas espécies de rápido crescimento, intolerantes à sombra e de vida curta apresentam elevada produtividade de madeira nos primeiros 20-30 anos de regeneração da floresta e se caracterizam como grandes impulsionadores da produtividade de madeira. Ao mesmo tempo, espécies tolerantes à sombra e de vida média e longa crescem no sub-bosque, e se valem de eventuais distúrbios, como queda, mortalidade ou corte de árvores do dossel, para terem o seu crescimento acelerado.

Portanto, a colheita seletiva de árvores pode alterar favoravelmente a dinâmica da floresta, principalmente acelerando o crescimento de árvores de espécies comerciais. Esse

impacto positivo foi constatado na análise dos dados da floresta estudada. Em um período de cinco anos antes da colheita, a produtividade de madeira foi alta e uma variedade de espécies contribuiu para esse incremento. Poucas espécies dominantes como *H. alchorneoides* foram responsáveis pelo grande estoque de madeira na floresta durante o período. Por ser uma espécie com madeira de alta qualidade, *H. alchorneoides* é uma espécie com elevada procura no mercado madeireiro em regiões de sua ocorrência. Na floresta estudada, ela foi responsável por 10% da dominância e pelo maior estoque de madeira da floresta. Outras espécies comerciais com esse potencial madeireiro podem ser encontradas no estágio médio de sucessão, também com boa produtividade de madeira, com destaque para *Miconia cinnamomifolia* e *Miconia formosa*.

A abertura do dossel causada pela colheita de árvores maduras e o consequente aumento da incidência luminosa pode promover o crescimento de árvores com diâmetros menores já estabelecidas no sub-bosque, ao mesmo tempo que pode promover o recrutamento de indivíduos das classes regenerantes. Este estudo evidenciou que a área basal remanescente é determinante para a dinâmica da floresta após uma colheita de árvores. Como era esperado, além das espécies de interesse comercial, outras espécies não madeireiras também podem ser beneficiadas com a colheita, como a *Cecropia glaziovii* e o *Euterpe edulis*. *E. edulis*, é uma espécie altamente desejável no manejo das florestas secundárias, para a produção de palmito e de polpa (açaí); um forte complemento à produção de madeira. Entretanto, a maior intensidade da dinâmica da floresta provocada pela abertura do dossel também beneficia outras espécies sem interesse comercial, inclusive do sub-bosque, e cuja alta densidade pode implicar grande competição com os regenerantes de espécies comerciais. Nesse caso, práticas silviculturais podem ser opção para evitar a redução do recrutamento e do crescimento das espécies de interesse.

### 5.1.1 O IMPACTO DA COLHEITA

Os resultados deste estudo mostraram que diferentes áreas basais da floresta, após uma colheita, implicam diferentes respostas para o recrutamento e a mortalidade de árvores. Taxas elevadas de recrutamento foram observadas em áreas onde a área basal foi menor, com o recrutamento de árvores de espécies comerciais, que foi maior que a mortalidade. Para o objetivo do manejo sustentável que visa a manutenção da floresta com a permanência de espécies comerciais, necessárias à recuperação do estoque de madeira, esse resultado é animador e reforça o potencial da floresta secundária para manejo policíclico.

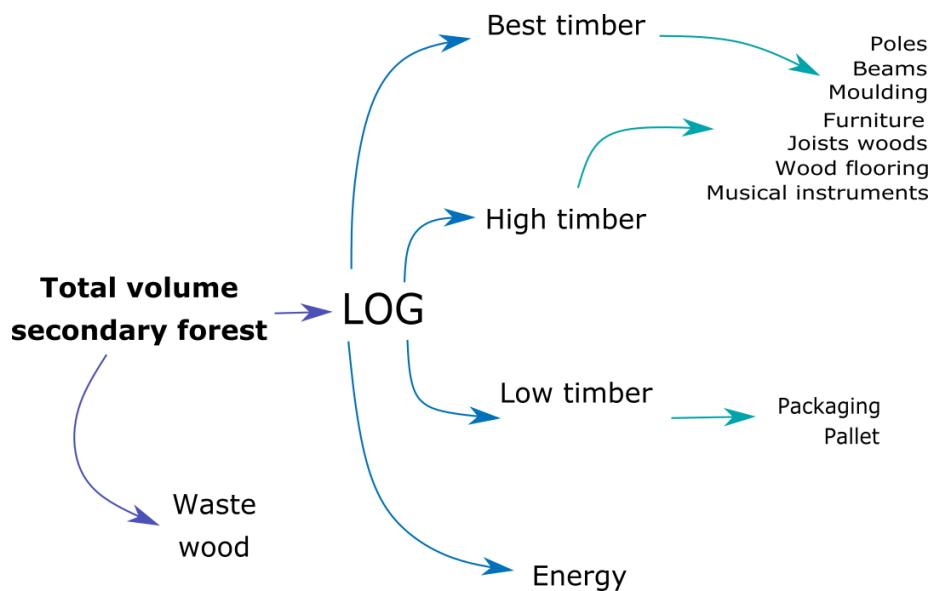
O crescimento da floresta é fortemente condicionado pela área basal da floresta. Na floresta estudada, em áreas onde a redução foi maior, a floresta cresceu mais, assim como as espécies comerciais. A abertura de espaço diminuiu a competição e árvores remanescentes crescem mais, principalmente aquelas de tamanho médio (entre 10 e 30 cm de dap). Por outro lado, não houve muitas alterações em áreas de baixa redução de área basal, onde o incremento em volume é proporcionado pelas árvores de maior diâmetro que permaneceram na floresta. O aumento do incremento de árvores individuais ficou evidente após a colheita, o que sugere que a redução de competidores vizinhos por meio de práticas silviculturais, como o corte de liberação (ASHTON; KELTY, 2018), é uma boa alternativa para o aumento da produtividade da floresta. Porém, nosso estudo não distinguiu o grau de isolamento das árvores remanescentes da colheita e a comprovação desse fato ainda está por ser realizada.

Mesmo com apenas sete anos de acompanhamento da floresta após a colheita de árvores, foi possível compreendermos alguns aspectos do impacto da colheita sobre a dinâmica da floresta, principalmente mudanças na riqueza, estrutura, taxa demográfica, crescimento da floresta e incremento das árvores. Entretanto, avaliações por mais longos períodos permitirão compor um cenário mais completo da recuperação do estoque de madeira e da permanência das espécies comerciais na floresta, além do tempo de recuperação para as diferentes áreas basais remanescentes. Entre os estudos que ainda podem ser realizados está o detalhamento do crescimento de árvores individuais após a colheita, com especial atenção ao grau de competição com os vizinhos. Também serão úteis estudos sobre o potencial das práticas silviculturais relacionadas a essa vizinhança, como os cortes e liberação e mesmo de refinamento. O estudo das classes de regenerantes com vistas ao melhoramento da floresta secundária para a produção de madeira também são ainda muito incipientes para a Mata Atlântica. O recrutamento de novos indivíduos e a mudança para a classe de adultos determina como as espécies presentes no sub-bosque mantêm a densidade de árvores adultas, tanto antes quanto após a colheita de árvores. Além da demografia dos regenerantes, o seu crescimento em diâmetro e altura é importante tema de estudo.

Ainda outro tema escassamente estudado é o rendimento em serraria das árvores típicas produzidas nas florestas secundárias, conhecimento fundamental para estimativas de valor esperado do uso da terra dessa atividade (Figura 5.2). Na floresta manejada para este estudo, foram colhidas 1.036 árvores de 54 espécies comerciais, totalizando 673 m<sup>3</sup> de madeira, que produziram 2.006 toras medindo entre 2 e 5 metros de comprimento. O rendimento de madeira

em peças serradas foi medido a partir do desdobro de 157 secções de tora em serra-fita, que geraram 1.983 peças serradas em diferentes dimensões, totalizando 19 m<sup>3</sup> de madeira serrada. Todos os dados ainda estão por serem analisados e irão fornecer importantes informações sobre o potencial econômico da colheita de árvores para a produção de madeira.

Figura 5.2. Classificação de espécies de floresta secundária e diferentes usos de madeira.



### 5.1.2 ESTRATÉGIA DE CONSERVAÇÃO E USO DE FLORESTAS SECUNDÁRIAS

Como parte das estratégias de conservação e promoção do desenvolvimento econômico sustentável, o uso múltiplo da terra é uma abordagem promissora. Uma das maneiras de aplicar essa abordagem é através da recuperação e manejo de áreas degradadas. Na Mata Atlântica, onde a paisagem é caracterizada por pequenas e médias áreas degradadas ou em regeneração após uso agrícola, o manejo de florestas secundárias pode ser uma opção viável para a produção de madeira e de outras atividades econômicas complementares. Na Amazônia, onde as áreas degradadas são vastas, a sua recuperação pode ser uma estratégia importante para evitar novos desmatamentos e promover a produção sustentável de madeira. Grandes áreas de pastagem abandonadas podem ser transformadas em florestas produtivas por meio da regeneração assistida e da formação de sistemas agroflorestais, inclusive combinando o cultivo de plantas e a criação de animais com o manejo florestal. Aumentar a produtividade de madeira em áreas degradadas pode trazer benefícios significativos tanto para o meio ambiente quanto para a

economia local. A produção de madeira certificada, por exemplo, pode gerar receita adicional para os proprietários de terra e contribuir para a conservação da floresta. Além disso, o manejo adequado da floresta pode ajudar a melhorar a qualidade do solo, aumentar a biodiversidade e reduzir a emissão de gases de efeito estufa.

Com o objetivo de promover a conservação dos ecossistemas florestais e ao mesmo tempo garantir o uso responsável dos recursos madeireiros, a seguir, há uma proposta manejo florestal sustentável para florestas secundárias. O manejo florestal sustentável é essencial para alcançar objetivos ambientais, sociais e econômicos de forma eficaz, com garantia de melhoria da produção de bens e serviços madeireiros. Planos de manejo em florestas secundárias devem levar em consideração os diferentes aspectos de cada região, com condições particulares ambientais e socioeconômicas. Inicialmente, é crucial realizar uma avaliação detalhada do potencial produtivo dessas florestas ao longo dos estágios médios e avançados de sucessão. Esse estudo deve considerar a diversidade de espécies presentes desde o início do processo de sucessão, incluindo aquelas de valor comercial. Com base nessa avaliação, será possível estabelecer diretrizes claras para o manejo adequado da floresta, considerando o tempo de vida das espécies dominantes e comerciais presentes nos primeiros 30-60 anos de sucessão. O planejamento é fundamental para determinar a estratégia a ser adotada ao longo dos anos, com benefícios na tomada de decisão e informações sobre o estado das florestas.

Umas das principais abordagens a serem adotadas é a colheita seletiva de árvores maduras, levando em consideração o impacto na dinâmica da floresta em estágio médio de sucessão. Essa prática deverá ser cuidadosamente planejada, analisando as mudanças na estrutura da floresta, o recrutamento de novas árvores e o crescimento das espécies comerciais. Com a colheita de árvores, será possível equilibrar a extração de madeira com a regeneração natural da floresta. Alguns métodos de regeneração podem ser adotados no manejo florestal para produção de madeira, como corte raso, o corte seletivo, o método de cobertura tropical (*shelterwood*), e método de árvores matrizes porta-sementes (*seed tree cutting*). Cada método é adequado para situações específicas de manejo florestal e possui vantagens e desvantagens. No caso da Mata Atlântica, a prática de corte raso é legalmente proibida em áreas de floresta com mais de 10 anos de regeneração natural.

Além disso, o manejo do sub-bosque desempenha um papel crucial na regeneração e no enriquecimento da floresta. A abertura do dossel resultante da colheita seletiva pode criar condições favoráveis para o crescimento de árvores no sub-bosque e o recrutamento de novos

indivíduos. Os planos de manejo podem adotar medidas para evitar a competição excessiva entre as espécies comerciais e outras espécies presentes, promovendo a diversidade e o equilíbrio no ecossistema. O desbaste florestal pode ser adotado para diminuir a competição entre árvores e promover o crescimento de indivíduos desejáveis de forma mais ativa.

Um aspecto essencial do manejo é o monitoramento contínuo do crescimento das árvores remanescentes após a colheita seletiva. Estudos de longo prazo permitirão melhor compreender a recuperação do estoque de madeira e a permanência das espécies comerciais na floresta. Também permitirão fundamentar a identificação de práticas silviculturais adequadas para promover o crescimento e o incremento do volume comercial da madeira. Outro ponto importante é determinar o tempo de recuperação necessário para diferentes áreas basais remanescentes, levando em conta a sustentabilidade do manejo florestal e a conservação da biodiversidade. Com base no tempo de recuperação para diferentes áreas basais remanescentes será possível estabelecer o período entre ciclos de corte em um sistema policíclico, além de diretrizes claras para garantir a regeneração adequada da floresta e a continuidade dos serviços ecossistêmicos.

A participação ativa dos proprietários rurais é fundamental para o sucesso desse manejo florestal sustentável, buscando envolvê-los principalmente através da sua capacitação técnica, mas com valorização dos conhecimentos tradicionais associados ao uso dessas florestas, com incentivo à conservação das florestas secundárias de forma permanente na paisagem. Essa participação fortalecerá os laços entre as comunidades e a floresta, tornando-as aliadas na busca pela sustentabilidade e em soluções baseadas na natureza.

A conservação da biodiversidade está integrada às práticas de manejo florestal, visando à proteção de espécies ameaçadas, à preservação de habitats importantes e à manutenção dos processos ecológicos essenciais. Esse enfoque garantirá a sustentabilidade do fornecimento de madeira e a preservação da diversidade biológica. A continuação do manejo dependerá de um sistema de monitoramento e avaliação contínuos para acompanhar os resultados da colheita seletiva de árvores para realizar ajustes necessários, em especial a eliminação de espécies invasoras e inibidoras de crescimento de espécies comerciais e a condução de árvores de espécies de interesse. Com base nessas avaliações, também é possível adaptar as estratégias para atender às mudanças nas condições ambientais e socioeconômicas.

Parcerias entre órgãos governamentais, organizações não governamentais, setor privado e comunidades locais podem fortalecer e favorecer a implementação do manejo florestal

sustentável. Essas cooperações são fundamentais para garantir o cumprimento das diretrizes estabelecidas e promover o uso responsável dos recursos florestais.

