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FERNANDO ELIAS DA SILVA

RECUPERAÇÃO DO CARBONO, DIVERSIDADE E ATRIBUTOS FUNCIONAIS DA VEGETAÇÃO LENHOSA EM FLORESTAS SECUNDÁRIAS NA AMAZÔNIA ORIENTAL

Belém, Pará
2020

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Tese apresentada ao Programa de Pós-Graduação em Ecologia do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito final para obtenção do título de Doutor em Ecologia.

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Á minha família e aos milhões de brasileiros que custearam essa formação.

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“Se soubesse que o mundo se acabaria amanhã, eu ainda hoje plantaria uma árvore.”

Martín Luther King

RECUPERAÇÃO DO CARBONO, DIVERSIDADE E ATRIBUTOS FUNCIONAIS DA VEGETAÇÃO LENHOSA EM FLORESTAS SECUNDÁRIAS NA AMAZÔNIA ORIENTAL

RESUMO

A conversão de florestas tropicais para outros tipos de uso da terra reduziu substancialmente a quantidade de florestas primárias nas últimas décadas, enquanto o contrário foi observado para florestas secundárias - áreas em regeneração após o desflorestamento. A recuperação de florestas secundárias é complexa e dependente de preditores variados entre as regiões, tais como o clima, solos, fragmentação e cobertura florestal remanescente. O objetivo geral dessa tese foi avaliar a recuperação dos estoques de carbono, diversidade arbórea e atributos funcionais da vegetação lenhosa de florestas secundárias de diferentes regiões na Amazônia Oriental, bem como suas relações com preditores ambientais locais (clima, solos e idade de abandono). No primeiro capítulo, avalio o estoque e as taxas de recuperação do carbono e da diversidade de árvores (riqueza de espécies rarefeita) em florestas secundárias antigas na região Bragantina e as comparo com estimativas para a região Neotropical e Amazônia. Além disso, avalio o histórico climático da região Bragantina e os efeitos de secas severas sobre a recuperação do carbono e na diversidade arbórea. A acumulação média de carbono nas florestas secundárias dessa região foi de 1,08 Mg ha^{-1} ano^{-1}, enquanto a riqueza rarefeita de espécies foi de 0,21 espécies ano^{-1}. O balanço de carbono e as taxas de crescimento foram menores em períodos mais secos, o que evidencia a vulnerabilidade dessas áreas ao estresse hídrico. Apenas 41,1% do carbono e 56% da diversidade de árvores foram recuperados aos níveis de florestas primárias, com as estimativas indicando um período de 150 anos para a recuperação completa. As taxas de acumulação do carbono das florestas secundárias da região Bragantina foram mais baixas do que as estimadas para a região Neotropical e para a Amazônia, o que reflete o elevado grau de degradação do solo e fragmentação da paisagem. Estes resultados sugerem que é improvável que as florestas secundárias dessa região retornem aos seus níveis originais em escalas de tempo politicamente significativas. No segundo capítulo, avalio a recuperação e as mudanças temporais de atributos funcionais, especificamente da área foliar específica (SLA), densidade da madeira, tamanho da semente e dispersão endozoocórica da vegetação lenhosa e suas relações com preditores ambientais ligados ao clima, solos e idade de abandono de florestas secundárias de diferentes regiões da Amazônia Oriental (região Bragantina, Marabá, Parauapebas e Santarém). As mudanças e a recuperação dos atributos funcionais de árvores em florestas secundárias são variáveis e respondem às variações no clima e solos, o que evidencia o papel da heterogeneidade ambiental durante a recuperação. Nossos resultados sugerem que florestas secundárias em paisagem altamente degradadas podem reduzir sua capacidade de mitigar as mudanças climáticas e de conservar a biodiversidade se forem ultrapassados limiares críticos de desflorestamento e extremos climáticos. Sugerimos que sejam criadas políticas emergenciais para garantir a permanência de florestas secundárias na paisagem, e que ações ativas de recuperação sejam implantadas em regiões críticas para reduzir o tempo de recuperação nessas áreas.

PALAVRAS-CHAVE: Amazônia, região Bragantina, biodiversidade, carbono, mudanças climáticas, florestas secundárias, desflorestamento.

CARBON RECOVERY, TREE DIVERSITY AND FUNCTIONAL ATTRIBUTES OF WOOD VEGETATION IN SECONDARY FORESTS IN THE EASTERN AMAZON

ABSTRACT

The conversion of tropical forests to other types of land use has substantially reduced the amount of primary forests in recent decades, while the opposite was observed for secondary forests - areas regenerating after cleared. The recovery of secondary forests is complex and depends on different predictors between regions, such as climate, soils, fragmentation and remaining forest cover. The objective of this thesis was to evaluate the recovery of carbon stocks, tree diversity and functional traits of the woody vegetation of secondary forests in different regions in the Eastern Amazon, as well as their relationship with local environmental predictors (climate, soils and age of abandonment). In the first chapter, I assess the stock and recovery rates of carbon and tree diversity (rarefied species richness) in older secondary forests in the Bragantina region and compare them with estimates for the Neotropical and Amazon regions. In addition, I assess the climate history of the Bragantina region and the effects of severe droughts on carbon recovery and tree diversity in secondary forests. The average carbon accumulation in the secondary forests of this region was 1.08 Mg ha-1 year-1, while the rarefied richness was 0.21 species year-1. The carbon balance and growth rates were lower in drier periods, which shows the vulnerability of these areas to water stress. Only 41.1% of carbon and 56% of tree diversity were recovered to primary forest levels, with estimates indicating a period of 150 years for total recovery. Carbon accumulation rates in secondary forests in the Bragantina region were lower than those estimated for the Neotropical and Amazon regions, which reflects the high soil degradation and landscape fragmentation. These results suggest that secondary forests in that region are unlikely to return to their original levels at politically significant time scales. In the second chapter, I evaluate the recovery and temporal changes of functional traits, specifically the specific leaf area (SLA), wood density, seed size and endozoochoric dispersion of woody vegetation, and their relationship with environmental predictors related to climate, soil and age abandonment of secondary forests in different regions of the Eastern Amazon (Bragantina, Marabá, Parauapebas and Santarém regions). Changes and recovery of functional tree traits in secondary forests are variable and respond to variations in climate and soils, which highlights the role of environmental heterogeneity during forest recovery. Our results suggest that secondary forests in highly degraded landscapes may reduce their ability to mitigate climate change and conserve biodiversity if critical deforestation thresholds and climatic extremes have been exceeded. Therefore, we suggest that emergency policies be created to guarantee the permanence of secondary forests in the landscape and that active recovery actions be implemented in critical regions to reduce the recovery time in these areas.

KEYWORDS: Amazon, Bragantina region, biodiversity, carbon, climate change, secondary forests, deforestation.

SUMÁRIO

1. INTRODUÇÃO GERAL

Florestas tropicais

Florestas tropicais são importantes centros de biodiversidade global, abrigando cerca de 60% de todas as espécies descritas. Devido ao isolamento biogeográfico na separação dos continentes, as florestas tropicais apresentam divergência na composição da fauna e flora evoluída entre as grandes regiões – América tropical, África, Sudeste da Ásia, Madagascar e Nova Guiné (Corlett and Primack 2006, Malhi et al. 2014). Em algumas regiões das florestas tropicais, como é o caso da Amazônia, as pesquisas são concentradas em poucos locais e mesmo após décadas de inventários biológicos muitas espécies ainda permanecem desconhecidas pela ciência (Wright 2010). Por exemplo, estimativas indicam que as florestas tropicais abrigam mais de 53.000 espécies de árvores (Slik et al. 2015) e 5-7 milhões de espécies artrópodes (Novotny et al. 2002).

Adicionalmente, essas florestas desempenham serviços ecossistêmicos relevantes, tais como a mitigação das mudanças climáticas. Florestas tropicais respondem por aproximadamente metade da produtividade primária do planeta; estoca cerca 90% do total de carbono nos ecossistemas terrestres; removem aproximadamente 30% do carbono introduzidos na atmosfera pelas atividades antrópicas anualmente (Pan et al. 2013, Brando et al. 2019); e retroalimentam as nuvens auxiliando no processo de formação de chuvas e controlam a temperatura em escala regional (Nobre et al. 2016). Existe um receio da comunidade científica de que as mudanças globais relacionadas ao clima e atividades antrópicas ameacem a sua existência (Lovejoy and Nobre 2018) e os serviços ecossistêmicos prestados pelas florestas tropicais (Brando et al. 2020).