Programas de manejo florestal podem destacar a importância da educação ambiental para conscientizar e promover a compreensão dos benefícios do manejo florestal sustentável, por meio do envolvimento da população em geral. Essa abordagem visa transmitir conhecimento sobre a conservação das florestas secundárias e a valorização dos recursos naturais. Planos de manejo em florestas secundárias devem conciliar a produção de madeira com a conservação dos ecossistemas, gerando benefícios econômicos, sociais e ambientais a longo prazo. Com a implementação dessas práticas de manejo florestal sustentável, poderemos garantir a preservação das florestas secundárias e promover o desenvolvimento sustentável de nossas comunidades.

Em conclusão, as florestas secundárias apresentam um considerável potencial produtivo de madeira de espécies comerciais, o que pode contribuir significativamente para a geração de renda e valorização dessas áreas cobertas de florestas. Embora ainda sejam escassos os estudos sobre manejo dessas florestas para múltiplos usos e o aumento da produtividade de madeira de qualidade, os resultados obtidos até o momento são promissores.

Com uma considerável diversidade de espécies desde o início do processo de sucessão, florestas secundárias apresentam espécies de rápido crescimento e bom volume de madeira. Aos 30 anos de sucessão, essas florestas já possuem um alto valor de volume comercial de madeira e árvores com tamanho adequado para a colheita. A colheita seletiva de árvores nessas florestas pode modificar sua estrutura, mas também pode impulsionar o crescimento de árvores de espécies comerciais, promovendo a recuperação do estoque de madeira para futuras colheitas.

A composição de espécies e as mudanças na dominância ao longo do processo sucesional podem ser indicativos de como a floresta se desenvolverá. Espécies comerciais produtoras de madeira estão presentes desde o início do processo sucesional, o que permite intervenções silviculturais precoces para promover o crescimento dessas espécies. Além disso, as florestas secundárias são dominadas por espécies de rápido crescimento, muitas das quais têm boa qualidade de madeira e tamanho adequado para produção de toras para serraria.

A colheita seletiva de árvores altera a dinâmica da floresta e, se bem planejada e executada, pode beneficiar o crescimento de árvores menores já estabelecidas no sub-bosque e

promover o recrutamento de novas árvores de interesse. A área basal resultante da colheita e a abertura do dossel são fatores determinantes nessa dinâmica, e pode influenciar o crescimento e o incremento do volume comercial das árvores remanescentes. O crescimento da floresta está diretamente relacionado à área basal, sendo que áreas com maiores redução apresentam maior crescimento, principalmente de espécies comerciais. A competição entre as árvores remanescentes pode ser reduzida por meio de práticas silviculturais, o que pode aumentar a produtividade da floresta. No entanto, são necessários estudos de longo prazo para compreender melhor a recuperação do estoque de madeira e a permanência das espécies comerciais após a colheita. Ainda são necessárias pesquisas sobre o crescimento individual das árvores após a colheita, a taxa demográfica e o crescimento dos regenerantes, além do rendimento em serraria das espécies típicas das florestas secundárias. Esses estudos contribuirão para o aperfeiçoamento do manejo das florestas secundárias para a produção de madeira de qualidade.

Florestas secundárias apresentam um potencial produtivo de madeira significativo e podem desempenhar um papel importante na oferta de madeira, especialmente em regiões onde a disponibilidade de florestas primárias é limitada ou onde a exploração madeireira sustentável é uma prioridade. No contexto das mudanças do clima, as florestas secundárias podem também contribuir para a mitigação e adaptação às emissões de gases do efeito estufa, uma vez que têm o potencial de sequestrar grandes quantidades de carbono atmosférico. Além disso, a restauração e o manejo adequado dessas florestas podem ajudar a aumentar sua resiliência frente aos impactos das mudanças do clima. Este estudo evidenciou que as florestas secundárias apresentam um grande potencial para a produção de madeiras de boa qualidade, para a conservação da biodiversidade e, por conseguinte, na mitigação das mudanças climáticas.

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# APÊNDICES

## Chapter 2

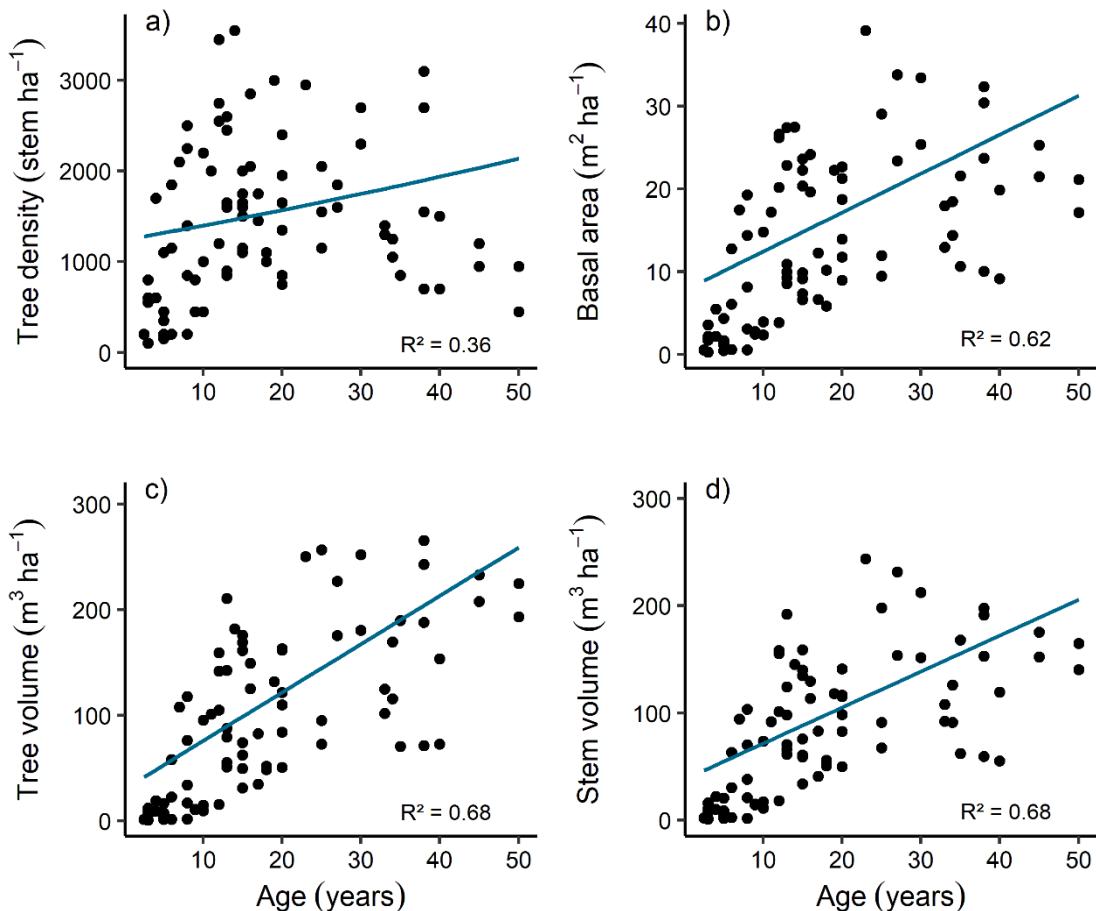
Appendix for

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

#### 1. APPENDIX FIGURES AND TABLES

##### 1.1. FIGURES

**Fig.A.1.** Tree density, basal area and volume of secondary forests from 2 to 50 years old. Data includes trees, palm trees and tree ferns with a diameter  $\geq 5$  cm at 1.3 m in height. Dots represent individual plots (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.



## 1.2. SUPPLEMENTARY TABLES

**Table A.1.** Timber products and market price by commercial timber species of the secondary forest in dense ombrophilous forest of the Brazilian Atlantic Forest. The classification was based on information provided literature, owners of the study area and the owner of a timber mill.

Species	Work quality	Timber quality	Timber products	US\$
<i>Alchornea glandulosa</i>	Soft wood	Low	crate; pallet	90
<i>Alchornea triplinervia</i>	Soft wood	High	beams; box board; joist wood	90
<i>Andira fraxinifolia</i>	Hard wood	High	beams; box board; furniture; wood flooring	330
<i>Annona neosericea</i>	Soft wood	Low	crate; pallet	140
<i>Aspidosperma parvifolium</i>	Hard wood	Best	beams; furniture; wood flooring	360
<i>Cabralea canjerana</i>	Hard wood	Best	pools; wooden board; wood flooring	416
<i>Calyptrothamnus lucida</i>	Hard wood	High	beams; joist wood	330
<i>Casearia decandra</i>	Hard wood	High	beams; joist wood; wooden board	330
<i>Casearia sylvestris</i>	Hard wood	High	beams; joist wood; wooden board	330
<i>Cedrela fissilis</i>	Intermediary	Best	furniture; wooden board; wooden ceiling	360
<i>Citharexylum myrianthum</i>	Soft wood	High	box board; crate; joist wood; wooden ceiling	330
<i>Cryptocarya moschata</i>	Hard wood	High	beams	310
<i>Cupania oblongifolia</i>	Hard wood	High	beams; joist wood; wooden board	330
<i>Guapira opposita</i>	Soft wood	Low	crate; pallet	90
<i>Hieronima alchorneoides</i>	Hard wood	Best	beams; box board; furniture; wood flooring	330
<i>Inga sessilis</i>	Soft wood	Low	box board; crate	140
<i>Jacaranda puberula</i>	Soft wood	High	box board; musical instrument; wooden ceiling	350
<i>Jacaranda micrantha</i>	Hard wood	Best	furniture; wood flooring	390
<i>Lonchocarpus campestris</i>	Soft wood	High	crate; joist wood; pallet; wooden ceiling	100
<i>Magnolia ovata</i>	Soft wood	High	box board; crate; wooden board	140
<i>Matayba intermedia</i>	Hard wood	High	beams; joist wood; wooden board	330
<i>Miconia cabucu</i>	Hard wood	Best	beams; joist wood; wooden board	330
<i>Miconia cinnamomifolia</i>	Hard wood	Best	beams; box board; furniture; wood flooring	330
<i>Myrcia tomentosa</i>	Hard wood	High	beams; joist wood	330
<i>Nectandra membranacea</i>	Soft wood	High	box board; joist wood; wooden board; wooden ceiling	330

<i>Nectandra oppositifolia</i>	Intermediary	Best	beams; furniture; wooden board; wood ceiling	350
<i>Ocotea catharinensis</i>	Hard wood	Best	furniture; wood flooring	360
<i>Ocotea pulchella</i>	Intermediary	Best	beams; joist wood; wooden board	350
<i>Pausandra morisiana</i>	Hard wood	High	beams; construction; joist wood	330
<i>Piptadenia gonoacantha</i>	Hard wood	High	beams; box board; furniture; wood flooring	330
<i>Piptocarpha axillaris</i>	Soft wood	Low	crate; pallet	90
<i>Posoqueria latifolia</i>	Hard wood	High	box board; joist wood; wood flooring	330
<i>Protium kleinii</i>	Hard wood	High	beams; construction; joist wood	330
<i>Psychotria carthagrenensis</i>	Intermediary	High	beams; joist wood	330
<i>Schizolobium parahyba</i>	Soft wood	Low	crate; pallet	90
<i>Sloanea guianensis</i>	Hard wood	High	beams; joist wood	330
<i>Tapirira guianensis</i>	Soft wood	Low	crate; pallet	90
<i>Trichilia lepidota</i>	Intermediary	High	beams; joist wood; wooden board; wooden ceiling	330
<i>Vernonanthura puberula</i>	Soft wood	Low	crate; pallet	140
<i>Vernonanthura discolor</i>	Soft wood	Low	crate; pallet	330
<i>Virola bicuhyba</i>	Soft wood	Low	crate; pallet	90
<i>Xylopia brasiliensis</i>	Hard wood	High	beams; box board; joist wood	330
<i>Zanthoxylum rhoifolium</i>	Soft wood	Low	crate; pallet	90

**Table A.2.** Number of individuals, dbh and height and timber quality by species in secondary forests in dense ombrophilous forest of the Brazilian Atlantic Forest.

Family	Species	Timber quality	N ind	dbh Max	Height Max
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	Low	2	20.3	8
Annonaceae	<i>Annona neosericea</i> H. Rainer	Low	7	19.2	12
	<i>Annona sericea</i> Dunal	Low	5	10.5	12
	<i>Annona</i> sp.	Low	1	5.7	5
	<i>Annona sylvatica</i> (A. St.-Hill.) Mart.	Low	5	21.5	12
	<i>Duguetia lanceolata</i> A. St.-Hill.	Low	3	10.0	16
	<i>Guatteria australis</i> A. St.-Hill.	Low	3	10.7	7
	<i>Xylopia brasiliensis</i> Spreng.	High	9	16.1	12
Apocynaceae	<i>Aspidosperma australe</i> Müell. Arg.	Best	1	6.4	8
	<i>Aspidosperma parvifolium</i> A. DC.	Best	4	46.0	19
	<i>Tabernaemontana catharinensis</i> A. DC.	Non-comm	1	9.0	10
Aquifoliaceae	<i>Ilex brevicuspis</i> Reissek	Non-comm	4	8.4	8
	<i>Ilex dumosa</i> Reissek	Non-comm	2	6.4	5
	<i>Ilex microdonta</i> Reissek	Non-comm	2	11.6	8
	<i>Ilex theezans</i> Mart.	Non-comm	7	8.3	13
Araliaceae	<i>Schefflera angustissima</i> (Marchal) Frodin	Non-comm	1	5.0	7
Arecaceae	<i>Bactris setosa</i> Mart.	Non-comm	2	5.8	4
	<i>Euterpe edulis</i> Mart.	Non-comm	62	19.0	15
	<i>Geonoma gamiova</i> Barb.	Non-comm	5	7.5	5
	<i>Geonoma schottiana</i> Mart.	Non-comm	4	8.0	2.2
	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Non-comm	2	9.4	5
Asteraceae	<i>Baccharis calvescens</i> A. P. Candole	Non-comm	12	13.2	6
	<i>Baccharis dracunculifolia</i> DC.	Non-comm	11	13.2	6
	<i>Baccharis elaeagnoides</i> Steud.	Non-comm	10	11.0	6
	<i>Baccharis</i> sp.	Non-comm	15	14.6	6.2
	<i>Piptocarpha angustifolia</i> Dusén ex Malme	Low	19	34.0	11
	<i>Piptocarpha axillaris</i> (Less.) Baker	High	3	14.3	12
	<i>Vernonanthura discolor</i> (Spreng.) H. Rob.	Low	32	20.2	12
	<i>Vernonanthura puberula</i> (Less.) H. Rob.	Low	4	10.3	10
Bignoniaceae	<i>Jacaranda micrantha</i> Cham.	Best	23	12.1	13.8
	<i>Jacaranda puberula</i> Cham.	High	13	10.5	7.5
	<i>Tabebuia</i> sp. Candl.	High	2	11.5	8
	<i>Tabebuia umbellata</i> (Sond.) Sandw.	High	1	7.2	7
Burseraceae	<i>Protium kleinii</i> Cuatrec.	High	2	10.8	14
Calophyllaceae	<i>Calophyllum brasiliense</i> Camb.	Best	3	13.0	13
Cannabaceae	<i>Trema micrantha</i> (L.) Blume	Low	2	8.9	7.8
Celastraceae	<i>Monteverdia robusta</i> Reiss.	High	2	6.2	5.5
Chlorantaceae	<i>Hedyosmum brasiliensis</i> Mart.	Low	6	15.0	7
Chrysobalanaceae	<i>Hirtella hebeclada</i> Moric. ex DC.	High	4	35.2	15
Clethraceae	<i>Clethra scabra</i> (Meiss.) Sleum	High	20	18.0	9
Clusiaceae	<i>Clusia criuva</i> Camb.	Non-comm	6	17.9	12
	<i>Clusia parviflora</i> (Saldanha) Engler	Non-comm	5	12.0	11.5
	<i>Garcinia Gardneriana</i> (Planch. & Triana) Zappi	Low	8	14.4	13
Combretaceae	<i>Terminalia australis</i> Camb.	Non-comm	2	8.1	6.5
Cunoniaceae	<i>Lamanonia ternata</i> Vell.	High	1	5.6	6.5
Cyatheaceae	<i>Cyathea corcovadensis</i> (Raddi) Domin	Non-comm	7	10.0	9
	<i>Cyathea delgadii</i> Sternb.	Non-comm	20	15.7	11
	<i>Cyathea</i> sp.	Non-comm	4	7.0	5

Ebenaceae	<i>Diospyros inconstans</i> Jacq.	Non-comm	2	5.2	7
Elaeocarpaceae	<i>Sloanea guianensis</i> (Aubl.) Benth.	High	19	38.0	18
Erythroxylaceae	<i>Erythroxylum myrsinoides</i> Mart.	High	3	8.7	8
Euphorbiaceae	<i>Actinostemon concolor</i> (Spreng.) Müell. Arg.	High	3	18.8	15
	<i>Alchornea glandulosa</i> Poepp. & Endl.	Low	2	10.0	13
	<i>Alchornea iricurana</i> Cesar.	High	1	7.2	7.5
	<i>Alchornea sidifolia</i> Müell. Arg.	High	1	6.0	5
	<i>Alchornea triplinervia</i> (Spreng.) Müell. Arg.	High	10	24.6	16
	<i>Manihot grahamii</i> Hook.	Non-comm	2	10.2	15
	<i>Maprounea guianensis</i> Aubl.	Low	1	15.4	13
	<i>Pausandra morisiana</i> (Casar.) Radlk.	High	2	6.3	6.5
	<i>Sapium glandulosum</i> (L.) Morong	High	1	6.6	5
	<i>Tetrorchidium rubrivenium</i> Poepp.	Non-comm	2	17.2	9
Fabaceae	<i>Abarema langsdorffii</i> (Benth.) Barneby & J. W. Grimes	Non-comm	3	8.5	8
	<i>Andira anthelmintica</i> Benth.	High	2	8.5	8.6
	<i>Andira fraxinifolia</i> Benth.	High	3	7.8	7
	<i>Copaifera trapezifolia</i> Hayne	High	2	7.8	11
	<i>Dalbergia frutescens</i> Britton	Non-comm	1	5.1	6
	Fabaceae sp.	Non-comm	1	13.2	11
	<i>Inga marginata</i> Willd.	Non-comm	7	35.5	12
	<i>Inga sessilis</i> (Vell.) Mart.	Low	4	32.0	16
	<i>Inga</i> sp.	Non-comm	3	15.4	15
	<i>Inga uruguensis</i> Hook. et Arn.	Non-comm	1	7.4	10
	<i>Inga virescens</i> Benth.	Non-comm	1	8.5	9
	<i>Lonchocarpus campestris</i> Mart. ex Benth.	High	6	10.2	7
	<i>Mimosa bimucronata</i> (DC.) O. Ktze.	Non-comm	11	34.0	12
	<i>Ormosia arborea</i> (Vell.) Harms	Non-comm	2	6.5	5
	<i>Piptadenia gonoacantha</i> (Mart.) J. F. Macbr.	High	3	36.0	20
	<i>Piptadenia paniculata</i> Benth.	High	1	5.5	10
	<i>Schizolobium parahyba</i> (Vell.) Blake	Low	1	15.4	7.5
Flacourtiaceae	<i>Zollernia ilicifolia</i> (Brongn.) Vogel	Non-comm	5	15.6	10
Lamiaceae	<i>Banara parviflora</i> (A. Gray) Benth.	Non-comm	3	11.1	7
Lauraceae	<i>Aegiphila integrifolia</i> (Jacq.) Moldenke	Low	5	15.5	14.2
	<i>Cryptocarya moschata</i> Mez. & Mart.	High	3	42.0	15
	<i>Endlicheria paniculata</i> (Spreng.) J. F. Macbr.	Low	2	11.4	11
	<i>Nectandra lanceolata</i> Nees et Mart. ex Nees	Best	10	27.0	14
	<i>Nectandra leucothrysus</i> Meisn.	Best	2	31.5	16
	<i>Nectandra megapotamica</i> Mez.	Best	8	43.0	13
	<i>Nectandra membranacea</i> (Sw.) Griseb.	High	8	52.0	17
	<i>Nectandra oppositifolia</i> Rol. ex Rottb.	Best	13	35.7	17
	<i>Nectandra rigida</i> (Kunth) Nees	High	1	15.8	13
	<i>Nectandra</i> sp.	High	1	8.0	10
	<i>Ocotea catharinensis</i> Mez.	Best	1	7.7	10
	<i>Ocotea pulchella</i> (Nees & Mart.) Mez	Best	14	20.3	12
	<i>Ocotea</i> sp.	High	3	26.7	20
	<i>Ocotea teleiandra</i> (Meisn.) Mez.	High	1	21.0	12
Loganiaceae	<i>Ocotea urbaniana</i> Mez.	Low	1	5.4	7
Magnoliaceae	<i>Strychnos brasiliensis</i> (Spreng.) Mart.	Non-comm	1	5.2	4.5
Malpighiaceae	<i>Magnolia ovata</i> (A. St.-Hill.) Spreng.	High	1	24.5	15
	<i>Byrsonima ligustrifolia</i> A. Juss.	Non-comm	1	21.1	14

Melastomataceae	<i>Huberia semiserrata</i> DC.	Non-comm	29	22.5	10
	<i>Miconia cinerascens</i> Miq.	Low	7	8.0	7.5
	<i>Miconia cinnamomifolia</i> (DC.) Naudin	Best	227	27.3	20
	<i>Miconia cubatanensis</i> Hoehne	Non-comm	5	11.0	12
	<i>Miconia flammea</i> Cesar.	Non-comm	2	6.0	7
	<i>Miconia formosa</i> Cogn	Best	100	34.6	18
	<i>Miconia latecrenata</i> (DC.) Naud.	Non-comm	8	19.1	20
	<i>Miconia ligustroides</i> (DC.) Naud.	Non-comm	6	15.9	10.5
	<i>Miconia rigidiuscula</i> Cogn.	High	56	22.6	11
	<i>Miconia</i> sp. 1	Non-comm	5	11.5	12
	<i>Miconia</i> sp. 2	Non-comm	2	7.4	6.9
	<i>Miconia valtheri</i> Ruiz & Pavón	Non-comm	4	7.0	4.5
	<i>Tibouchina granulosa</i> (Desr.) Cogn.	Non-comm	5	6.4	5.5
	<i>Tibouchina pulchra</i> Cogn.	Low	594	35.2	18
	<i>Tibouchina sellowiana</i> (Cham.) Cogn.	Non-comm	8	14.3	9
	<i>Tibouchina trichopoda</i> Baill.	Non-comm	7	12.7	10
Meliaceae	<i>Cabralea canjerana</i> (Vell.) Mart.	Best	7	37.0	17
	<i>Cedrela fissilis</i> Vell.	Best	3	11.7	9
	<i>Guarea macrophylla</i> Vahl	Low	15	10.9	9
	<i>Trichilia elegans</i> A. Juss.	High	3	9.6	18
	<i>Trichilia lepidota</i> Mart.	High	5	10.2	7
Monimiaceae	<i>Mollinedia</i> sp.	Non-comm	2	6.4	5
	<i>Mollinedia triflora</i> (Spreng.) Tul.	Non-comm	2	17.8	11
Moraceae	<i>Brosimum lactescens</i> (S. Moore) C. C. Berg	Non-comm	4	23.7	11
	<i>Ficus luschnathiana</i> (Miq.) Miq.	Non-comm	3	11.2	7
	<i>Ficus organensis</i> (Miq.) Miq.	Non-comm	3	32.5	10.5
	<i>Sorocea bonplandii</i> (Baill.) W. C. Burger et al.	Low	3	10.0	5.5
Morfo specie	Morfo specie 1	Non-comm	1	6.9	8
Myristicaceae	<i>Virola bicuhyba</i> (Schott ex Spreng.) Warb.	Low	13	21.3	15
Myrtaceae	<i>Campomanesia guaviroba</i> (DC.) Kaiaerskou	Non-comm	2	12.4	10
	<i>Campomanesia reitziana</i> Legr.	Non-comm	2	24.0	15
	<i>Campomanesia</i> sp. Legr.	Non-comm	4	16.2	11
	<i>Campomanesia xanthocarpa</i> (Mart.) O. Berg	Non-comm	4	29.8	7
	<i>Eugenia playtsema</i> O. Berg.	Non-comm	1	12.4	6.5
	<i>Myrcia eugeniosioides</i> (Kaus. & Legr.) Legr.	Low	15	29.4	15
	<i>Myrcia excoriata</i> (Mart.) E. Lucas & C. E. Wilson	Non-comm	1	8.7	3
	<i>Myrcia gracilis</i> Berg.	Non-comm	3	6.3	6
	<i>Myrcia lucida</i> Mart. ex DC.	Non-comm	1	10.0	8
	<i>Myrcia palustris</i> (DC.) D. Legrand	Non-comm	1	5.0	4
	<i>Myrcia rostrata</i> (Sw.) DC.	Non-comm	6	9.2	7
	<i>Myrcia spectabilis</i> DC.	Non-comm	3	6.5	11
	<i>Myrcia splendens</i> (Sw.) DC.	Non-comm	11	11.7	11
	<i>Myrcia strigipes</i> O. Berg	Non-comm	3	20.0	12
	<i>Myrcia tomentosa</i> (Aubl.) DC.	High	8	12.7	9
	<i>Myrciaria pliniodoides</i> C. D. Legrand	Non-comm	1	6.0	3
	Myrtaceae sp. 1	Non-comm	1	9.0	8.1
	Myrtaceae sp. 2	Non-comm	5	11.0	12
	<i>Psidium cattleianum</i> Sabine	High	3	10.0	12
Nyctaginaceae	<i>Guapira hirsuta</i> (Choisy) Lundell	Low	6	14.0	8.5
	<i>Guapira opposita</i> (Vell.) Reitz	Low	26	32.5	18

	<i>Pisonia ambigua</i> Heimerl.	High	2	33.3	17
Ochnaceae	<i>Ouratea parviflora</i> (A. DC.) Baill.	Non-comm	7	16.5	11
Olacaceae	<i>Heisteria silvianii</i> Schwacke	Non-comm	8	18.7	13
Oleaceae	<i>Chionanthus filiformis</i> (Vell.)	Non-comm	1	7.4	4.5
Peraceae	<i>Pera labrata</i> (Schott) Poepp. ex Baill.	High	51	18.1	13
Phyllanthaceae	<i>Hyeronima alchorneoides</i> Allem.	Best	85	31.0	24
Phytolaccaceae	<i>Phytolacca dioica</i> L.	Non-comm	2	9.5	10
Piperaceae	<i>Piper gaudichaudianum</i> Kuntze	Non-comm	1	5.7	9
Polygonaceae	<i>Coccoloba warmingii</i> Meisn.	Non-comm	1	6.5	4.5
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R. Br.	Low	141	22.5	15
	<i>Myrsine parvifolia</i> A. DC.	Low	6	10.4	10
	<i>Myrsine umbellata</i> Mart. ex DC.	Low	7	15.5	14
Proteaceae	<i>Roupala brasiliensis</i> Klotzsch	High	1	12.5	7.8
Quiinaceae	<i>Quiina glaziovii</i> Engl.	Non-comm	1	5.8	5
Rosaceae	<i>Prunus sellowii</i> Koehne	High	1	6.3	9
Rubiaceae	<i>Alibertia concolor</i> (Cham.) K. Schum.	Non-comm	4	15.0	13
	<i>Amaioua guianensis</i> Aubl.	Non-comm	3	10.7	14
	<i>Bathysa australis</i> (A. St.-Hill.) K. Schum.	Non-comm	15	10.8	14
	<i>Chomelia pedunculosa</i> Benth.	Non-comm	3	15.8	14
	<i>Posoqueria latifolia</i> (Rudge) Schult.	High	4	14.9	10
	<i>Psychotria carthagrenensis</i> Jacq.	High	8	15.2	10
	<i>Psychotria leiocarpa</i> Cham.	Non-comm	1	7.7	6.5
	<i>Psychotria longipes</i> Müell. Arg.	Non-comm	26	29.5	17
	<i>Psychotria nuda</i> (Cham. & Schltl.) Wawra	Non-comm	8	12.0	8
	<i>Psychotria officinalis</i> (Aubl.) Raeusch. ex Sandwith	Non-comm	2	7.6	11
	<i>Psychotria</i> sp. 1	Non-comm	1	7.5	6
	<i>Psychotria</i> sp. 2	Non-comm	1	7.3	6.5
	<i>Psychotria stenocalyx</i> Müell. Arg.	Non-comm	2	15.5	10
	<i>Psychotria suterella</i> Müell. Arg.	Non-comm	13	14.4	12
	<i>Rudgea jasminoides</i> (Cham.) Müell. Arg.	Non-comm	9	12.4	15
Rutaceae	<i>Esenbeckia grandiflora</i> Mart.	High	2	12.0	12
	<i>Zanthoxylum rhoifolium</i> Lam.	Low	16	23.4	18
Salicaceae	<i>Casearia decandra</i> Jacq.	High	15	11.0	12
	<i>Casearia sylvestris</i> Sw.	High	28	15.8	16
Sapindaceae	<i>Allophylus edulis</i> (A. St.-Hill., Camb. & A. Juss.) Radlk. ex Warm.	Non-comm	2	5.9	7.7
	<i>Allophylu spetiolulatus</i> Radlk.	Non-comm	3	9.5	7
	<i>Cupania oblongifolia</i> Mart.	High	3	14.4	10.5
	<i>Cupania vernalis</i> Camb.	Best	25	21.1	10
	<i>Dodonaea viscosa</i> (L.) Jacq.	Non-comm	9	8.3	5
	<i>Matayba elaeagnoides</i> Radlk	High	1	11.4	7.5
	<i>Matayba guianensis</i> Aubl.	High	12	25.6	14
	<i>Matayba intermedia</i> Radlk.	High	12	21.5	16
Sapotaceae	<i>Pouteria venosa</i> (Mart.) Baehni	High	2	17.7	8
Solanaceae	<i>Solanum mauritianum</i> Scop.	Non-comm	1	12.3	9
	<i>Solanum sanctae-catharinae</i> Dunal	Non-comm	1	13.1	8
Styracaceae	<i>Styrax leprosus</i> Hook. & Arn.	Low	1	5.0	8.5
Symplocaceae	<i>Symplocos laxiflora</i> Benth.	Non-comm	2	6.5	12
	<i>Symplocos tenuifolia</i> Brand	Non-comm	1	8.5	6
Theaceae	<i>Gordonia fruticosa</i> (Schrad.) H. Keng.	High	3	12.5	7
Tiliaceae	<i>Luehea divaricata</i> Mart.	High	1	6.2	2
Unidentified	Unidentified	Non-comm	11	28.4	16
Urticaceae	<i>Cecropia glaziovii</i> Snethl.	Non-comm	26	25.0	15