As florestas tropicais americanas (ex. Amazônia) lideram o ranking das taxas de perdas anuais absolutas com cerca de 39.900 Km², seguida pelas florestas asiáticas (com 22.000 Km²) e africanas (com 11.000 Km²) (Malhi et al. 2014). No Brasil, as perdas pelo desflorestamento estão concentradas no sul da Amazônia – com cerca de 5.000 km² anuais no passado recente – devido às constantes alterações antrópicas ligadas a agricultura, pecuária, mineração e criação de hidrelétricas na região conhecida como

“Arco do Desflorestamento” (Fearnside and Figueiredo 2017, Fearnside 2018). A produção agropecuária e urbanização têm sido os principais fatores antrópicos relacionados com o aumento da conversão de áreas nativas (Fearnside 2006, 2008). As mudanças da cobertura florestal para outros tipos de uso da terra, acima dos 40% da paisagem, tem sido relacionada com a redução da disponibilidade de água e nos padrões regionais de chuvas, tal como o aumento da estação seca e das enchentes anuais (Gloor et al. 2013, Spracklen 2015, Nobre et al. 2016, Spracklen et al. 2018). O desflorestamento e as mudanças climáticas potencializam as queimadas em um círculo vicioso (Brando et al. 2020), além do que a degradação das florestas pela combinação de queimadas, exploração de madeira e fragmentação (Barlow et al. 2016), incluindo a defaunação e a perda de interações ecológicas importantes, representam um sério risco para a manutenção do armazenamento de carbono (Bello et al. 2015) e da biodiversidade nessas florestas (Barlow et al. 2016).

As mudanças no uso da terra nas florestas tropicais associadas com o desflorestamento reduziu substancialmente a quantidade de florestas primárias nas últimas décadas, enquanto que as florestas secundárias - áreas em regeneração após o desflorestamento - aumentaram proporcionalmente (Chazdon 2014, 2017). Florestas secundárias respondem por cerca de 23% das áreas desflorestadas da Amazônia, com área total entre 120.000 e 230.000 Km² (TerraClass 2014, MapBiomas 2020). Em 2017, somente o estado do Pará representava cerca de 42% (5 Mha) de florestas secundárias da Amazônia brasileira (Nunes et al. 2020). Embora essas florestas não sejam equivalentes às florestas primárias, elas têm um papel importante, especialmente em termos de conectividade em áreas muito desflorestadas. Além disso, existe uma esperança da comunidade científica de que elas possam mitigar de maneira econômica as mudanças climáticas e a perda de biodiversidade (Chazdon 2014, Lewis et al. 2019).

Articulação internacional para reduzir a perda e degradação de florestas: Acordo de Paris e Desafio de Bonn

As mudanças climáticas consistem na principal preocupação da sociedade humana atualmente, à frente do terrorismo e dos ataques cibernéticos, devido às implicações negativas associadas com o comércio global e a vida na terra (Poushter and Huang 2019). De maneira geral, os ecossistemas florestais desempenham um papel importante na mitigação das mudanças climáticas devido a sua capacidade de estocar carbono. No Brasil, o desflorestamento desenfreado associado com queimadas coloca essas florestas como a principal fonte de emissões de gases do efeito estufa (GEE) (Brando et al. 2020).

Diante disso, várias articulações internacionais vêm sendo feitas, em particular foi firmado em Paris um acordo global assinado por 195 países na Convenção-Quadro das Nações Unidas sobre Mudança do Clima (UNFCCC) durante a COP21 em 2015 (Conferência das Partes). O intuito desse acordo é reduzir as emissões de gases GEE no contexto do desenvolvimento sustentável, e prevê a manutenção da temperatura média global abaixo de 2°C acima dos níveis pré-industriais. O Brasil é um dos países signatários, com metas ambiciosas de redução de 43% de GEE até 2030. Para tanto, o país deve aumentar os investimentos em bioenergia sustentável (em 18%), restaurar 12 milhões de hectares de florestas e zerar o desflorestamento até 2030, i.e., implementar a proposta REDD+, de redução de emissões por desflorestamento e degradação (MMA 2015, Euler 2016).

Em 2016, o governo brasileiro reforça o compromisso do acordo de Paris e também adere ao Desafio de Bonn (bonnchallenge.org) – um esforço internacional que prevê a recuperação florestal de 350 milhões de hectares até 2030 ao nível global. O desafio foi lançado em 2011 na cidade alemã de Bonn, onde o Brasil endossou o compromisso de restaurar 12 milhões de hectares de florestas firmado no acordo de Paris, além de 5 milhões de hectares extras em sistemas agrícolas integrados (ex.: sistema de integração LPF - lavoura, pecuária e floresta). Essas metas foram ratificadas no Plano Nacional de Recuperação da Vegetação Nativa (PLANAVEG). O Brasil é um país pioneiro e líder em ações mitigatórias das mudanças climáticas e de conservação ambiental (Ferreira et al. 2014). Entretanto, esse legado está correndo sérios riscos diante do cenário político atual, que coloca em dúvidas a capacidade do país em honrar os compromissos feitos no acordo de Paris e do Desafio de Bonn (Strassburg 2019, Escobar 2019).

Para honrar esses compromissos o governo brasileiro terá que investir, no contexto amplo, em ações de restauração e conservação de florestas, grande parte delas na Amazônia. As pesquisas sobre recuperação florestal têm sido constantemente atualizadas devido às mudanças globais associadas ao clima (Chang and Turner 2019) e com a necessidade de acelerar todo o processo (Chazdon and Guariguata 2016). A regeneração natural de florestas secundárias é o método mais barato e efetivo de restaurar grandes áreas de florestas (Crouzeilles et al. 2017). Entretanto, ainda existem lacunas quanto a sua efetividade em paisagens altamente degradadas.

Florestas secundárias são extremamente importantes nas paisagens onde ocorrem devido ao seu papel socioeconômico e na manutenção e proteção da biodiversidade relictual. Essas florestas desempenham diversas funções relacionadas com a 1) *provisão de recursos* tais como a água (ex.: água potável, segura e limpa; fornecimento estável de água para uso doméstico, irrigação, fins industriais ou geração de eletricidade), alimentação (coleta de peixes, caça, frutas), medicina popular (plantas medicinais), matéria-prima (construção, artesanato, carvão, palha); 2) *regulação de serviços ecossistêmicos* ligados ao carbono (sequestro de carbono na vegetação e no solo), eventos climáticos extremos (controle de enchentes e proteção do vento), qualidade do ar (interceptação de poeira, produtos químicos pela cobertura vegetal), prevenção de erosão (redução de erosões e assoreamento), controle de pragas (promove o controle ambiental pela manutenção das cadeias tróficas), polinização e dispersão de semente (manutenção dos dispersores e polinizadores bióticos), ciclagem de nutrientes (manutenção da liteira); e serviços culturais (recreação, estado de espírito, herança cultural e educação ambiental) (Cremaschi et al. 2012, Brancalion et al. 2014, Chazdon 2014). Por exemplo, para a diversidade de árvores, essas florestas podem recuperar até 90% dos valores relativos aos níveis de florestas primárias próximas em apenas 31 anos (Rozendaal et al. 2019). Da mesma forma, a dominância de espécies pioneiras e secundárias de crescimento rápido na composição florística dessas áreas favorece as taxas de acumulação de carbono - um dos GEE mais importantes. Estimativas indicam que o acúmulo anual de carbono dessas áreas seja 11 vezes maior que o das florestas primárias neotropicais (Poorter et al. 2016), fornecendo um sumidouro de carbono global estimado de 130 Pg entre 2016 e 2100, que ajuda na mitigação das mudanças climáticas globais (Houghton and Nassikas 2018). Esse espectro demonstra a importância dessas áreas nas paisagens onde ocorrem, o que justifica ações para a manutenção e manejo sob a perspectiva das ações do REDD+. Contudo, essas áreas são desprotegidas pela legislação e vêm sendo constantemente ameaçadas por novos ciclos de corte. Por exemplo, na Amazônia brasileira, estima-se que 19,6 milhões de hectares de florestas secundárias foram desflorestadas entre 1987 e 2017 (Nunes et al. 2020, Wang et al. 2020), o que pode ameaçar a capacidade dessas florestas em remover carbono atmosférico e evidencia o quanto esses ecossistemas são desprotegidos.

Síntese do arcabouço teórico sobre sucessão ecológica nas florestas em regeneração

O processo ecológico que baseia a recuperação de florestas secundárias é a sucessão ecológica secundária, i.e., a regeneração de uma comunidade após uma perturbação parcial ou completa (Ricklefs 2016). Nesse processo, as espécies são classificadas de acordo com grupos distintos, baseando em características morfológicas e de exigências de luminosidade ao longo dos estágios de sucessão (Denslow 1978, 1980). Existem diversas classificações de grupos ecológicos para floresta tropical enfocando visões e tipos de sucessão. Entretanto, esses grupos definem resumidamente as alterações na composição de espécies vegetais nos estágios de sucessão inicial, intermediário e final, e seus requerimentos ambientais necessários ao estabelecimento (Denslow 1978, Kageyama and Gandara 2003).

As espécies são classificadas em: 1) *Pioneiras*, definidas como as espécies iniciais que recobrem o solo e são dependentes de luz (ou heliófilas), e nos estágios avançados de sucessão o recrutamento dessas espécies é raro e associado às clareiras. Estas espécies podem ser divididas em *pioneiras típicas*, com ciclo de vida curto (5 a 15 anos), sementes pequenas e de fácil dispersão e com prevalência anemocórica, reprodução abundante e precoce; e *pioneiras longevas* ou *secundárias iniciais*, com ciclo de vida longo (10 a 30 anos) e potencial para atingir e permanecer no dossel da floresta por longos períodos. 2) *Secundárias* ou *secundárias tardias*, definidas como espécies arbóreas naturalmente emergentes ou de dossel, com ciclo de vida médio a longo (40 ou >100 anos), sementes com prevalência anemocórica, sem dormência, germinam na sombra, mas, seu desenvolvimento é associado a clareiras. 3) *Climácicas*, definidas como as espécies com ciclo de vida médio a longo prazo (40 a >100 anos), geralmente zoocóricas, desenvolvimento tolerante à sombra e, portanto, são massivamente representadas por espécies de subdossel, embora algumas conseguem atingir e permanecer no dossel da floresta (Budowski 1965). O processo de sucessão é contínuo, complexo, variável entre regiões, zonas climáticas e usos da terra, sendo que a delimitação padronizada desses estágios é sem dúvidas, uma ciência imprecisa (Chazdon 2014). É importante ponderar os impactos da variação ambiental durante a extrapolação de resultados em contextos amplos. Para evitar generalizações, alguns estudos indicam a definição dos caminhos sucessionais em cada caso, via análise conjunta da composição florística, biomassa, idade de abandono e as taxas demográficas das comunidades (Chazdon et al. 2007, Chazdon 2014).

A sucessão ecológica é uma disciplina antiga, mas, ainda continua tendo um papel chave e impactos diretos na aplicação da Ecologia moderna (Chang and Turner 2019). Por exemplo, a análise da relação dos filtros ambientais, fragmentação e mudanças no uso da terra sobre o *pool* de espécies e dispersores em florestas secundárias (Jakovac et al. 2016a, Magnago et al. 2017, Lennox et al. 2018), é um dos exemplos da aplicação da sucessão ecológica para elucidar os mecanismos ligados à perda de espécies e mudanças temporais na biodiversidade nesses ambientes. Vale destacar que esse processo não é restrito às florestas secundárias, ao passo que florestas primárias intactas exibem mudanças sucessionais na composição florística (Esquivel-Muelbert et al. 2019) e no crescimento e acúmulo do carbono diante de secas severas ao longo do tempo (Phillips and Lewis 2014, Brienen et al. 2015). Desse modo, as assembleias de espécies durante a sucessão ecológica secundária podem ser agrupadas conforme fatores determinísticos, que suportam as expectativas baseadas no nicho ecológico (Norden et al. 2009, Nuñez et al. 2019).

Em termos gerais, os caminhos sucessionais em florestas secundárias são múltiplos e complexos, o que dificulta as previsões de recuperação dessas áreas (Arroyo-Rodríguez et al. 2017). Diversos fatores podem atuar sobre a resiliência de florestas secundárias, entretanto, alguns são essenciais para a compreensão do processo de sucessão nessas áreas. Dentre eles destacam-se as:

1) *Mudanças climáticas globais* – Três tipos de evidências sugerem que as florestas secundárias tropicais são sensíveis a essas mudanças. Primeiro, as estimativas das florestas primárias mostram uma diminuição no sumidouro de carbono durante secas extremas (Brienen et al. 2015). Segundo, estudos em larga escala em florestas secundárias indicam um forte efeito do clima nas taxas de recuperação de carbono e biodiversidade (Anderson-Teixeira et al. 2013, Poorter et al. 2016, Rozendaal et al. 2019). Terceiro, estudos longitudinais revelaram como as secas modulam a velocidade de recuperação, aumentam a mortalidade e reduzem o recrutamento e o crescimento (Chazdon et al. 2005, Maza-Villalobos et al. 2013, Martínez-Ramos et al. 2018), devido aos efeitos negativos sobre a recuperação, balanço hídrico e taxas fotossintéticas das árvores, especialmente nos estágios iniciais da sucessão (Bretfeld et al. 2018).

2) Fatores edáficos – As variações edáficas e topográficas respondem pela distribuição e seleção de espécies durante a sucessão em diferentes escalas, especialmente nos estágios iniciais. Isto porque nos estágios avançados o principal recurso limitante é a luminosidade (van Breugel et al. 2019). A intensificação do processo de regeneração em solos férteis pode estar relacionada com a elevada substituição de espécies condicionada pela disponibilização de recursos (Moran et al. 2000, Lu et al. 2002) e mortalidade (De Toledo et al. 2011). Por exemplo, alguns estudos observaram que em solos pobres a recuperação da biomassa, da diversidade e composição florística de florestas secundárias é mais lenta (Lu et al. 2002, Jakovac et al. 2015, 2016b, Poorter et al. 2016), enquanto que em outros estudos essa relação não foi significativa (Lennox et al. 2018, Jones et al. 2019).

3) *Idade sucessional* – A composição de espécies da fauna e flora são variáveis ao longo da sucessão secundária. Essa dinâmica relaciona-se com as variações na disponibilidade de recursos no hábitat, tais como a luz e nutrientes do solo, e com as interações entre as espécies (Chazdon 2014). A composição florística de florestas jovens é dominada por espécies pioneiras de crescimento rápido, enquanto que nos estágios intermediárias e avançados de sucessão essas espécies são gradualmente substituídas por espécies secundárias e de crescimento lento. Essas mudanças garantem que

florestas secundárias jovens apresentem maiores taxas de crescimento e rotatividade do que floresta antigas (Poorter et al. 2016, Jones et al. 2019).

4) *Paisagem* – A influência da paisagem sobre a recuperação de florestas está relacionada principalmente com as mudanças na cobertura e seus impactos sobre a fauna e flora. Em paisagens menos fragmentadas e com maior cobertura florestal primária a recuperação da biodiversidade é mais rápida (Lennox et al. 2018). Neste caso, a limitação de propágulos e a maior intensidade dos efeitos de borda nas paisagens mais fragmentadas influenciam negativamente o processo de sucessão das espécies e o acúmulo de carbono (Magnago et al. 2017). Desse modo, florestas secundárias nessas paisagens podem levar centenas de anos para que se recupere aos níveis de florestas primárias.

5) Uso da terra anterior – O uso da terra anterior ao abandono associado ao número de ciclos são fatores importantes para considerar durante a recuperação de florestas secundárias (Villa et al. 2018). O uso intensivo e manejo inadequado prejudica a estrutura e propriedades do solo, o que interfere no processo de sucessão ecológica secundária nessas áreas (Jakovac et al. 2015, 2016b). Por exemplo, o crescimento de florestas secundárias em áreas de pastagens é mais lenta do que em áreas de cultivo itinerante, com tendências a dominância de poucas espécies nessas comunidades (Fearnside and Guimarães 1996).

6) *Persistência* – Embora a quantidade de florestas secundárias esteja aumentando ao longo do tempo devido a intenso desflorestamento, uma tendência diferente é observada quanto a persistência dessas áreas nas paisagens amazônicas. Estimativas indicam que na Amazônia, o tempo de permanência da maioria dos fragmentos de florestas secundárias é de aproximadamente 5 anos (Davidson and Martinelli 2013, Aguiar et al. 2016), podendo chegar até 20 anos em algumas regiões como a Costa Rica (Reid et al. 2019). Desse modo, essas áreas são consideradas bastante efêmeras, uma vez que sofrem novos cortes parciais ou totais, em curtos intervalos de tempo. Para exemplificar, entre 2008 e 2014, houve um aumento de 187(±48) % nas perdas de florestas secundárias na Amazônia brasileira, o que indica uma mudança estratégica na preferência de desmate nesse ecossistema menos protegido pela legislação (Wang et al. 2020). Essa inconstância reduz categoricamente

a sua capacidade de regeneração, tendo em vista que a sucessão é interrompida indefinidamente após vários ciclos de uso (Jakovac et al. 2015, 2016b).

7) *Falta de estudos longitudinais* – Florestas tropicais são paisagens bastante heterogêneas no que diz respeito a variação nas condições ambientais. Essa heterogeneidade de hábitats é refletida na biodiversidade, o que garante a megadiversidade observada nesse ecossistema (Wright 2010). Ao avaliar a biodiversidade nessas áreas é muito importante considerar as variações no hábitat, especialmente nas comparações em ampla escala (Mora et al. 2015). A maioria dos estudos que avaliam a recuperação de florestas secundárias nos trópicos são baseados em cronosequências, i.e., inferências temporais baseadas em dados espaciais (Poorter et al. 2016, Rozendaal et al. 2019). Essa abordagem é importante e útil nos estudos de resiliência, ao permitir comparações temporais múltiplas com maior facilidade. Entretanto, ao desconsiderar a heterogeneidade de hábitat e rotatividade das espécies, as estimativas a partir de cronosequências podem ser tendenciosas (Chazdon et al. 2007, Johnson and Miyanishi 2008, França et al. 2016). Por outro lado, a baixa persistência de florestas secundárias na paisagem e a dificuldade nas estimativas de idade dos fragmentos, não facilitam a localização e determinação de fragmentos antigos, o que justifica a escassez de estudos longitudinais.