Verbenaceae	<i>Citharexylum myrianthum</i> Cham. <i>Vitex megapotamica</i> (Spreng.) Moldenke	High Best	3 1	24.0 15.0	14 1.5
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**Table A.3.** Importance values (IV) of the forty most dominant species in secondary forest stands of Brazilian Atlantic Forest. C = commercial, NC = non-commercial, DA = Density, DR = Relative density, DoA = Dominance, DoR = Relative dominance, FA = Frequency, FR = Relative frequency, IV = Importance Value.

Species	Comm use	DA	DR	DoA	DoR	FA	FR	VI
<i>Tibouchina pulchra</i>	C	362.2	24.9	3.8	27.1	36.6	3.7	18.54
<i>Miconia cinnamomifolia</i>	C	138.4	9.5	1.2	8.6	53.7	5.4	7.83
<i>Myrsine coriacea</i>	C	86.0	5.9	0.5	3.4	42.7	4.3	4.53
<i>Hyeronima alchorneoides</i>	C	51.8	3.6	0.7	5.0	42.7	4.3	4.28
<i>Miconia cabucu</i>	C	61.0	4.2	0.6	4.2	32.9	3.3	3.88
<i>Euterpe edulis</i>	NC	37.8	2.6	0.3	1.9	25.6	2.6	2.34
<i>Miconia rigidiuscula</i>	C	34.2	2.4	0.2	1.5	22.0	2.2	2.01
<i>Cecropia glaziovii</i>	NC	15.9	1.1	0.3	2.1	23.2	2.3	1.83
<i>Pera glabrata</i>	C	31.1	2.1	0.2	1.2	19.5	2.0	1.77
<i>Psychotria longipes</i>	NC	15.9	1.1	0.2	1.5	14.6	1.5	1.36
<i>Vernonanthura discolor</i>	C	19.5	1.3	0.2	1.1	15.9	1.6	1.33
<i>Guapira opposita</i>	C	15.9	1.1	0.2	1.2	12.2	1.2	1.18
<i>Piptocarpha angustifolia</i>	C	11.6	0.8	0.2	1.2	13.4	1.3	1.10
<i>Casearia sylvestris</i>	C	17.1	1.2	0.1	0.8	13.4	1.3	1.09
<i>Cupania vernalis</i>	C	15.2	1.1	0.1	0.9	12.2	1.2	1.04
<i>Sloanea guianensis</i>	C	11.6	0.8	0.1	1.0	9.8	1.0	0.93
<i>Huberia semiserrata</i>	NC	17.7	1.2	0.2	1.3	2.4	0.2	0.92
<i>Nectandra oppositifolia</i>	C	7.9	0.5	0.2	1.3	7.3	0.7	0.86
<i>Clethra scabra</i>	C	12.2	0.8	0.1	0.5	12.2	1.2	0.84
<i>Jacaranda micrantha</i>	C	14.0	1.0	0.1	0.4	11.0	1.1	0.82
<i>Nectandra membranacea</i>	C	4.9	0.3	0.2	1.3	7.3	0.7	0.80
<i>Casearia decandra</i>	C	9.2	0.6	0.0	0.3	14.6	1.5	0.78
<i>Nectandra megapotamica</i>	C	4.9	0.3	0.2	1.2	7.3	0.7	0.76
<i>Ocotea pulchella</i>	C	8.5	0.6	0.1	0.9	7.3	0.7	0.75
<i>Nectandra lanceolata</i>	C	6.1	0.4	0.1	1.0	8.5	0.9	0.75
<i>Virola bicuhyba</i>	C	7.9	0.5	0.1	0.8	8.5	0.9	0.73
unidentified	NC	6.7	0.5	0.1	0.6	11.0	1.1	0.72
<i>Zanthoxylum rhoifolium</i>	C	9.8	0.7	0.1	0.8	6.1	0.6	0.70
<i>Cyathea delgadii</i>	NC	12.2	0.8	0.1	0.6	6.1	0.6	0.69
<i>Alchornea triplinervia</i>	C	6.1	0.4	0.1	0.7	9.8	1.0	0.69
<i>Matayba guianensis</i>	C	7.3	0.5	0.1	0.7	8.5	0.9	0.68
<i>Guarea macrophylla</i>	C	9.2	0.6	0.0	0.3	11.0	1.1	0.67
<i>Baccharis</i> sp.	NC	9.2	0.6	0.0	0.3	11.0	1.1	0.67
<i>Myrcia eugeniosioides</i>	C	9.2	0.6	0.1	0.7	6.1	0.6	0.64
<i>Matayba intermedia</i>	C	7.3	0.5	0.1	0.5	7.3	0.7	0.58
<i>Mimosa bimucronata</i>	NC	6.7	0.5	0.1	0.7	6.1	0.6	0.58
<i>Cryptocarya moschata</i>	C	1.8	0.1	0.2	1.2	3.7	0.4	0.56
<i>Cabralea canjerana</i>	C	4.3	0.3	0.1	0.6	7.3	0.7	0.55
<i>Baccharis calvescens</i>	NC	7.3	0.5	0.0	0.2	8.5	0.9	0.53
<i>Baccharis dracunculifolia</i>	NC	6.7	0.5	0.0	0.2	8.5	0.9	0.51

**Table A.4.** Stem volume, basal area and number of individuals of commercial and non-commercial species by plot in three drivers of successional pathways in Brazilian Atlantic Forest. Each plot has 200 m<sup>2</sup> of sampled area.

Code Plot	Successional pathway	Age (years)	Number of plants		Basal area (m <sup>2</sup> .ha <sup>-1</sup> )		Stem volume (m <sup>3</sup> .ha <sup>-1</sup> )	
			Comm	Non-comm	Comm	Non-comm	Comm	Non-comm
21	DOF 1	50	9	10	16.5	4.7	138.2	26.6
22	DOF 1	45	10	9	18.3	3.2	136.7	15.7
23	DOF 1	40	6	8	6.4	2.8	41.2	14.0
25	DOF 1	45	15	9	22.1	3.2	159.8	15.7
26	DOF 1	50	6	3	15.3	1.9	129.8	10.8
27	DOF 1	34	16	5	16.7	1.8	117.3	8.8
28	DOF 1	30	25	21	14.0	11.4	83.5	67.9
31	DOF 1	34	11	14	6.7	7.7	45.0	46.3
32	DOF 1	20	14	13	14.4	4.3	95.5	21.3
33	DOF 1	15	28	7	6.2	1.2	29.3	4.8
36	DOF 1	3	2	14	0.3	3.3	1.2	14.9
37	DOF 1	5	0	7	0.0	1.2	0.0	5.1
38	DOF 1	9	9	0	2.5	0.0	14.5	0.0
39	DOF 1	18	17	3	5.3	0.5	48.8	2.1
40	DOF 1	33	13	15	9.6	8.4	60.0	48.1
41	DOF 1	18	15	7	6.1	4.1	33.6	22.5
42	DOF 1	25	17	6	7.8	1.6	59.5	7.9
43	DOF 1	13	13	4	2.9	6.4	25.4	45.3
44	DOF 1	15	30	3	21.8	0.4	157.3	1.8
45	DOF 1	3	1	11	0.2	2.0	2.5	8.3
46	DOF 1	20	12	5	4.7	9.2	29.5	69.0
48	DOF 1	17	33	2	11.7	0.5	80.9	2.5
49	DOF 1	17	28	1	6.5	0.1	40.5	0.5
50	DOF 1	6	11	12	2.8	3.3	14.5	15.9
52	DOF 1	13	17	1	8.2	1.7	54.7	11.6
53	DOF 1	35	10	7	17.0	4.6	140.3	27.8
54	DOF 1	13	32	1	8.4	0.1	61.1	0.5
55	DOF 1	20	12	3	10.2	1.6	74.3	8.7
56	DOF 1	15	21	1	8.4	1.5	51.4	9.6
57	DOF 1	35	10	7	6.4	4.2	39.5	22.8
60	DOF 1	10	17	3	3.5	0.4	15.7	1.7
62	DOF 1	12	23	1	3.7	0.2	17.5	0.8
63	DOF 1	8	4	0	0.5	0.0	2.0	0.0
64	DOF 1	5	9	0	1.7	0.0	8.7	0.0
65	DOF 1	15	22	1	8.4	0.8	71.7	4.2
67	DOF 1	6	1	3	0.2	0.5	0.6	1.9
69	DOF 1	40	21	9	15.4	4.5	93.6	25.8
70	DOF 1	8	13	4	2.0	1.1	15.8	5.2
71	DOF 1	15	23	7	4.8	1.8	50.8	8.2
72	DOF 1	20	26	7	7.5	1.5	43.8	6.2
73	DOF 1	5	2	1	0.2	0.2	0.8	1.0
74	DOF 1	5	0	4	0.0	1.2	0.0	5.5

76	DOF 1	3	0	2	0.0	0.3	0.0	1.0
79	DOF 1	33	15	11	9.1	3.9	71.3	21.1
80	DOF 1	13	32	0	10.9	0.0	98.1	0.0
81	DOF 1	9	6	10	0.7	2.1	6.1	9.0
82	DOF 1	25	27	4	9.9	2.0	79.4	11.9
1	DOF 2	25	35	6	27.1	1.9	188.2	9.8
2	DOF 2	13	49	3	21.7	1.1	119.0	5.5
3	DOF 2	8	50	0	14.4	0.0	70.1	0.0
4	DOF 2	7	41	1	16.9	0.5	91.5	2.7
5	DOF 2	11	30	10	13.3	3.9	70.4	21.5
6	DOF 2	6	28	9	11.1	1.7	56.3	7.2
7	DOF 2	12	22	29	11.9	14.8	71.2	84.1
8	DOF 2	27	25	7	24.8	9.0	163.8	67.9
9	DOF 2	5	18	4	3.3	1.0	15.8	5.0
10	DOF 2	10	5	4	0.7	1.6	2.9	8.6
11	DOF 2	12	44	11	22.7	3.5	140.3	18.0
12	DOF 2	20	42	6	18.7	2.5	101.8	13.4
13	DOF 2	12	66	3	19.6	0.6	98.8	2.4
14	DOF 2	23	53	6	36.3	2.9	229.2	14.8
16	DOF 2	15	27	5	19.1	1.3	129.1	5.7
18	DOF 2	30	47	7	30.8	2.7	198.6	13.7
19	DOF 2	13	42	7	25.1	2.3	180.9	11.3
20	DOF 2	16	36	5	18.6	1.1	108.9	4.7
114	DOF 2	38	34	28	21.7	10.7	142.9	54.8
115	DOF 2	38	20	34	21.7	8.7	151.1	40.2
121	DOF 2	38	8	6	6.2	3.9	37.5	22.0
122	DOF 2	38	10	21	10.7	13.0	75.3	77.9
100	DOF 3	14	60	11	25.7	1.8	138.2	7.3
101	DOF 3	4	10	2	1.6	0.6	7.5	2.9
102	DOF 3	3	11	0	1.7	0.0	7.0	0.0
103	DOF 3	27	35	2	22.7	0.7	150.4	3.4
104	DOF 3	8	44	1	17.0	2.3	87.3	16.0
105	DOF 3	10	44	0	14.8	0.0	73.8	0.0
106	DOF 3	16	52	5	23.4	0.8	126.3	3.2
107	DOF 3	20	36	3	21.9	0.8	137.7	3.4
108	DOF 3	8	27	1	8.0	0.2	37.5	0.7
110	DOF 3	4	29	5	4.8	0.6	19.8	2.4
111	DOF 3	19	42	18	18.4	3.9	101.1	17.1
112	DOF 3	15	36	4	21.8	1.8	131.0	9.3
113	DOF 3	2	4	0	0.5	0.0	2.1	0.0
<b>Total</b>		<b>1846</b>	<b>540</b>					

**Table A.5.** Akaike and *delta*-Akaike Information Criterion (AIC;  $\Delta$ AIC) values, log-likelihood (logLik) and degrees of freedom (df) of the models fitted to richness, diversity, density, basal area, and stem volume for secondary forests in the Brazilian Atlantic Forest.

Variable	AIC	$\Delta$ AIC	logLik	df
<b>Species richness</b>				
A*ComU + (1 Pathway)	820.8	0.0	-404.4	6
A*ComU + (1 Pathway /ComU)	822.6	1.7	-404.3	7
A + ComU + (1 Pathway)	823.8	3.0	-406.9	5
A + ComU + (1 Pathway /ComU)	825.8	5.0	-406.9	6
A + 1 + (1 Pathway)	902.9	82.0	-448.4	3
<b>Shannon index</b>				
A*ComU + (1 Pathway /ComU)	288.7	0.0	-138.4	6
A*ComU + (1 Pathway)	290.7	2.0	-138.4	7
A + ComU + (1 Pathway)	293.4	4.7	-141.7	5
A + 1 + (1 Pathway/ComU)	295.4	6.7	-141.7	6
A + ComU + (1 Pathway)	366.8	78.1	-180.4	3
<b>Simpson index</b>				
A*ComU + (1 Pathway)	46.5	0.0	-17.3	6
A*ComU + (1 Pathway/ComU)	48.5	2.0	-17.3	7
A + ComU + (1 Pathway)	51.4	4.9	-20.7	5
A + ComU + (1 Pathway/ComU)	53.4	6.9	-20.7	6
A + 1 + (1 Pathway)	68.1	21.6	-31.1	3
<b>Density (stem ha<sup>-1</sup>)</b>				
A + (1 Pathway)	613.5	0.0	-302.8	4
1 + (1 Pathway)	617.9	4.4	-305.9	3
<b>Basal area (m<sup>2</sup> ha<sup>-1</sup>)</b>				
A + (1 Pathway)	544.6	0.0	-268.3	3
1 + (1 Pathway)	593.4	48.8	-293.7	4
<b>Tree volume (m<sup>3</sup> ha<sup>-1</sup>)</b>				
A + (1 Pathway)	872.7	0.0	-432.3	3
1 + (1 Pathway)	944.5	71.8	-469.3	4
<b>Stem volume (m<sup>3</sup> ha<sup>-1</sup>)</b>				
A + (1 Pathway)	852.6	0.0	-422.3	3
1 + (1 Pathway)	907.9	55.2	-450.9	4
<b>Density for dbh class</b>				
A + DC + (1 Pathway/DC)	3625.4	0.0	-1805.7	7
A*DC + (1 Pathway/DC)	3627.5	2.1	-1804.7	9
A + DC + (1 Pathway)	3664.7	39.4	-1826.4	6
A* DC + (1 Pathway)	3666.4	41.1	-1825.2	8
A + 1 + (1 Pathway)	3921.2	295.8	-1957.6	3
<b>Basal area for dbh class</b>				
A* DC + (1 Pathway/DC)	1351.0	0.0	-666.5	9
A + DC + (1 Pathway/DC)	1363.4	12.4	-674.7	7
A* DC + (1 Pathway)	1366.9	15.9	-675.4	8
A + DC + (1 Pathway)	1379.8	28.8	-638.9	6
A + 1 + (1 Pathway)	1491.4	140.4	-742.7	3
<b>Stem volume for dbh class</b>				
A* DC + (1 Pathway/ DC)	2305.8	0.0	-1143.9	9

A* DC + (1 Pathway)	2313.3	7.5	-1148.7	8
A + DC + (1 Pathway/ DC)	2322.9	17.1	-1154.5	7
A + DC + (1 Pathway)	2330.5	24.7	-1159.3	6
A + 1 + (1 Pathway)	2416.3	110.5	-1205.1	3
<b>Density for commercial use</b>				
A*ComU + (1 Pathway/ComU)	3685.1	0.0	-1833.6	9
A + ComU + (1 Pathway/ComU)	3693.4	8.3	-1839.7	7
A*ComU + (1 Pathway)	3705.0	19.9	-1844.5	8
A + ComU + (1 Pathway)	3716.2	34.1	-1853.6	6
A + 1 + (1 Pathway)	3747.4	62.3	-1870.7	3
<b>Basal area for commercial use</b>				
A*ComU + (1 Pathway/ComU)	1412.5	0.0	-697.2	9
A + ComU + (1 Pathway/ComU)	1422.7	10.2	-704.4	7
A*ComU + (1 Pathway)	1443.6	31.1	713.8	8
A + ComU + (1 Pathway)	1457.0	44.5	-722.5	6
A + 1 + (1 Pathway)	1521.6	109.1	-757.8	3
<b>Stem volume for commercial use</b>				
A*ComU + (1 Pathway/ComU)	2359.9	0.0	-1170.9	9
A + ComU + (1 Pathway/ComU)	2374.5	14.6	-1180.2	7
A*ComU + (1 Pathway)	2376.6	16.7	-1180.3	8
A + ComU + (1 Pathway)	2392.9	33.0	-1190.5	6
A + 1 + (1 Pathway)	2465.8	105.9	-1229.9	3
<b>Density for timber quality</b>				
A*TQ + (1 Pathway/TQ)	3622.1	0.0	-1802.0	9
A + TQ + (1 Pathway/ TQ)	3623.4	1.3	-1804.7	7
A* TQ + (1 Pathway)	3664.7	42.7	-1824.4	8
A + TQ + (1 Pathway)	3672.9	50.9	-1830.5	6
A + 1 + (1 Pathway)	3695.2	73.2	-1844.6	3
<b>Basal area for timber quality</b>				
A*TQ + (1 Pathway/TQ)	1379.8	0.0	-680.9	9
A + TQ + (1 Pathway/ TQ)	1385.9	6.1	-685.9	7
A* TQ + (1 Pathway)	1422.4	42.5	-703.2	8
A + TQ + (1 Pathway)	1435.1	55.3	-711.6	6
A + 1 + (1 Pathway)	1474.3	94.5	-734.2	3
<b>Stem volume for timber quality</b>				
A*TQ + (1 Pathway/TQ)	2330.9	0.0	-1156.5	9
A + TQ + (1 Pathway/ TQ)	2337.4	6.5	-1161.7	7
A* TQ + (1 Pathway)	2359.0	28.1	-1171.5	8
A + TQ + (1 Pathway)	2371.4	40.4	-1179.7	6
A + 1 + (1 Pathway)	2411.0	80.1	-1202.5	3

Note: A = Age (years); ComU = Commercial use; DC = Diameter class; TQ = Timber quality.

**Table A.6.** Description of the linear mixed-effects models with the best fit to richness, diversity, density, basal area and volume variables. The model fitted for each variable is the result of the selection of the best model with fixed and random effects. For all the models of richness, diversity, density, basal area, and volume the fixed effect was age and random effect was successional pathway. We present the test statistic, the number of observations (*n*), marginal/conditional  $R^2$ , full model Chi-squared statistics ( $\chi^2$ ), number of model parameters (Par.) and *p*-value.

Response variable	n	$R^2_{m/c}$	$\chi^2$	Par	p-value	Fixed effect	Interactions
<b>Richness and diversity</b>							
Species richness	164	0.40/0.45	4.981	6	0.026	Age ComU	Age:ComU
Shannon index (H')	164	0.39/0.44	6.672	6	0.010	Age ComU	Age:ComU
Simpson index (1-D)	164	0.16/0.18	6.919	6	0.009	Age ComU	Age:ComU
<b>Total values</b>							
Density (ind.ha <sup>-1</sup> )	82	0.06/0.36	6.38	4	0.012	Age	--
Basal area (m <sup>2</sup> .ha <sup>-1</sup> )	82	0.35/0.62	50.81	4	1.02e-12	Age	--
Tree volume (m <sup>3</sup> .ha <sup>-1</sup> )	82	0.52/0.68	73.85	4	<2.2e-16	Age	--
Stem volume (m <sup>3</sup> .ha <sup>-1</sup> )	82	0.52/0.68	57.24	4	3.86e-14	Age	--
<b>dbh class</b>							
Density (ind.ha <sup>-1</sup> )	246	0.69/0.78	41.354	7	1.27e-10	Age DC	--
Basal area (m <sup>2</sup> .ha <sup>-1</sup> )	246	0.43/0.58	17.913	9	2.31e-5	Age DC	Age:DC
Stem volume (m <sup>3</sup> .ha <sup>-1</sup> )	246	0.38/0.49	9.506	9	0.002	Age DC	Age:DC
<b>Commercial species</b>							
Density (ind.ha <sup>-1</sup> )	246	0.25/0.43	21.884	9	2.90e-6	Age ComU	Age:ComU
Basal area (m <sup>2</sup> .ha <sup>-1</sup> )	246	0.35/0.53	33.073	9	8.88e-9	Age ComU	Age:ComU
Stem volume (m <sup>3</sup> .ha <sup>-1</sup> )	246	0.37/0.49	18.696	9	1.533e-5	Age ComU	Age:ComU
<b>Timber quality</b>							
Density (ind.ha <sup>-1</sup> )	246	0.24/0.50	44.680	9	2.32e-11	Age TQ	Age:TQ
Basal area (m <sup>2</sup> .ha <sup>-1</sup> )	246	0.28/0.51	44.547	9	2.48e-11	Age TQ	Age:TQ
Stem volume (m <sup>3</sup> .ha <sup>-1</sup> )	246	0.25/0.43	30.074	9	4.16e-8	Age TQ	Age:TQ

Note: Age = years; ComU = Commercial use; DC = Diameter class; TQ = Timber quality.

**Table A.7.** Parameters of models to predict values richness, diversity, density, basal area, tree volume and stem volume of secondary forests in the Brazilian Atlantic Forest. The model fitted for each response variable is the result of the selection of the best model with fixed and random effects. For all the models of richness, diversity, density, basal area, and volume the fixed effect was age and random effect was successional pathway. For all variables, the curve fitting procedure was used to select the best-fit predictors model.

Response variable	Fixed effect					Random effect		
		Estimate	Std. error	t value	p-value	Groups	Variance	Std. Dev.
Species richness for commercial use	Intercept	3.537	0.737	4.796	<0.001	Pathway	0.703	0.839
	Age	0.179	0.254	7.034	<0.001		7.873	2.806
	TQ-NC	-1.736	0.783	-2.218	0.028	Residual		
	Age:TQ-NC	-0.080	0.036	-2.249	0.026			
Shannon index for commercial use	Intercept	0.574	0.149	3.862	0.004	Pathway	0.030	0.174
	Age	0.041	0.001	8.237	<0.001		0.360	0.554
	TQ-NC	-0.078	0.154	-0.560	0.614	Residual		
	Age:TQ-NC	-0.183	0.007	-2.610	0.010			
Simpson index for commercial use	Intercept	0.382	0.060	6.382	<0.001	Pathway	0.002	0.049
	Age	0.013	0.002	5.265	<0.001		0.071	0.266
	TQ-NC	0.124	0.074	1.667	0.097	Residual		
	Age:TQ-NC	-0.009	0.003	-2.659	0.009			
Density for total	Intercept	35.211	4.097	8.595	<0.001	Pathway	40.09	6.332
	Age	0.220	0.085	2.584	0.012		86.04	9.276
Basal area for total	Intercept	7.738	3.202	2.417	0.078	Pathway	26.39	5.137
	Age	0.471	0.056	8.461	<0.001		36.60	6.049
Tree volume for total	Intercept	30.104	20.381	1.477	0.213	Pathway	1005.0	31.7
	Age	4.578	0.413	11.076	<0.001		2025.0	45.0
Stem volume	Intercept	38.030	17.777	2.139	0.098	Pathway	758.7	27.54
	Age	3.357	0.366	9.172	<0.001		1588.2	39.85
Density for dbh class	Intercept	1364.575	146.535	9.688	<0.001	DC: Pathway	43490	208.5
	Age	4.194	1.893	239.337	0.028		11914	109.2
	DC 15<30	-1223.8	181.508	6.387	<0.001		127314	356.8
	DC ≥30	-1419.7	181.508	6.387	<0.001			
Basal area for dbh class (cm)	Intercept	7.172	1.388	5.167	<0.001	DC: Pathway	2.086	1.444
	Age	0.061	0.032	1.912	0.057		2.237	1.496
	DC 15<30	-5.251	1.537	-3.417	0.005		12.247	3.500
	DC ≥30	-8.528	1.537	-5.549	<0.001			
	Age:DC 15<30	0.187	0.045	4.121	<0.001			
	Age:DC ≥30	0.100	0.045	2.213	0.028			
Stem volume for dbh class (cm)	Intercept	38.023	8.112	4.687	<0.001	DC: Pathway	62.90	7.931
	Age	0.277	0.224	1.236	0.218		62.86	7.928
	DC 15<30	-25.911	9.469	-2.737	0.015		602.89	24.554
	DC ≥30	-50.194	9.469	-5.301	<0.001			
	Age:DC 15<30	1.411	0.317	4.457	<0.001			
	Age:DC ≥30	1.112	0.317	3.512	<0.001			
Density for commercial use (ComU)	Intercept	287.218	153.563	12.139	0.086	ComU: Pathway	38004	194.9
	Age	8.061	3.684	241.056	0.030		13513	116.2
	ComU-Dominants	726.132	195.316	9.663	0.004	Pathway	161407	401.8
	CoU-NC	-139.382	195.316	9.663	0.492			
	Age:ComU-Dominants	-14.501	5.205	241.299	0.006			

	Age:ComU-NC	2.823	5.205	241.299	0.588			
Basal area for commercial use (ComU)	Intercept	-0.345	1.637	-0.211	0.837	ComU: Pathway	4.900	2.214
	Age	0.268	0.036	7.400	<0.001	Pathway	1.278	1.130
	ComU-Dominants	7.840		3.694	0.005	Residual	15.576	3.947
	CoU-NC	0.915	2.122	0.431	0.677			
	Age:ComU-Dominants	-0.185	2.122	-3.614	<0.001			
	Age:ComU-NC	-0.149	0.051	-2.911	0.004			
Stem volume for commercial use (ComU)	Intercept	-8.885	9.381	-0.947	0.359	ComU: Pathway	138.6	11.773
	Age	2.014	0.250	8.055	<0.001	Pathway	36.7	6.058
	ComU-Dominants	52.890	12.308	4.297	0.001	Residual	745.0	27.295
	CoU-NC	11.597	12.308	0.942	0.366			
	Age:ComU-Dominants	-1.358	0.353	-3.846	<0.001			
	Age:ComU-NC	-1.330	0.353	-3.765	<0.001			
Density for timber quality (TQ)	Intercept	879.736	159.395	5.519	<0.001	TQ: Pathway	61049.0	247.08
	Age	-5.501	3.220	-1.708	0.089	Pathway	521.7	22.84
	TQ-high	-702.532	224.646	-3.127	0.015	Residual	122857.4	350.51
	TQ-best	-633.754	224.646	-2.821	0.024			
	Age: TQ-high	9.287	4.554	2.040	0.043			
	Age: TQ-best	9.023	4.554	1.981	0.049			
Basal area for timber quality (TQ)	Intercept	7.079	1.634	11.883	<0.001	TQ: Pathway	5.947	2.439
	Age	0.031	0.034	239.914	0.358	Pathway	0.452	0.672
	TQ-high	-7.327	2.245	8.021	0.011	Residual	13.547	3.681
	TQ-best	-6.746	2.245	8.021	0.017			
	Age: TQ-high	0.111	0.048	239.942	0.021			
	Age: TQ-best	0.147	0.048	239.942	0.002			
Stem volume for timber quality (TQ)	Intercept	37.690	9.617	3.919	0.002	TQ: Pathway	197.522	14.054
	Age	0.274	0.235	1.168	0.244	Pathway	1.734	1.317
	TQ-high	-43.331	13.5558	-3.196	0.011	Residual	656.340	25.619
	TQ-best	-34.533	13.558	-2.547	0.031			
	Age: TQ-high	0.817	0.332	2.458	0.015			
	Age: TQ-best	1.035	0.332	3.115	0.002			

## Chapter 3

Appendix for

### The effect of the tree harvesting on secondary forest dynamics in the Brazilian Atlantic Forest

#### 1. SUPPLEMENTARY TABLES

**Table A.1.** Akaike (AIC) values, log-likelihood (logLik) and degrees of freedom (df) of the models fitted using lmem to analyse richness, Shannon and Simpson diversity, density, commercial volume, recruitment and mortality to whole forest and commercial species for secondary forests with harvesting in the Brazilian Atlantic Forest.