Por fim, os caminhos sucessionais em florestas secundárias são bastante variáveis, com os fatores descritos acima aliados a outros não descritos aqui (ex.: banco de sementes, rebrota, dispersores), atuam em conjunto ao longo do tempo, fazendo com que cada fragmento tenha uma trajetória específica. Além disso, considerando a dimensão do Bioma Amazônia, é de se esperar que a heterogeneidade ambiental seja bastante variável entre as regiões, o que vai influenciar no processo de recuperação de florestas secundárias.

Atributos funcionais nas florestas em recuperação

Os atributos funcionais são características que podem ser utilizadas na compreensão de funções específicas da biodiversidade. Essas características podem fornecer *insights* importantes sobre mecanismos de sucessão e recuperação de serviços ecossistêmicos (Chazdon 2017, Berenguer et al. 2018, Chua and Potts 2018, Poorter et al. 2019), e sua compreensão diante da perspectiva das mudanças climáticas atuais é essencial para análise abrangente do futuro das florestas secundárias. Algumas características, como tipo de dispersão e tamanho da semente, demonstram os fatores limitantes para a recuperação de florestas devido à sua forte relação com a colonização e estabelecimento das espécies (Wijdeven and Kuzee 2000, Reid et al. 2015, Hawes et al. 2020). Nesse caso, árvores com sementes maiores e dispersão zoocórica tendem a ter maior distância de dispersão e maiores chances de colonização de novas áreas (Russo and Augspurger 2004, Clark et al. 2005, Lozada et al. 2007).

Por outro lado, outras características como a área foliar específica, podem fornecer informações sobre a perda de água e o desempenho da planta (Wright et al. 2004, Poorter and Bongers 2006), enquanto que a densidade da madeira está diretamente relacionada ao ciclo biogeoquímico do carbono e com a resistência dos tecidos (Berenguer et al. 2018, Phillips et al. 2019). As espécies de crescimento rápido tendem a ter menor densidade de madeira e maior área foliar específica devido ao baixo investimento nos tecidos e metabolismo acelerado, enquanto que para espécies de vida longa é o contrário (Poorter and Bongers 2006).

A avaliação da dinâmica de características funcionais pode indicar diferentes estratégias de espécies durante a recuperação e tendências sucessionais, embora ainda seja pouco compreendida (Stan and Sanchez-Azofeifa 2019). Por exemplo, ao longo dos estágios de sucessão é possível observar espécies arbóreas funcionalmente similares ou divergentes, tais como as pioneiras ou dependentes de luz nos estágios iniciais, e as clímaces e tolerantes à sombra nos estágios avançados (Chazdon et al. 2010, Chazdon 2017). A trajetória de sucessão é variável e impulsionada por diferentes processos estocásticos e determinísticos (Nuñez et al. 2019). Fatores ambientais como clima, solo e severidade do distúrbio podem ser responsáveis pela variação na recuperação das características funcionais das plantas ao longo do tempo (Boukili and Chazdon 2017, Pinho et al. 2018, Chua and Potts 2018, Estrada-Villegas et al. 2019). Por exemplo, florestas secundárias mais úmidas se recuperam mais rapidamente do que as secas (Poorter et al. 2016). Desse modo, diferentes trajetórias para a sucessão de características funcionais podem ser encontradas entre regiões, o que pode ajudar a esclarecer o papel desse componente na avaliação da resiliência das florestas tropicais.

Integração dos capítulos

Essa tese é composta por dois capítulos, sendo que no primeiro capítulo, apresento a avaliação do estoque e das taxas de recuperação do carbono e da diversidade arbórea em florestas secundárias antigas na região Bragantina – a região de colonização mais antiga da Amazônia -, onde a paisagem é altamente fragmentada e os níveis de cobertura florestal são mínimos. Para dimensionar os nossos resultados, comparamos as taxas de recuperação do carbono da região Bragantina com as principais estimativas da literatura vigente para as regiões tropicais.

No segundo capítulo, apresento uma avaliação da recuperação e das mudanças temporais dos atributos funcionais de área foliar específica, densidade da madeira, tamanho da semente e dispersão endozoocórica de florestas secundárias em diferentes regiões da Amazônia Oriental (região Bragantina, Marabá, Parauapebas e Santarém). Essas regiões apresentam grandes variações nas condições ambientais ligadas ao clima, idade, paisagem e características edáficas e, portanto, faço uma análise da relação desses filtros ambientais com a recuperação e mudanças nos atributos funcionais avaliados.

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CAPÍTULO 1

ASSESSING THE GROWTH AND CLIMATE SENSITIVITY OF SECONDARY FORESTS IN HIGHLY DEFORESTED AMAZONIAN LANDSCAPES

O primeiro capítulo dessa tese foi submetido e publicado na revista Ecology e está disponível em: https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.2954.

Abstract

Tropical forests hold 30% of Earth's terrestrial carbon and at least 60% of its terrestrial biodiversity, but forest loss and degradation are jeopardizing these ecosystems. Although the regrowth of secondary forests has the potential to offset some of the losses of carbon and biodiversity, it remains unclear if secondary regeneration will be affected by climate changes such as higher temperatures and more frequent extreme droughts. We used a dataset of 10 repeated forest inventories spanning two decades (1999-2017) to investigate carbon and tree species recovery and how climate and landscape context influence carbon dynamics in an older secondary forest located in one of the oldest post-Columbian agricultural frontiers in the Brazilian Amazon. Carbon accumulation averaged 1.08 Mg ha^{-1} yr^{-1}, while species richness was effectively constant over the studied period. Moreover, we provide evidence that secondary forests are vulnerable to drought stress: carbon balance and growth rates were lower in drier periods. This contrasts with drought responses in primary forests, where changes in carbon dynamics are driven by increased stem mortality. These results highlight an important climate change-vegetation feedback, whereby the increasing dry-season lengths being observed across parts of Amazonia may reduce the effectiveness of secondary forests in sequestering carbon and mitigating climate change. In addition, the current rate of forest regrowth in this region was low compared with previous pan-tropical and Amazonian assessments – our secondary forests reached just 41.1% of the average carbon and 56% of the tree diversity in the nearest primary forests — suggesting that these areas are unlikely to return to their original levels on politically meaningful timescales.

Keywords

Amazon, Bragantina region, biodiversity, carbon, climate change, secondary forests

Introduction

Secondary forests regenerating after land clearance represent > 50% of all tropical forests (Chazdon et al. 2009), and there is hope that they can cost-effectively mitigate climate change and biodiversity loss (Chazdon 2014, Lewis et al. 2019) – two of the defining crises of the Anthropocene (Malhi et al. 2014). For example, secondary forest carbon uptake is estimated to be 11 times higher than that of Neotropical primary forests (Poorter et al. 2016), providing an estimated global carbon sink of 130 Pg between 2016 and 2100 (Houghton and Nassikas 2018). Secondary forests can also provide important biodiversity co-benefits in landscapes otherwise devoid of primary forests or with high levels of deforestation (Vieira and Gardner 2012, Lennox et al. 2018, Matos et al. 2019). However, to realize their potential to mitigate climate change and biodiversity loss, tropical secondary forests must be able to recover under novel climatic conditions.

Global climate change is affecting the humid tropics through higher temperatures and levels of atmospheric CO_2 (Malhi et al. 2014), increases in dry-season length (Fu et al. 2013) and the frequency and intensity of climate extremes (Brando et al. 2019). These climate changes may be exacerbated by declines in precipitation and increases in temperature linked to regional deforestation (Spracklen et al. 2018, Baker and Spracklen 2019). Three types of evidence suggest tropical secondary forests will be sensitive to these changes. First, primary forest estimates show a decrease in the carbon sink during extreme droughts (Brienen et al. 2015). Second, large-scale studies of secondary forests indicate a strong effect of climate on the recovery rates of carbon and biodiversity (Anderson-Teixeira et al. 2013, Poorter et al. 2016, Rozendaal et al. 2019). Third, longitudinal studies have revealed how droughts modulate recovery speed, increase mortality and reduce recruitment and growth (Chazdon et al. 2005, Maza-Villalobos et al. 2013, Martínez-Ramos et al. 2018), due to the negative effects on the water balance and photosynthetic rates of trees, especially in the earlier stages of succession (Bretfeld et al. 2018).

While these studies provide a useful knowledge base, there are some important limitations. First, secondary forests are likely to be even more sensitive than primary forests to changes in precipitation (Uriarte et al. 2016) because pioneer species are more vulnerable to embolism (Markesteijn et al. 2011). Second, the large-scale studies that have inferred temporal trends from spatial data (i.e. the chronosequence approach) are complicated by factors such as species turnover and natural variation between samples (Johnson and Miyanishi 2008, Norden et al. 2015, França et al. 2016) and idiosyncratic determinants of recovery (Chazdon et al. 2007, Arroyo-Rodríguez et al. 2017). Third, most longitudinal studies focus on short-term assessments restricted to a single drought event (Chazdon et al. 2005, Maza-Villalobos et al. 2013, Bretfeld et al. 2018, Martínez-Ramos et al. 2018), which cannot detect responses to longer-term increases in temperature or post-drought growth compensation (Berenguer et al. 2018). Furthermore, the few longer-term studies relating secondary forest carbon dynamics to climate focus on tropical dry forests (e.g., Álvarez-Yépiz et al. 2018, Martínez-Ramos et al. 2018), meaning there is a lack of research in humid tropical regions where species may be even more sensitive to drought (Esquivel-Muelbert et al. 2019).