Variable	AIC	logLik	df	R <sup>2</sup> m/c
<b>Richnesswhole forest</b>				
Richness ~ Basal area initial + (Intensity-1 Growth period)	212.4	-101.377	4	0.20/0.49
<b>Richness commercial species</b>				
Richness ~ Basal area initial + Intensity + (Intensity-1 Growth period)	175.7	-81.591	5	0.24/0.78
<b>Shannon diversity whole forest</b>				
Shan ~ Basal area initial + (Intensity-1 Growth period)	6.2	1.696	4	0.10/-0.18
<b>Shannon diversity commercial species</b>				
Shan ~ Basal area initial + Growth period + (1 Growth period/Intensity)	15.6	1.730	7	0.14/-0.12
<b>Simpson diversity whole forest</b>				
Simp ~ Basal area initial	-114.3	60.152	30	0.23
<b>Simpson diversity commercial species</b>				
Simp ~ Basal area initial + Growth period + (1 Growth period/Intensity)	-106.2	62.661	7	0.15/0.00
<b>Densitywhole forest</b>				
Density ~ Basal area initial + Intensity + Growth period + (1 Growth period/ Intensity)	415.22	-200.61	1	0.56/0.58
<b>Density commercial species</b>				
Density ~ Basal area initial + Growth period + (Intensity-1 Growth period)	391.26	-190.63	1	0.50/0.88
<b>Commercial volume whole forest</b>				
CVol ~ Basal area initial*Intensity*Growth period + (Intensity-1 Growth period)	261.2	-119.169	8	0.03/0.99

<b>Commercial volume for commercial species</b>					
CVol ~ Basal area initial + (Intensity-1 Growth period)	269.0	-129.698	4	0.75/0.75	
<b>Recruitment whole forest</b>					
Rec ~ Basal area initial + (1 Growth period)	-49.5	29.666	4	0.23/0.49	
<b>Recruitment commercial species</b>					
Rec ~ Basal area initial + (Intensity -1 Growth period)	-46.6	28.204	4	0.42/0.66	
<b>Mortalitywhole forest</b>					
Mort ~ Basal area initial + Growth period + (1 Growth period)	-21.8	17.333	5	0.46/0.51	
<b>Mortalitycommercial species</b>					
Mort ~ Basal area initial + Growth period + (Intensity -1 Growth period)	-39.9	26.398	5	0.85/0.85	

**Table A.2.** Number of individuals per family, ecological group and timber quality by species in secondary forest in dense ombrophilous forest of the Brazilian Atlantic Forest. Ecological groups: PI: Pioneer; ES: Early secondary; LS: Late secondary; CL: Climax.

Family	Species	Ecological group	Timber quality	Number of individuals
Annonaceae	<i>Annona cacans</i>	ES	Low	1
	<i>Annona emarginata</i>	ES	Energy	19
	<i>Annona neosericea</i>	PI	Low	121
	<i>Annona rugulosa</i>	ES	Energy	4
	<i>Annona</i> sp.	ES	Low	4
	<i>Xylopia brasiliensis</i>	LS	High	2
Apocynaceae	<i>Aspidosperma australe</i>	LS	Best	4
	<i>Aspidosperma ramiflorum</i>	LS	High	2
	<i>Aspidosperma tomentosum</i>	ES	High	3
	<i>Tabernaemontana catharinensis</i>	PI	Energy	4
Arecaceae	<i>Euterpe edulis</i>	LS	Energy	1241
	<i>Syagrus romanzoffiana</i>	ES	Energy	1
Asteraceae	<i>Asteraceae</i> sp.	PI	Energy	5
	<i>Piptocarpha axillaris</i>	PI	Low	24
	<i>Vernonanthura discolor</i>	PI	High	2
	<i>Vernonanthura puberula</i>	ES	Low	34
Bignoniaceae	<i>Handroanthus albus</i>	ES	High	2
	<i>Jacaranda micrantha</i>	ES	Best	1
	<i>Jacaranda puberula</i>	ES	High	1
Burseraceae	<i>Protium kleinii</i>	LS	High	1
Canellaceae	<i>Cinnamodendron dinisii</i>	CL	Low	2
Cannabaceae	<i>Trema micrantha</i>	ES	Low	31
Caricaceae	<i>Jacaratia spinosa</i>	PI	Energy	2
Celastraceae	<i>Monteverdia tetragona</i>	LS	High	10
Chrysobalanaceae	<i>Hirtella hebeclada</i>	LS	High	2
	<i>Histeria silviani</i>	LS	High	1
	<i>Clusia criuva</i>	PI	Energy	48
Clusiaceae	<i>Garcinia gardneriana</i>	LS	Low	10
	<i>Cordia silvestris</i>	ES	Low	15
Cunoniaceae	<i>Lamanonia ternata</i>	ES	Energy	1
Cyatheaceae	<i>Cyathea delgadii</i>	CL	Energy	40
	<i>Cyathea</i> sp. 1	CL	Energy	353
	<i>Cyathea</i> sp. 2	CL	Energy	1
	<i>Cyathea</i> sp. 3	CL	Energy	1
	<i>Cyathea</i> sp. 4	CL	Energy	1
	<i>Cyathea</i> sp. 5	CL	Energy	1
	<i>Sloanea guianensis</i>	CL	High	38
Elaeocarpaceae	<i>Solanaceae</i>	CL	Energy	1
	<i>Alchornea glandulosa</i>	PI	Low	12
	<i>Alchornea sidifolia</i>	ES	High	2
	<i>Alchornea</i> sp.	ES	High	3

	<i>Alchornea triplinervia</i>	ES	High	78
	<i>Pausandra morisiana</i>	CL	High	7
	<i>Sapium glandulosum</i>	PI	High	12
	<i>Tetrorchidium rubrivenium</i>	ES	Energy	30
Fabaceae	<i>Andira fraxinifolia</i>	LS	High	13
	<i>Bauhinia forficata</i>	PI	Low	31
	<i>Centrolobium robustum</i>	LS	High	13
	<i>Copaifera trapezifolia</i>	CL	High	1
	<i>Dahlstedtia muehlbergiana</i>	ES	Low	6
	<i>Dahlstedtia pinnata</i>	ES	Low	41
	<i>Dalbergia brasiliensis</i>	ES	High	2
	<i>Fabaceae sp.</i>	NC	Energy	1
	<i>Fabaceae sp. 1</i>	NC	Energy	1
	<i>Fabaceae sp. 2</i>	NC	Energy	1
	<i>Faramea monte</i>	NC	Energy	1
	<i>Inga edulis</i>	ES	Energy	7
	<i>Inga marginata</i>	ES	Energy	30
	<i>Inga sp. 2</i>	ES	Energy	1
	<i>Inga vera</i>	ES	Energy	1
	<i>Machaerium hirtum</i>	ES	Energy	3
	<i>Machaerium sp.</i>	ES	Energy	1
	<i>Mouriri chamissoana</i>	ES	High	1
	<i>Myrocarpus frondosus</i>	ES	High	6
	<i>Ormosia arborea</i>	LS	Energy	2
	<i>Piptadenia gonoacantha</i>	ES	High	3
	<i>Piptadenia paniculata</i>	ES	High	8
	<i>Platymiscium floribundum</i>	LS	High	37
	<i>Pterocarpus rohrii</i>	LS	Low	1
	<i>Schizolobium parahyba</i>	PI	Low	43
	<i>Sebastiana klotzschiana</i>	PI	Low	5
	<i>Senna multijuga</i>	PI	Low	6
	<i>Zollernia ilicifolia</i>	LS	Energy	11
Laminaceae	<i>Aegiphila integrifolia</i>	PI	Low	3
Lauraceae	<i>Aniba firmula</i>	LS	High	11
	<i>Cryptocarya mandiocanna</i>	CL	High	1
	<i>Cryptocarya sp. 1</i>	CL	High	5
	<i>Endlicheria paniculata</i>	CL	Low	3
	<i>Lauraceae sp. 2</i>	ES	Low	1
	<i>Leandra dasytricha</i>	ES	Low	1
	<i>Leandra regnelli</i>	ES	Low	3
	<i>Leandra sp.</i>	ES	Low	1
	<i>Lonchocarpus campestris</i>	ES	Low	45
	<i>Nectandra leucantha</i>	CL	Low	7
	<i>Nectandra membranacea</i>	ES	High	76
	<i>Nectandra oppositifolia</i>	ES	Best	15
	<i>Nectandra sp. 1</i>	LS	High	1

	<i>Nectandra</i> sp. 2	LS	High	30
	<i>Ocotea catharinensis</i>	CL	Best	3
	<i>Ocotea mandiocana</i>	ES	High	7
	<i>Ocotea puberula</i>	CL	Best	4
	<i>Ocotea pulchella</i>	LS	Best	1
	<i>Ocotea teleiandra</i>	CL	High	1
	<i>Persea venosa</i>	CL	Low	1
Lecythidaceae	<i>Cariniana estrellensis</i>	LS	Low	14
Magnoliaceae	<i>Magnolia ovata</i>	LS	High	43
Malpighiaceae	<i>Byrsonima ligustrifolia</i>	ES	Energy	1
Malvaceae	<i>Pseudobombax grandiflorum</i>	ES	Low	1
Melastomataceae	<i>Melastomataceae</i> sp.	NC	Energy	1
	<i>Miconia cinnamomifolia</i>	ES	Best	85
	<i>Miconia darisica</i>	ES	Best	3
	<i>Miconia formosa</i>	ES	Best	46
	<i>Miconia</i> sp.	ES	Energy	1
	<i>Miconia tristis</i>	ES	Energy	1
	<i>Miconia valtheri</i>	CL	Energy	1
Meliaceae	<i>Cabralea canjerana</i>	LS	Best	150
	<i>Cedrela fissilis</i>	ES	Best	27
	<i>Guarea macrophylla</i>	LS	Low	47
	<i>Trichilia lepidota</i>	ES	High	60
	<i>Trichilia pallens</i>	CL	Energy	4
Monimiaceae	<i>Mollinedia schottiana</i>	CL	Energy	35
	<i>Mollinedia</i> sp.	CL	Energy	1
	<i>Mollinedia</i> sp. 1	CL	Energy	44
	<i>Mollinedia</i> sp. 2	CL	Energy	8
	<i>Mollinedia</i> sp. 3	CL	Energy	11
	<i>Mollinedia triflora</i>	LS	Energy	54
Moraceae	<i>Ficus adhatodifolia</i>	PI	Energy	2
	<i>Ficus cestrifolia</i>	PI	Energy	1
	<i>Ficus luschnathiana</i>	LS	Energy	6
	<i>Ficus</i> sp.	LS	Energy	4
	<i>Maclura tinctoria</i>	PI	Energy	1
	<i>Sorocea bonplandii</i>	ES	Low	8
Myristicaceae	<i>Virola bicuhyba</i>	LS	Low	112
Myrtaceae	<i>Campomanesia xanthocarpa</i>	LS	Energy	7
	<i>Capsicodendrom</i> sp.	LS	Energy	1
	<i>Eugenia beaurepairiana</i>	PI	Energy	4
	<i>Eugenia burkartiana</i>	CL	Energy	5
	<i>Eugenia catharinensis</i>	ES	Low	1
	<i>Eugenia cerasiflora</i>	CL	Energy	3
	<i>Eugenia involucrata</i>	LS	High	1
	<i>Eugenia melanogyna</i>	LS	Energy	1
	<i>Eugenia</i> sp.	CL	Energy	1
	<i>Eugenia verticillata</i>	CL	Energy	1

	<i>Myrcia ferruginosa</i>	CL	Energy	4
	<i>Myrcia glabra</i>	PI	Energy	2
	<i>Myrcia hatschbachii</i>	LS	Energy	1
	<i>Myrcia lucida</i>	LS	Energy	27
	<i>Myrcia neoriedeliana</i>	CL	Energy	2
	<i>Myrcia pubipetala</i>	LS	Energy	52
	<i>Myrcia</i> sp.	LS	Energy	1
	<i>Myrcia spectabilis</i>	LS	Energy	61
	<i>Myrcia splendens</i>	ES	Energy	15
	<i>Myrcia strigipes</i>	LS	Energy	37
	<i>Myrcia tijucensis</i>	LS	Energy	4
	<i>Myrcia tomentosa</i>	ES	High	13
	<i>Myrtaceae</i> sp. 1	CL	Energy	3
	<i>Myrtaceae</i> sp. 10	CL	Energy	2
	<i>Myrtaceae</i> sp. 11	CL	Energy	1
	<i>Myrtaceae</i> sp. 2	CL	Energy	1
	<i>Myrtaceae</i> sp. 3	CL	Energy	1
	<i>Myrtaceae</i> sp. 4	CL	Energy	1
	<i>Myrtaceae</i> sp. 5	CL	Energy	1
	<i>Myrtaceae</i> sp. 6	CL	Energy	1
	<i>Myrtaceae</i> sp. 7	CL	Energy	1
	<i>Myrtaceae</i> sp. 9	CL	Energy	2
	<i>Plinia rivularis</i>	LS	Energy	1
Nyctaginaceae	<i>Guapira opposita</i>	ES	Low	116
	<i>Pisonia ambigua</i>	ES	High	3
Ochnaceae	<i>Ouratea parviflora</i>	CL	Energy	1
	<i>Quiina glaziovii</i>	LS	Energy	3
Olacaceae	<i>Heisteria silvianii</i>	LS	Energy	23
Peraceae	<i>Pera glabrata</i>	ES	High	6
Phyllanthaceae	<i>Hieronyma alchorneoides</i>	ES	Best	386
Phytolaccaceae	<i>Seguieria langsdorffii</i>	CL	Energy	10
Piperaceae	<i>Piper aduncum</i>	ES	Energy	7
	<i>Piper arborium</i>	LS	Energy	1
	<i>Piper cernuum</i>	ES	Energy	3
	<i>Piper</i> sp. 1	NC	Energy	2
	<i>Piper</i> sp. 2	NC	Energy	1
Polygonaceae	<i>Coccoloba warmingii</i>	CL	Energy	1
	<i>Ruprechtia laxiflora</i>	ES	Energy	2
Primulaceae	<i>Myrsine coriacea</i>	PI	Low	2
	<i>Myrsine hermogenesii</i>	ES	Energy	2
	<i>Myrsine umbellata</i>	ES	Energy	1
	<i>Myrtaceae</i> sp.	ES	Energy	1
Proteaceae	<i>Roupala montana</i> var. <i>brasiliensis</i>	ES	High	3
Rosaceae	<i>Eriobotrya japonica</i>	ES	Energy	3
	<i>Prunus myrtifolia</i>	ES	Energy	7
	<i>Rosaceae</i> sp.	NC	Energy	1

Rubiaceae	<i>Alseis floribunda</i>	LS	Energy	5
	<i>Amaioua intermedia</i>	ES	Low	3
	<i>Bathysa australis</i>	ES	Energy	189
	<i>Cordiera concolor</i>	CL	Energy	2
	<i>Posoqueria latifolia</i>	ES	High	37
	<i>Psychotria carthagensis</i>	LS	High	24
	<i>Psychotria nemorosa</i>	CL	Energy	3
	<i>Psychotria nuda</i>	CL	Energy	309
	<i>Psychotria sp.</i>	CL	Energy	5
	<i>Psychotria suterella</i>	CL	Energy	187
	<i>Psychotria viridis</i>	LS	Energy	1
	<i>Rubiaceae sp.</i>	CL	Energy	1
	<i>Rudgea jasminoides</i>	CL	Energy	15
Rutaceae	<i>Citrus sp.</i>	ES	Energy	3
	<i>Citrus reticulata</i>	ES	Energy	2
	<i>Zanthoxylum rhoifolium</i>	ES	Low	10
	<i>Zanthoxylum sp. 1</i>	PI	Energy	2
	<i>Zanthoxylum sp. 2</i>	PI	Energy	1
Sabiaceae	<i>Meliosma sellowii</i>	CL	Energy	1
Salicaceae	<i>Casearia decandra</i>	ES	High	28
	<i>Casearia obliqua</i>	ES	Energy	121
	<i>Casearia sp.</i>	ES	Energy	1
	<i>Casearia sylvestris</i>	ES	High	79
Sapindaceae	<i>Allophylus petiolulatus</i>	CL	Energy	125
	<i>Cupania oblongifolia</i>	ES	High	67
	<i>Cupania sp.</i>	LS	Energy	4
	<i>Cupania vernalis</i>	ES	Best	11
	<i>Matayba intermedia</i>	ES	High	45
Sapotaceae	<i>Chrysophyllum inornatum</i>	LS	Energy	1
	<i>Chrysophyllum viride</i>	CL	Energy	3
	<i>Pouteria venosa</i>	LS	High	2
Solanaceae	<i>Sessea regnellii</i>	LS	Energy	3
	<i>Solanum pseudoquina</i>	ES	Energy	2
	<i>Solanum sp.</i>	ES	Energy	1
unidentified	NI	NC	Energy	231
Urticaceae	<i>Boehmeria caudata</i>	PI	Energy	5
	<i>Cecropia glaziovii</i>	PI	Energy	263
	<i>Coussapoa microcarpa</i>	ES	Low	7
Verbenaceae	<i>Citharexylum myrianthum</i>	PI	High	16
	<i>Citronela paniculata</i>	PI	High	8

**Table A.3.** Parameters of models to predict values richness, Shannon and Simpson diversity, density, commercial volume, recruitment and mortality to whole forest and commercial species of secondary forests with harvest in the Brazilian Atlantic Forest. The model fitted for each response variable is the result of the selection of the best model using linear mixed effect models with fixed and random effects. For all variables, the curve fitting procedure was used to select the best-fit predictors model.

Response variable	Fixed effect					Random effect		
		Estimate	Std. error	t value	p-value	Groups/ Name	Variance	Std. Dev.
Richness all species	Intercept	31.3790	1.1196	4.034	<0.001	GP/Intensity	0.05225	0.2286
	Basal area initial	0.6855	0.2645	2.594	0.015	Residual	52.39093	7.2382
Richness commercial species	Intercept	14.1023	4.6809	3.013	0.006	GP/Intensity	0.06328	0.2516
	Basal area initial	0.3612	0.1420	2.544	0.017	Residual	14.143	3.7608
	Growth period	4.5028	2.0607	2.185	0.038			
Shannon - all species	Intercept	2.9455	0.1418	20.779	<0.001	GP/Intensity	0.000	0.000
	Basal area initial	0.0095	0.00532	1.793	0.0839	Residual	0.0356	0.189
Shannon - commercial species	Intercept	3.1741	0.1643	19.314	<0.001	Intensity:GP	0.000	0.000
	Basal area initial	-0.0109	0.0067	-1.619	0.118	Growth period	0.001	0.033
	Growth period	-0.5860	0.2742	-2.137	0.042	Residual	0.0258	0.160
	BAI*GP	0.0208	0.0100	2.073	0.048			
Simpson - all species	Intercept	0.8878	1.907	50.514	0.000	GP/Intensity	--	--
	Basal area initial	0.0014	0.061	2.0584	0.049	Residual	--	--
Simpson - commercial species	Intercept	0.9503	0.0158	60.159	<0.001	Intensity:GP	0.000	0.000
	Basal area initial	-0.001	0.0006	-1.978	0.059	Growth period	<0.001	0.003
	Growth period	-0.056	0.0263	-2.110	0.045	Residual	<0.001	0.015
	BAI*GP	0.002	0.0009	2.085	0.047			
Density - all species	Intercept	106.856	270.004	0.396	0.696	Intensity:GP	0.000	0.000
	Basal area initial	47.141	7.963	5.920	<0.001	Growth period	2501	50.01
	Intensity	16.176	3.794	4.264	<0.001	Residual	43439	208.42
	Growth period	308.323	135.971	2.268	0.032			
Density - commercial species	Intercept	-298.006	170.057	-1.752	0.091	GP/Intensity	106.1	10.3
	Basal area initial	29.270	5.147	5.687	<0.001	Residual	18489.9	136.0
	Growth period	257.470	74.772	3.443	0.002			
Commercial volume - all species	Intercept	-0.0101	38.26	-2.648	0.014	GP/Intensity	112.2	10.59
	Basal area initial	0.116	1.272	9.140	<0.001	Residual	252.0	15.87
	Growth period	0.013	43.87	2.917	0.008			
	Intensity	4.288	10.63	0.403	1.000			
	BAI*GP	-4.652	1.470	-3.164	0.004			
	BAI*Intensity	-0.158	0.0036	-4.320	<0.001			
Commercial volume - commercial species	Intercept	15.579	15.473	1.007	0.323	Growth period	<0.001	<0.001
	Basal area initial	5.462	0.581	9.407	<0.001	(intercept)	<0.001	<0.001
						Intensity		
						Residual	424.10	20.59
	Intercept	0.9181	0.062	14.730	<0.001	GP/Intensity	0.0017	0.041

Recruitment - all species	Basal area initial	-0.005	0.002	-2.744	0.011	Residual	0.0034	0.058
Recruitment - commercial species	Intercept	0.8994	0.085	10.56	<0.001	GP/Intensity	<0.001	0.002
	Basal area initial	-0.0095	0.003	-3.55	0.002	Residual	<0.001	0.061
Mortality - all species	Intercept	0.8353	0.084	9.938	<0.001	GP (Intercept)	0.0009	0.030
	Basal area initial	-0.0014	0.003	-0.423	0.676	Residual	0.0084	0.092
	Growth period	-0.1643	0.063	-2.616	0.015			
Mortality - commercial species	Intercept	0.8776	0.175	5.029	<0.001	GP/Intensity	0.000	0.000
	Basal area initial	0.0034	0.0053	-0.645	0.526	Growth period	0.005	0.072
	Intensity	0.0008	0.0037	0.218	0.829	Residual	0.004	0.066
	Growth period	0.3487	0.235	-1.485	0.152			
	BAI*Intensity	-0.00008	0.00015	-0.532	0.600			
	BAI*GP	0.00184	0.00683	0.269	0.790			

## Chapter 4

### Appendix for

## The effect of the tree harvesting on secondary forest dynamics in the Brazilian Atlantic Forest

### 1. SUPPLEMENTARY TABLES

**TableA.1.** Timber products and market price by commercial timber species of the secondary forest in dense ombrophilous forest of the Brazilian Atlantic Forest. The classification was based on information provided literature, owners of the study area and the owner of a timber mill.

Species	Work quality	Timber products	US\$
Best quality timber			
<i>Aspidosperma parvifolium</i>	Hard wood	beams; furniture; wood flooring	360
<i>Cabralea canjerana</i>	Hard wood	pools; wooden board; wood flooring	416
<i>Cedrela fissilis</i>	Intermediary	furniture; wooden board; wooden ceiling	360
<i>Cupania oblongifolia</i>	Hard wood	beams; joist wood; wooden board	330
<i>Hieronyma alchorneoides</i>	Hard wood	beams; box board; furniture; wood flooring	330
<i>Jacaranda micrantha</i>	Hard wood	furniture; wood flooring	390
<i>Miconia formosa</i>	Hard wood	beams; joist wood; wooden board	330
<i>Miconia cinnamomifolia</i>	Hard wood	beams; box board; furniture; wood flooring	330
<i>Nectandra oppositifolia</i>	Intermediary	beams; furniture; wooden board; wood ceiling	350
<i>Ocotea catharinensis</i>	Hard wood	furniture; wood flooring	360
<i>Ocotea pulchella</i>	Intermediary	beams; joist wood; wooden board	350
High quality timber			
<i>Alchornea triplinervia</i>	Soft wood	beams; box board; joist wood	90
<i>Andira fraxinifolia</i>	Hard wood	beams; box board; furniture; wood flooring	330
<i>Calyptrotes lucida</i>	Hard wood	beams; joist wood	330
<i>Casearia decandra</i>	Hard wood	beams; joist wood; wooden board	330
<i>Casearia sylvestris</i>	Hard wood	beams; joist wood; wooden board	330
<i>Citharexylum myrianthum</i>	Soft wood	box board; crate; joist wood; wooden ceiling	330
<i>Cryptocarya moschata</i>	Hard wood	beams	310
<i>Lonchocarpus campestris</i>	Soft wood	crate; joist wood; pallet; wooden ceiling	100
<i>Magnolia ovata</i>	Soft wood	box board; crate; wooden board	140
<i>Matayba intermedia</i>	Hard wood	beams; joist wood; wooden board	330

<i>Myrcia tomentosa</i>	Hard wood	beams; joist wood	330
<i>Nectandra membranacea</i>	Soft wood	box board; joist wood; wooden board; wooden ceiling	330
<i>Pausandra morisiana</i>	Hard wood	beams; construction; joist wood	330
<i>Piptadenia gonoacantha</i>	Hard wood	beams; box board; furniture; wood flooring	330
<i>Posoqueria latifolia</i>	Hard wood	box board; joist wood; wood flooring	330
<i>Protium kleinii</i>	Hard wood	beams; construction; joist wood	330
<i>Psychotria carthagenaensis</i>	Intermediary	beams; joist wood	330
<i>Sloanea guianensis</i>	Hard wood	beams; joist wood	330
<i>Trichilia lepidota</i>	Intermediary	beams; joist wood; wooden board; wooden ceiling	330
<i>Xylopia brasiliensis</i>	Hard wood	beams; box board; joist wood	330
Low quality timber			
<i>Alchornea glandulosa</i>	Soft wood	crate; pallet	90
<i>Annona neosericea</i>	Soft wood	crate; pallet	140
<i>Guapira opposita</i>	Soft wood	crate; pallet	90
<i>Piptocarpha axillaris</i>	Soft wood	crate; pallet	90
<i>Schizolobium parahyba</i>	Soft wood	crate; pallet	90
<i>Virola bicuhyba</i>	Soft wood	crate; pallet	90
<i>Zanthoxylum rhoifolium</i>	Soft wood	crate; pallet	90

**Table A.2.** Number of individuals per period of inventory, ecological group, and timber quality by species in secondary forest in dense ombrophilous forest of the Brazilian Atlantic Forest. Ecological groups: PI: Pioneer; ES: Early secondary; LS: Late secondary; CL: Climax.