Initiatives such as the Bonn Challenge highlight two additional knowledge gaps linked to management. It seems likely that the increase in landscape-scale restoration will also increase secondary forest permanence, moving beyond the current situation where secondary forests are often cleared again within 5-20 years (Aguiar et al. 2016, Reid et al. 2018). Although our current understanding of younger forests is good (Poorter et al. 2015, 2016, 2019, Martínez-Ramos et al. 2018, Villa et al. 2018, Rozendaal et al. 2019), and the non-linear response of forest recovery over time is well established (Poorter et al. 2016, Ferreira et al. 2018, Lennox et al. 2018, Requena Suarez et al. 2019, Rozendaal et al. 2019), there is far too much variation in the relationship to use young forests to accurately predict recovery rates in older forests. Moreover, the relative recovery rates of carbon and biodiversity are unclear. While some regional assessments report a tight coupling at all stages of succession (Lennox et al. 2018), continent-scale assessments suggest a much faster recovery of biodiversity: plots recovered 80% of tree species richness 20 years after abandonment (Rozendaal et al. 2019) and only 27% of the carbon stock (Poorter et al. 2016). As recovery of both carbon and biodiversity are mediated by factors such as stand age and landscape and local conditions (Jakovac et al. 2015, Magnago et al. 2017, Villa et al. 2018, Ferreira et al. 2018, Lennox et al. 2018, Matos et al. 2019), it is not clear how these rates compare in heavily deforested landscapes.

Here, we address these knowledge gaps by investigating secondary forest recovery in the Bragantina region, the oldest deforestation frontier in the Brazilian Amazon (Almeida et al. 2010). We undertook 10 repeated censuses of 3 ha of older secondary forests (~60 years) over 18 years and addressed four questions: 1) What are the recovery rates of carbon stocks and tree species richness, and what is the relationship between these measures? 2) Does variation in seasonal temperature, water stress and landscape context influence carbon dynamics? 3) How does carbon recovery in the Bragantina region compare to estimates from other tropical regions? 4) What is the timeframe for carbon to return to typical primary forest levels?

Methods

Study area and landscape context

Our study focused on the eastern-Amazonian municipality of Bragança (Appendix S1: Fig. S1). This municipality has lost 90.2% of its native forests and mangrove areas. Secondary forest covers 28.8% of the landscape, accounting for 67.5% of the total forest cover (including mangrove areas) (Appendix S1: Fig. S1). Primary and secondary forests (established post-1985) are situated in small, isolated, and selectively logged fragments (~30 to 60 hectares; MapBiomas 2019).

We established three study-plot classes. In 1999, we began inventories in 12 secondary forest plots (50 x 50 m = 0.25 ha; Appendix S1: Fig. S1, Table S1; hereafter, "*long-term plots*"). These plots were separated by a mean distance of 265 m (range 70-590 m). In 2017, we established an additional four secondary forest plots (250 x 10 m = 0.25 ha; hereafter, "*extra plots*") in different fragments of the Bragança municipality. In 2017, we also established three plots in primary forests (250 x 10 m 0.25 ha; Appendix S1: Fig. S1; hereafter "*primary forest plots*").

Both long-term and extra secondary forest plots were abandoned after successive cycles of slash-and-burn agriculture (for manioc, maize, and rice cultivation). There was no record of wildfires after agricultural abandonment at our plots. Given that undisturbed primary forests are extremely rare in the region, to select primary forest plots we conducted interviews with local people to identify sites that retain the structural characteristics of Amazonian old-growth forests; nonetheless, it is likely that selective logging and edge effects have already altered our primary forest plots. All plots were located in *terra-firme* areas. The predominant soils across all plots are oxisols with low fertility and 15-35% clay in the superficial layers (Da Silva Castro et al. 2013). Plots were flat, and average elevation was 35 m (range: 30-66 m).

Age of secondary forests

We used two approaches to evaluate secondary forest age. The long-term plots are older than the existing satellite record and were provisionally aged by interviews conducted by the researchers who established them in 1999. The estimated age in 2017 was c. 48-58 years old. Unfortunately, Landsat 1 images from the region (1974) were also too cloudy to support these interviews. We therefore estimated ages by back casting the non-linear growth trajectories (Question 4). For the extra plots recovering post 1985, we used the MapBiomas 3.1 dataset to estimate their ages (details in Appendix S1; MapBiomas 2019).

Tree censuses

The long-term secondary forest plots were established with a full tree census in 1999, with repeated surveys taking place annually between 2000-2004 then subsequently in 2006, 2011, 2014 and 2017, while a full tree census was undertaken in the extra and primary forest plots when they were established in 2017. In all plots, we measured all trees ≥ 10 cm diameter at breast height (DBH). In the last census, we also estimated tree height by visual assessment. Plant identification was conducted in the field and when necessary botanical samples were collected for comparisons from the Herbário IAN

(Embrapa Amazônia Oriental) collection. Tree census data are available at ForestPlots.net (Lopez-Gonzalez et al. 2011).

Estimation of carbon stocks and tree species richness

We used three approaches to estimate the above-ground biomass (AGB) of individual stems. First, we calculated AGB using the allometric equation: $AGB = 0.637 \times (\rho D^2 H)^{0.976}$ where ρ represents tree wood density (g cm^{-3}), D represents stem DBH (cm) and H represents stem height (Chave et al. 2014). Stem wood densities were taken from the Global Wood Density Database (Chave et al. 2009). We subset the data to entries for South America and used the mean wood density across entries at the lowest available taxonomic level (e.g. where no data was available for a species, we used the genus average).

To estimate the height of stems for censuses prior to 2017, we used non-linear least-squares to determine height-DBH relationships at each study plot. Using the 2017 height and DBH values as training data, we assumed a functional relationship described by the Michaelis-Menten model: $H = \frac{a \times D}{b \times D}$, where a and b are estimated from the training data. Second, due to potential errors in the tree height sample caused by our visual assessment approach, we applied correction functions to the 2017 stem heights then determined pre-2017 tree heights as described above. The height-correction functions were derived from large primary and second secondary forest tree samples (c. 500 individuals in both forest types) from the eastern Brazilian Amazon for which visual and laser-based heights were estimated. These data suggest that visual assessments tend to underestimate stem height, especially stems < 15 m tall in secondary forests (Appendix

S1: Fig. S2). Finally, we also estimated stem biomass using the following allometric equation that does not include a height parameter: $AGB = exp\,[-1.803 - 0.976E + 0.976\, ln\,(\rho) + 2.673\, ln\,(D) - 0.299\, ln\,(D)^2]$, where E is a measure of environmental stress, defined by cumulative water deficit and temperature and precipitation seasonality (Chave et al. 2014).

Results across these approaches suggest that use of the uncorrected values of stem height values underestimates plot-level carbon by around 10-20%, so we do not report results from this approach. In the main text, we focus on results from the height-corrected estimation technique because including height is known to improve AGB estimates (Sullivan et al. 2018). However, the height-corrected approach returned highly similar carbon estimates to those obtained using the allometric equation that does not include height (mean root square difference < 1.5 Mg C ha^{-1}). The results for this latter approach can be found in Appendix S1: Fig. S6. We assumed that the carbon content of the individuals represents 50% of the AGB. Tree species richness (of individuals > 10 cm DBH) in each plot was assessed by rarefying richness to 100 individuals, the minimum abundance in the sampled plots.

Climatological and landscape predictors of carbon dynamics

Monthly precipitation and temperature for each census year were determined using data collected at a local meteorological station (INMET 2018; Appendix S1: Fig. S1). These data show that the study region has annual precipitation of 1,850 mm, with a rainy season from December to July (222 mm month^{-1}) and a dry season from August to November (19.5 mm month^{-1}).

We calculated three climatological predictors of carbon dynamics: the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010), the Maximum Climatological Water Deficit (MCWD; Malhi et al. 2009), and the maximum dry season temperature (MDST). SPEI is a measure of water stress based on the difference between monthly precipitation and potential evapotranspiration expressed as a standardized index, with negative values representing drier periods over the timescale considered relative to median values for a long-term reference time-series. To account for medium-term water deficit, we estimated monthly SPEI values for a 12-month moving window from May to April. MCWD is the most negative accumulated value of the climatological water deficit (CWD) over each one-year period (between May and April; 1973-2017). CWD is defined as monthly precipitation, minus evapotranspiration, minus the CWD of the previous month (Malhi et al. 2009). MDST was measured as the highest monthly temperature value during the dry season (i.e., between August and November). Finally, we used edge distance as our predictor of landscape context effects on carbon dynamics. For each secondary forest plot, edge distance was calculated as the distance from the plot centroid to the nearest forest edge using images from Google Earth 7.1.7.2600 (earth.google.com).