Species	Ecological group	Timber quality	Trees numbers	
			pre-harvest	post-harvest
<i>Aegiphila integrifolia</i>	PI	Low	2	--
<i>Alchornea glandulosa</i>	PI	Low	4	7
<i>Alchornea sidifolia</i>	ES	High	1	1
<i>Alchornea</i> sp.	ES	High	3	2
<i>Alchornea triplinervia</i>	ES	High	38	45
<i>Amaioua intermedia</i>	ES	Low	2	2
<i>Andira fraxinifolia</i>	LS	High	7	9
<i>Aniba firmula</i>	LS	High	9	8
<i>Annona cacans</i>	ES	Low	1	1
<i>Annona neosericea</i>	PI	Low	75	75
<i>Annona</i> sp.	ES	Low	2	2
<i>Aspidosperma australe</i>	LS	Best	4	3
<i>Aspidosperma ramiflorum</i>	LS	High	--	1
<i>Aspidosperma tomentosum</i>	ES	High	1	2
<i>Bauhinia forficata</i>	PI	Low	20	15
<i>Cabralea canjerana</i>	LS	Best	83	94
<i>Cariniana estrellensis</i>	LS	Low	7	7
<i>Casearia decandra</i>	ES	High	16	13
<i>Casearia sylvestris</i>	ES	High	41	39
<i>Cedrela fissilis</i>	ES	Best	15	17
<i>Centrolobium robustum</i>	LS	High	10	10
<i>Cinnamodendron dinisii</i>	CL	Low	2	2
<i>Citharexylum myrianthum</i>	PI	High	7	8
<i>Citronela paniculata</i>	PI	High	5	7
<i>Copaifera trapezifolia</i>	CL	High	1	1
<i>Cordia silvestris</i>	ES	Low	3	4
<i>Coussapoa microcarpa</i>	ES	Low	1	--
<i>Cryptocarya mandiocana</i>	CL	High	--	1
<i>Cryptocarya</i> sp.	CL	High	3	3
<i>Cupania oblongifolia</i>	ES	High	47	45
<i>Cupania vernalis</i>	ES	Best	3	5
<i>Dahlstedtia muehlbergiana</i>	ES	Low	5	5

<i>Dahlstedtia pinnata</i>	ES	Low	25	32
<i>Dalbergia brasiliensis</i>	ES	High	--	2
<i>Endlicheria paniculata</i>	CL	Low	2	--
<i>Eugenia catharinensis</i>	ES	Low	--	1
<i>Garcinia Gardneriana</i>	LS	Low	5	4
<i>Guapira opposita</i>	ES	Low	36	59
<i>Guarea macrophylla</i>	LS	Low	23	16
<i>Handroanthus albus</i>	ES	High	2	2
<i>Hieronyma alchorneoides</i>	ES	Best	279	246
<i>Jacaranda micrantha</i>	ES	Best	--	1
<i>Lonchocarpus campestris</i>	ES	High	35	21
<i>Magnolia ovata</i>	LS	High	18	27
<i>Matayba intermedia</i>	ES	High	32	26
<i>Miconia cinnamomifolia</i>	ES	Best	71	36
<i>Miconia formosa</i>	ES	Best	30	22
<i>Monteverdia tetragona</i>	LS	High	4	7
<i>Myrcia tomentosa</i>	ES	High	--	3
<i>Myrocarpus frondosus</i>	ES	High	6	4
<i>Nectandra leucantha</i>	CL	Low	5	2
<i>Nectandra membranacea</i>	ES	High	41	20
<i>Nectandra oppositifolia</i>	ES	Best	8	8
<i>Nectandra</i> sp.	LS	High	23	5
<i>Ocotea catharinensis</i>	CL	Best	2	1
<i>Ocotea mandiocana</i>	ES	High	5	4
<i>Ocotea puberula</i>	CL	Best	3	--
<i>Ocotea pulchella</i>	LS	Best	1	1
<i>Ocotea teleiandra</i>	CL	High	1	--
<i>Pausandra morisiana</i>	CL	High	4	3
<i>Pera glabrata</i>	ES	High	5	--
<i>Persea venosa</i>	CL	Low	--	1
<i>Piptadenia gonoacantha</i>	ES	High	1	3
<i>Piptadenia paniculata</i>	ES	High	8	8
<i>Piptocarpha axillaris</i>	PI	Low	7	5
<i>Pisonia ambigua</i>	ES	High	3	1
<i>Platymiscium floribundum</i>	LS	High	22	30
<i>Posoqueria latifolia</i>	ES	High	29	14
<i>Pouteria venosa</i>	LS	High	2	2

<i>Protium kleinii</i>	LS	High	1	1
<i>Pseudobombax grandiflorum</i>	ES	Low	--	1
<i>Psychotria carthagagenensis</i>	LS	High	17	11
<i>Roupala montana</i> var. <i>brasiliensis</i>	ES	High	3	2
<i>Sapium glandulosum</i>	PI	High	7	9
<i>Schizolobium parahyba</i>	PI	Low	6	3
<i>Sebastiana klotzschiana</i>	PI	Low	2	2
<i>Sloanea guianensis</i>	CL	High	24	24
<i>Sorocea bonplandii</i>	ES	Low	6	6
<i>Trema micrantha</i>	ES	Low	8	--
<i>Trichilia lepidota</i>	ES	High	37	42
<i>Vernonanthura discolor</i>	PI	High	1	1
<i>Virola bicuhyba</i>	LS	Low	66	57
<i>Xylopia brasiliensis</i>	LS	High	2	--
<i>Zanthoxylum rhoifolium</i>	ES	Low	7	4

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**Table A.3.** Akaike (AIC) values, log-likelihood (logLik) and degrees of freedom (df) of the models fitted using lmem to analyse relative growth rate (RGR) in diameter and periodic annual increment (PAI) in commercial volume to all species and commercial species for secondary forests with harvesting in the Brazilian Atlantic Forest.

Variable	AIC	logLik	df	R <sup>2</sup> m/c
<b>RGR all species</b>				
RGR ~ Basal area initial + (Intensity-1 Growth period)	-232.52	120.261	4	0.44/0.49
<b>RGR commercial species</b>				
RGR ~ Basal area initial + (Intensity-1 Growth period)	-237.354	122.677	4	0.34/0.34
<b>PAI commercial volume all species</b>				
PAIcv ~ Basal area initial + Growth period + (Intensity-1 Growth period)	92.008	-40.004	6	0.57/0.85
<b>PAI commercial volume all species</b>				
PAIcv ~ Basal area initial + (1 Growth period)	88.389	-40.194	4	0.29/0.35

**Table A.4.** Parameters of models to predict values relative growth rate (RGR) in diameter and periodic increment annual (PAI) in commercial volume of secondary forests with harvest in the Brazilian Atlantic Forest. The model fitted for each response variable is the result of the selection of the best model using linear mixed effect models with fixed and random effects. For all variables, the curve fitting procedure was used to select the best-fit predictors model.

Response variable		Fixed effect				Random effect			
		Estimate	Std. error	t value	p-value	Groups/ Name	Variance	Std. Dev.	
RGR species	all	Intercept	0.01697	0.0017	10.106	0.002	GP/Intensity	3.717e-10	1.928e-5
		Basal area initial	-0.00024	0.0001	-3.966	0.010	Residual	2.526e-10	1.589e-3
RGR species	commercial	Intercept	1.359e-2	1.202e-3	11.313	<0.001	GP/Intensity	0.000	0.000
		Basal area initial	-1.664e-4	4.577e-5	-3.635	0.001	Residual	2.127e-6	0.001
PAI commercial volume - all species		Intercept	-1.518	1.907	-0.796	0.436	GP/Intensity	0.003	0.051
		Basal area initial	0.282	0.061	4.596	<0.001	Residual	0.831	0.912
		Growth period	9.359	2.457	3.810	0.001			
		BAI*GP	-0.295	0.081	-3.618	0.001			
PAI commercial volume - commercial species		Intercept	2.275	0.872	2.609	0.021	GP/Intensity	0.085	0.292
		Basal area initial	0.104	0.032	3.244	0.004	Residual	0.943	0.971

**Table A.5.** Akaike (AIC) values, log-likelihood (logLik) and degrees of freedom (df) of the models fitted using glm to analyse periodic annual increment (PAI) in commercial volume to dbh class (5-15; 15-30; <30cm), and timber quality (low, high and best) for secondary forests with harvesting in the Brazilian Atlantic Forest.

Variable	AIC	logLik	df	Null deviance	Residual deviance	R <sup>2</sup>
<b>PAI commercial volume - dbh class</b>						
PAIcv ~ Basal area initial	80.972	-27.486	13	33.266	8.939	0.73
*Intensity*dbh class						
<b>PAI commercial volume - timber quality</b>						
PAIcv ~ Initial basal area + timber quality	85.969	-37.985	5	23.027	14.253	0.38

**Table A.6.** Parameters of models to predict values periodic increment annual (PAI) in commercial volume of secondary forests with harvest in the Brazilian Atlantic Forest. The model fitted using glm for each response variable is the result of the selection of the best model using linear mixed effect models with fixed and random effects. For all variables, the curve fitting procedure was used to select the best-fit predictors model.

Response variable		Fixed effect		t value	<i>p</i> -value
		Estimate	Std. error		
PAI commercial volume - dbh class	Intercept	2.8453	1.2841	2.216	0.034
	Initial basal area (IBA)	-0.0344	0.0426	-0.807	0.425
	Intensity	-0.0826	0.0300	-2.755	0.009
	dbh class 15<30	-5.7492	1.8160	-3.166	0.003
	dbh class 5<15	-3.4198	1.8160	-1.883	0.069
	IBA*Intensity	0.0027	0.0013	2.144	0.040
	IBA*dbh class 15<30	0.1986	0.0602	3.300	0.002
	IBA*dbh class5<15	0.0802	0.0602	1.332	0.192
	Intensity*dbh class15<30	0.1216	0.0424	2.867	0.007
	Intensity*dbh class5<15	0.1014	0.0424	2.389	0.023
	IBA*Intensity*dbh class 15<30	-0.0022	0.0018	-1.267	0.214
	IBA*Intensity*dbh class5<15	-0.0028	0.0018	-1.570	0.126
PAI commercial volume - timber species	Intercept	0.6718	0.3730	1.801	0.079
	Initial basal area (IBA)	0.0444	0.0147	3.021	0.004
	Timber high	0.0559	0.2153	0.260	0.796
	Timber Low	-0.7189	0.2153	-3.339	0.002

**Table A.7.** Akaike (AIC) values, log-likelihood (logLik) and degrees of freedom (df) of the models fitted using glm to analyse growth rate to single-trees, ecological groups, timber quality and the nine selected commercial species for secondary forests with harvesting in the Brazilian Atlantic Forest.

Variable	AIC	logLik	df	Null deviance	Residual deviance	R <sup>2</sup>
<b>Growth tree - glm</b>						
GR ~ Initial dbh	1664.5	-829.2	3	293.8	286.4	0.02
<b>Ecological groups to trees - glm</b>						
GR ~ Initial dbh + Ecological group	1651.4	-819.7	6	293.8	284.3	0.03
<b>Timber quality - glm</b>						
GR ~ Initial dbh + Growth period + Timber quality	1657.2	-822.6	6	293.8	284.9	0.03
<i>Hieronyma alchorneoides</i> (n=538)						
GR ~ Initial dbh + Growth period	380.15	-186.1	4	64.101	62.451	0.03
<i>Cabralea canjerana</i> (n=178)						
GR ~ Initial dbh	85.5	-39.7	3	16.586	16.228	0.02
<i>Virola bicuhyba</i> (n=126)						
GR ~ Initial dbh + Growth period	103.8	-47.9	4	17.760	15.692	0.11
<i>Miconia cinnamomifolia</i> (n=114)						
GR ~ Initial dbh + Growth period	10.05	-1.023	4	7.327	6.386	0.13
<i>Cupania oblongifolia</i> (n=99)						
GR ~ Initial dbh	63.64	-28.820	3	10.346	10.079	0.03
<i>Alchornea triplinervia</i> (n=88)						
GR ~ Initial dbh + Growth period	125.52	-58.760	4	20.816	20.023	0.04
<i>Nectandra membranacea</i> (n=69)						
GR ~ Initial dbh	39.481	-16.741	3	6.487	6.183	0.05
<i>Miconia formosa</i> (n=52)						
GR ~ Initial dbh	38.179	-16.089	3	5.687	5.653	0.01
<i>Cedrela fissilis</i> (n=33)						
GR ~ Initial dbh	36.613	-15.306	3	5.140	4.877	0.05

Note: GR = Growth rate (cm.cm<sup>-1</sup>.years<sup>-1</sup>).

**Table A.8.** Parameters of models to predict values growth rate to trees, ecological groups, and timber quality of secondary forests with harvest in the Brazilian Atlantic Forest. The model fitted for each response variable is the result of the selection of the best model using glm with fixed effects. For all variables, the curve fitting procedure was used to select the best-fit predictors model.

Response variable	Coefficients	Fixed effect			
		Estimate	Std. error	t value	p-value
Growth tree	Intercept	0.2353	0.014	17.448	<0.001
	Initial dbh	0.0059	0.001	8.127	<0.001
Ecological group	Intercept	0.2550	0.024	10.729	<0.001
	Initial dbh	0.0065	0.001	8.826	<0.001
	Early secondary	-0.0527	0.022	-2.392	0.017
	Late secondary	0.0112	0.025	0.454	0.650
	Climax	0.0098	0.042	0.237	0.813
Timber quality	Intercept	0.1914	1.907e <sup>-02</sup>	10.039	<0.001
	Initial dbh	0.00658	7.518e <sup>-04</sup>	8.760	<0.001
	Post-harvest	-6.965e <sup>-02</sup>	1.325e <sup>-02</sup>	-0.005	0.996
	High quality timber	0.05446	1.562e <sup>-02</sup>	3.486	<0.001
	Low quality timber	0.04644	1.775e <sup>-02</sup>	2.616	0.009

**Table A.9.** Parameters of models to predict values of trees of nine species of secondary forests with harvest in the Brazilian Atlantic Forest. The model fitted for each response variable is the result of the selection of the best model using glm with fixed effects. For all variables, the curve fitting procedure was used to select the best-fit predictors model.

Response variable	Coefficients	Fixed effect			
		Estimate	Std. error	t value	p-value
<i>Hieronyma alchorneoides</i>	Intercept	0.209	0.043	4.816	<0.001
	Initial dbh	0.005	0.002	3.084	0.002
	Growth period	-0.070	0.030	-2.318	0.021
<i>Cabralea canjerana</i>	Intercept	0.237	0.046	5.137	<0.001
	Initial dbh	0.007	0.003	1.965	0.051
<i>Virola bicuhyba</i>	Intercept	0.219	0.066	3.336	0.001
	Initial dbh	0.011	0.004	3.106	0.002
	Post-harvest	0.158	0.065	2.417	0.017
<i>Miconia cinnamomifolia</i>	Intercept	0.153	0.070	2.163	0.033
	Initial dbh	0.010	0.003	3.398	0.001
	Post-harvest	0.120	0.051	2.355	0.020
<i>Cupania oblongifolia</i>	Intercept	0.293	0.077	3.823	<0.001
	Initial dbh	0.007	0.004	1.545	0.126
<i>Alchornea triplinervia</i>	Intercept	0.176	0.133	1.325	0.189
	Initial dbh	0.004	0.006	0.642	0.523
	Post-harvest	0.177	0.111	1.604	0.113
<i>Nectandra membranacea</i>	Intercept	0.184	0.102	1.807	0.076
	Initial dbh	0.009	0.005	1.703	0.094
<i>Miconia formosa</i>	Intercept	0.411	0.118	3.471	0.001
	Initial dbh	-0.004	0.008	-0.549	0.586
<i>Cedrela fissilis</i>	Intercept	0.170	0.155	1.098	0.281
	Initial dbh	0.009	0.007	1.271	0.213