Carbon anomalies

We calculated the amount of carbon incorporated by growth (G) and recruitment (R), as well as that lost by mortality (M) for each census interval, thus obtaining periodic carbon balance (B = G + R - M). We used anomalies to subtract the expected natural carbon accumulation that occurs through time. Censuses occurred at varying intervals (1, 2, 3 and 5 years). Let $i \in 1, 2, \ldots, 9$ be one of the intervals, let T_{-i} be the total length of the time series minus the length of interval i, let C_{-i} be the change in carbon balance or one of its components over all intervals not including i, let n_i be the number of years in interval i, and let a_i be the observed change C in interval i. Therefore, the expected change in C in interval i is $E(C_i) = \frac{n_i \times C_{-i}}{T_{-i}}$, and the anomaly is $a_t - E(C_t)$.

Statistical analysis

We used Bayesian piecewise linear splines to estimate i) carbon recovery with time; ii) tree species richness recovery with time; and iii) the relationship between carbon and tree species richness recovery (Question 1). Bayesian model comparison with reversible jump Markov Chain Monte Carlo simulations (Lunn et al. 2009) was used to average multiple piecewise-linear models to produce smoothed curvilinear relationships (Thomson et al. 2010). The number and location of change-points were assigned hierarchical prior distributions that included zero changepoints as a possibility. In each simulation, the spline function was comprised of up to $k = 6$ linear coefficients (i.e., between zero and six) and $k - 1$ corresponding changepoints. The resulting posterior distributions yielded model-averaged parameter estimates and 95% credible intervals that account for uncertainties about model structure. The model for long-term secondary forest recovery included plot-level random effects to account for expected similarities between plots.

To explore whether variation in maximum dry season temperature, water stress (SPEI and MCWD) and landscape context (edge distance) influence tree growth, recruitment, mortality and carbon dynamics (Question 2), we used Bayesian variable selection with nonlinear covariate effects (Thomson et al. 2010). We used the lowest recorded value of MCWD in a given period as our measure of one-off drought severity (see also Esquivel-Muelbert et al. 2019). We used SPEI values (Vicente-Serrano et al. 2010) as a measure of the longer-term (here 12-month) water balance, which is known to be significant for tree growth (Greenwood et al. 2017). The relative importance of an explanatory variable was assessed by the posterior probability of a non-zero effect. We considered posterior probabilities > 0.75 to be indicative of a statistical association.

We compared the average carbon accumulation rates of our secondary forest plots (both long-term and extra plots) to estimates of carbon accumulation from leading tropical and global assessments (Bonner et al. 2013, Poorter et al. 2016, Lennox et al. 2018, Requena Suarez et al. 2019) and pan-Amazonian estimates in old-growth and logged primary forests (Brienen et al. 2015, Rutishauser et al. 2015) (Question 3). To investigate secondary forest recovery timeframes (Question 4), we fit monotonically increasing and marginally decreasing rational functions, based on third-order polynomials as the numerator and second-order polynomials as the denominator, to the median and lower and upper bounds of the 95% credible intervals for carbon levels in the long-term plots (Fig. 1A).

Results

Climate variation over the time-series (1972-2017)

The maximum dry season temperature increased by 0.1 °C per decade across our time series (Appendix S1: Fig. S5). Water stress (MCWD and SPEI values) was highly variable, declined weakly, and was highest (lowest values of MCWD and SPEI) in strong

El-Niño years. MCWD and SPEI were only weakly related ($r = 0.44$ across the 1973-2017 time series; $r = 0.19$ during census years – Appendix S1: Fig. S3).

Carbon and tree species richness recovery

The average carbon stock in 2017 was 141.7 (±16.3 SE), 58.3 (±2.7) and 4.27 (±1.19) Mg ha^{-1} in, respectively, the primary forest, long-term, and extra plots, whereas rarefied richness was 60.05 (±4.07), 41.2 (±1.4) and 33.9 (±3.5) (Appendix S1: Table S1). In the long-term secondary forest plots, the recovery of carbon and rarefied richness showed different trajectories among census (Fig. 1A-B). The mean accumulation of carbon in our long-term plots was 1.08 Mg ha^{-1} yr^{-1} between 1999 and 2017. Carbon and time were associated at the 0.07 level (i.e., 93% of the R^2 posterior mass was greater than zero). Rarefied richness displayed a much weaker relationship with time, being associated only at the 0.33 level and with a mean trend of 0.21 species yr^{-1}. Carbon stock in the long-term secondary forest plots reached only 41.1% of the average primary forest level in 2017, while rarefied richness recovered to 56%. Above-ground carbon stocks and plant diversity were not related to each other over time (Fig. 1).

Influence of climate and edge distance on carbon anomalies

Carbon balance was positively related to SPEI in the long-term plots. These changes were driven by variation in stem growth, with lower than average carbon accumulation in drier periods (Fig. 2). Although the maximum dry season temperature did not affect the overall carbon balance, it had countervailing effects on carbon growth and recruitment: growth was highest and recruitment lowest in the warmest years and vice versa. Carbon loss from mortality was not associated with any of the predictors (Fig 2), and edge distance and MCWD were not associated with any of the carbon anomalies (Appendix S1: Fig. S7).

Comparison between carbon recovery rates

The carbon recovery rate in the long-term plots was lower than most estimates of secondary forest recovery from the Amazon or across the tropics, and our younger extra plots had even lower recovery rates than the older long-term plots (Fig. 3). Recovery rates at our study plots were also below Amazon-wide estimates of primary forest recovery after selective logging and were only slightly higher than the average carbon uptake rate of tropical primary forests (Fig. 3).

Extrapolating carbon recovery timeframes

Our backwards extrapolation (to zero) gives approximate ages for the long-term secondary forests of 39 and 48 years in 2017 (Fig. 4), which is marginally lower but generally consistent with the ages reported during interviews (c. 48-58 years old in 2017). As a consequence of the low carbon recovery rates of the long-term plots, our extrapolation of future carbon levels — aimed at providing a rough estimate of a plausible recovery window under present-day conditions — suggests that it will take at least another century (c. 150 years since abandonment) until the site regains carbon levels similar to local primary forests (Fig. 4).

Discussion

Influence of climate on carbon recovery in secondary forests

Our results show for the first time that secondary forest carbon accumulation in the Amazon can be influenced by periods of water deficit. This suggests that the role of water availability in regulating carbon uptake observed in humid primary forests (e.g., Phillips et al. 2009, Anderson et al. 2018), dry primary (Mendivelso et al. 2014, Álvarez-Yépiz et al. 2018) and dry secondary forests (Maza-Villalobos et al. 2013, Martínez-Ramos et al. 2018) also extends to humid secondary forests. The generality of this finding is consistent with the strong link between the evapotranspiration index SPEI and spatial variation in carbon recovery in tropical forests (Schwalm et al. 2017). Indeed, secondary forests in the humid tropics may be even more sensitive than those in tropical dry regions given that the former show longer recovery times in the face of seasonal water availability (Poorter et al. 2019). Despite the similarity of the findings across forest types, our results also suggest that different mechanisms may underpin the sensitivity of the carbon balance to water deficit. Drought-mediated changes in primary forest carbon balance are driven by increased mortality (Phillips et al. 2009, Anderson et al. 2018), while the changes in the carbon balance observed in this study were primarily driven by reduced growth (Fig. 2).

Although the maximum dry season temperature (MDST) had no influence on the carbon balance of the studied secondary forests, increasing MDST increased the growth of established stems while reducing recruitment. The mechanistic explanation for such contrasting results requires further investigation. However, it might indicate a differential temperature effect between stems size classes. For example, higher temperatures exacerbate the physiological consequences of acute water stress (Lloyd and Farquhar 2008, Markesteijn et al. 2011), and shallow-rooted smaller stems (<10cm DBH) may be more sensitive to drought effects than the medium-sized stems (10-30 cm DBH) (Elias et al. 2018). The increase in growth also suggests that established stems that can cope with higher temperatures may also benefit from factors associated with hotter years, such as better light conditions (Bentos et al. 2017) or faster litter decomposition rates and nutrient cycling (Eichenberg et al. 2013).

The positive relationship between temperature and growth in the assessed secondary forest contrasts with findings in tropical primary forests, where negative relationships (e.g. Feeley et al 2007) and a lack of any relationship (e.g. Rowland et al. 2014) have been detected. This difference may be explained by the dominance in secondary forests of fast growing, heliophilic species (Vieira et al. 1994, Chazdon 2014), which tend to show relatively high optimum temperature points (Slot et al. 2014). A more complete understanding of secondary forest temperature responses is crucial given their importance as a climate change mitigation technology.

Carbon recovery

Carbon accumulation rates in our long-term study plots (48-58 years old) were low compared to most other studies (Fig. 3), and only around twice that recorded in Amazonia’s primary forests. Although this rate of carbon accumulation is comparable to recent continental-scale estimates of biomass recovery in older (20-80 years old) tropical secondary rainforests in the Americas (Requena Suarez et al. 2019; Fig. 3), this similarity masks one important difference: our long-term plots had a much lower lifetime recovery rate than the same continent-scale estimates (Fig. 4B). Combining the mean < 20- and 20-80-year-old accumulation rates of Requena Suarez et al. (2019) suggests that a typical American tropical secondary rainforest will accumulate the median carbon seen at our study site (Fig. 1) in just 20-21 years, less than half the site's estimated age (Fig 4B). Moreover, even the lower bound of the Requena Suarez et al. (2019) 95% accumulation rate confidence intervals suggests that American tropical secondary rainforests should attain our site's median carbon in 28 years.

The low lifetime recovery rate and equivalent rates of recovery over the last two decades can only be reconciled if forests in the Bragantina region have a very slow rate of early forest succession (Fig 4B). This is supported by the four younger extra secondary forest plots, which displayed even lower recovery rates than the long-term plots and are far below the predictions of Requena Suarez et al. (2019) for age-equivalent plots (Fig. 3). Furthermore, our backward extrapolation of growth tended to underestimate the secondary forest age when compared to interview data – if we assume the interview-based dates are correct, this would be consistent with slower than predicted growth rates when the forests were younger.

Such slow early-successional recovery rates could reduce the effectiveness of climate mitigation strategies in regions that have a long history of human occupation, have lost most of the original forest cover, and have suffered the widespread defaunation of large-bodied vertebrates through hunting (Almeida et al. 2010, Moura et al. 2014). These factors reduce the dispersal and colonization of forest tree species (Hooper et al. 2005), reduce carbon stocks (Bello et al. 2015) and increase recovery times (Jakovac et al. 2015, Chazdon 2014, Villa et al. 2018). Moreover, it is important to note that these measures of carbon recovery were observed under the climatic and landscape conditions over the lifetimes of the secondary forest plots. Future recovery could be slower if the last forest remnants are lost, further decreasing forest connectivity (Aguiar et al. 2016, Reid et al. 2018, Matos et al. 2019), if the frequency of farm-fallow cycles increases (Jakovac et al. 2015, Villa et al. 2018), or if deforestation and climate change further increase water deficits (Fu et al. 2013, Spracklen et al. 2018).

Interesting insights can be drawn from the two predictors – the Maximum Climatological Water Deficit (MCWD) and edge distance – that had no discernible impact on carbon balance. First, MCWD is one of the most frequently used measures of water deficit in studies of tropical forests (e.g., Malhi et al. 2009, Anderson et al. 2018, Berenguer et al. 2018, Esquivel-Muelbert et al. 2017, 2019), but it appears that longer-term measures such as the 12-month SPEI index can reveal ecological processes that are not influenced by inter-period water deficit maximums. Second, edge effects have been detected in a wide range of contexts, including in secondary forests (e.g. Magnago et al. 2017); the lack of any effect in our study could be due to the limited range of distance-to-edge (62-266 m) or the possibility that all long-term study plots were under some form of edge influence in this highly deforested landscape.

The recovery of biodiversity

Although rarefied richness exhibited greater convergence to primary forest levels (56%) than carbon (41.1%), there was a near-zero increase in secondary forest rarefied richness between 1999 and 2017. Richness therefore responds differently to carbon recovery, as tree diversity appears to have increased quickly in the initial stages of succession (see also Lennox et al. 2018) before reaching a state of impeded or arrested succession (Arroyo-Rodríguez et al. 2017). This slowdown could be due to the absence of diverse seed inputs and the slow generation time of trees limiting the recruitment of older-growth species. It also suggests that the strong carbon-biodiversity relationships observed in recovering forests elsewhere (Gilroy et al. 2014, Ferreira et al. 2018, Lennox et al. 2018) may not occur in older secondary forests or in highly deforested landscapes. Finally, it is also likely that we are overestimating the relative recovery of biodiversity: although we rarefied richness by 100 stems, which is two to five times higher than previous studies assessing biodiversity recovery (Rozendaal et al. 2019), the absolute difference between primary and secondary forest would likely be much greater if we considered larger plots that capture more of the high beta diversity of primary forest (e.g., Solar et al. 2015).

Conclusion

The capacity of regenerating tropical secondary forests to sequester carbon and provide habitat for tropical species has profound implications for global climate change and biodiversity conservation. Our study is among the first to utilize data collected over two decades through periodic resampling and finds that the ability of secondary forests to mitigate climate change and limit biodiversity loss are likely to be negatively affected by increases in the rate of tropical deforestation and ongoing climate change. Understanding the generality and future climate sensitivity of these responses will require further investment in long term studies in human modified tropical forests.

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Figures

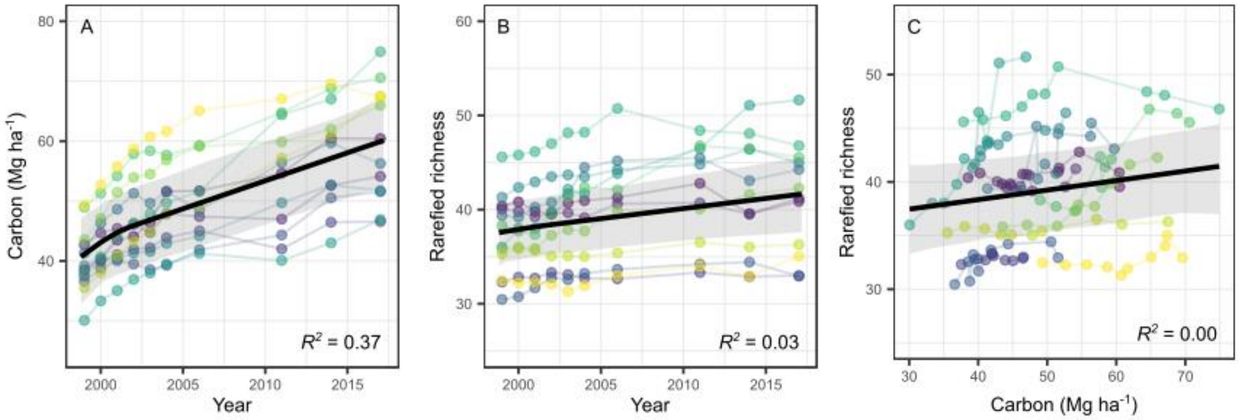

Figure 1: The recovery of secondary forests in Bragança. Carbon (A) and rarefied species richness (B) and the relationship between carbon and rarefied richness (C) between 1999 and 2017 in the twelve long-term study plots. Points show results at each census. Points and lines are color-coded by plot. The black line shows the median trend. The grey band shows the 95% credible interval.

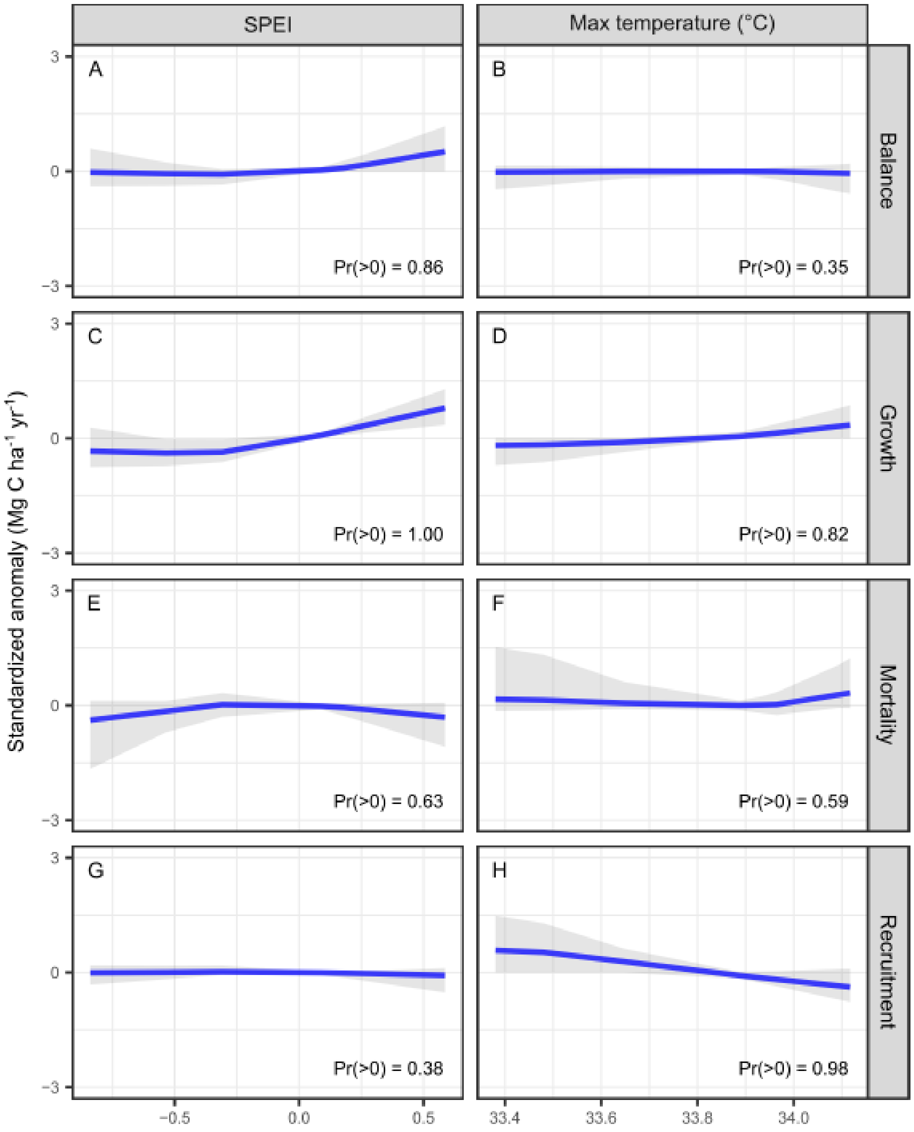

Figure 2: Climate and secondary forest carbon dynamics. The marginal effect of the standardized precipitation-evapotranspiration index (SPEI; A, C, E, G) and the maximum dry season temperature (Max temperature; B, D, F, H) on carbon balance (A-B), growth (C-D), mortality (E-F) and recruitment (G-H) in the twelve long-term secondary forest study plots. Lines show the median relationship. Bands show the 95% credible interval. A statistical association was assumed for posterior probabilities of a non-zero effect (*Pr(>0)*) > 0.75.

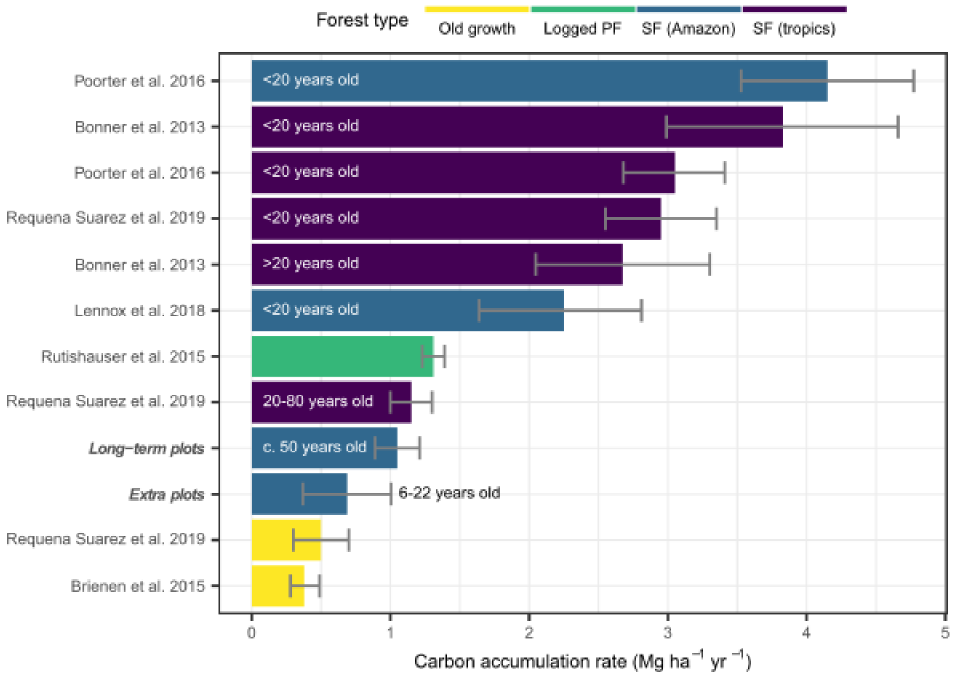

Figure 3: Estimates of carbon accumulation rates from previous studies compared to those from the twelve long-term and four extra secondary forest study plots. Bars show median values (or the mean where the median was unavailable). Error bars show 95% confidence/credible intervals. The Poorter et al. (2016) tropical secondary forest estimate uses only Neotropical plots. For the Requena Suarez et al. (2016) study, we used their estimates from tropical rainforests in the Americas. The Rutishauser et al. (2015) and Brienen et al. (2015) studies are from the Amazon.

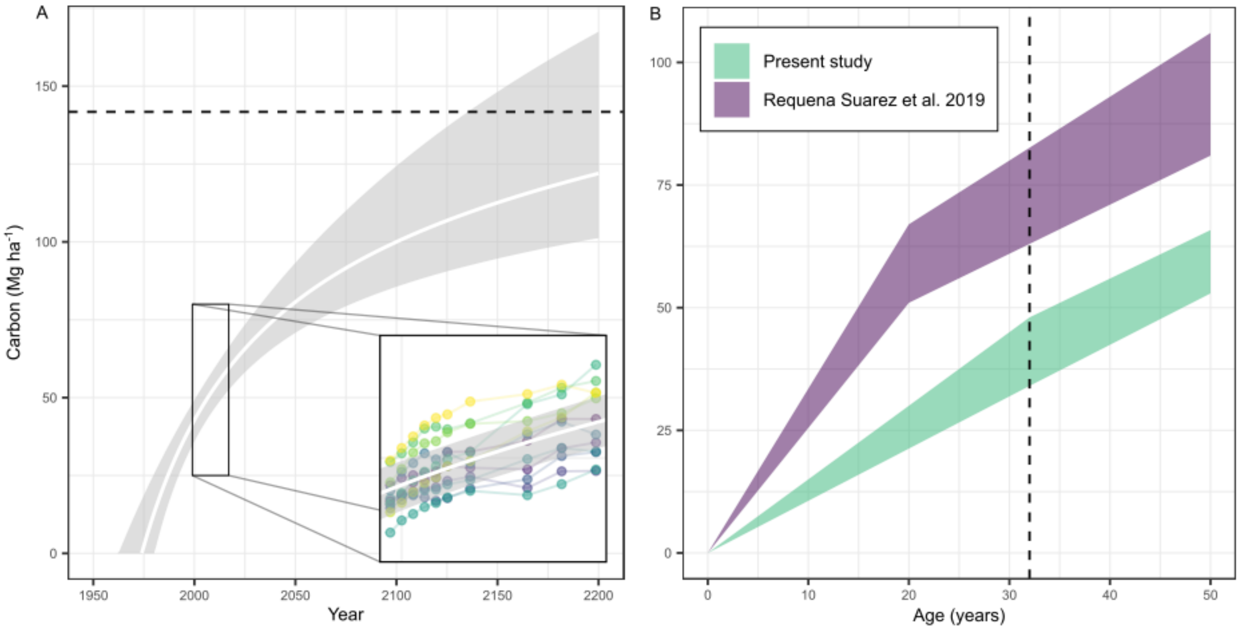

Figure 4. (A) Extrapolation of past and future carbon levels for the 12 long-term study plots. The white line shows median carbon; the grey band shows a possible range. These estimates were derived by fitting rational functions to the median and 95% credible lower and upper bounds of carbon recovery shown in Fig. 1A. The inset shows the data. Points shows carbon levels at each census. Points and lines are color coded by plot. The black dashed line shows mean primary forest carbon. (B) Comparison of carbon recovery trajectories from the present study and Requena Suarez et al. (2019). For this comparison, we used the Requena Suarez et al. (2019) 95% confidence interval carbon accumulation rates for <20- and >20-year-old tropical American secondary rainforests. For the present study, we assumed the 12 long-term study plots were 50 years old, meaning that the first census occurred (in 1999) at age 32 (shown by the vertical dashed line). Carbon recovery rates post this age were taken from the 95% credible lower and upper bounds (Fig. 1A). Rates prior to this age were extrapolated linearly from the 32-year-old 95% credible lower and upper bound values.

Supporting Information

Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes

ECOLOGY

Appendix S1

Measuring landscape disturbance

We calculated forest loss and fragmentation for the municipality of Bragança, Eastern Amazon. We used 30-m spatial resolution Landsat land-use data from Brazil's National Institute for Space Research (TerraClass 2014). To calculate forest loss, we first produced a binary (0-1) raster of primary forest cover and non-forest land, such as water bodies and savannah, using the GRASS *r.mapcalc* function in QGIS 3.2. Then, using shapefiles of Bragança, we ran the zonal statistics tool in QGIS 3.2 to calculate the total number of pixels (p), the total number of primary forest pixels (f) and the total number of non-forest pixels (nf). Percentage forest loss (l) is then given by $l = 100(1 - f/(p - nf))$.

To calculate forest fragmentation, we created a binary primary forest raster for Bragança. The municipality forest cover raster was then fed to the GUIDOS toolbox. This toolbox provides mathematical morphological operators that estimate the proportion of pixels that fall into several fragmentation classes (Vogt and Riitters 2017).

Estimating secondary forest age from the MapBiomas dataset

We classified pixels as secondary forests from the first year that they returned to one of the MapBiomas ‘forest’ classes following a period being classified as one of the ‘non-forest’ classes. Age was then calculated as the number of consecutive years that a pixel was classified as SF. We then used ArcGIS Pro to extract the age of each pixel intersected by the 10 x 250 m vegetation transects (Number of pixels = 13). Age was then calculated as the number of consecutive years that a pixel was classified as secondary forest and ranged from 8 to 33 years (Appendix S1: Table S1). We used the median of these values as the best representation of transect age. MapBiomas dataset 3.1 is available on the MapBiomas platform (www.mapbiomas.org; MapBiomas 2019). Note that the MapBiomas data is limited to the ageing of SFs established post-1985, which in our case means only the extra plots and not the twelve long-term study plots.

Correcting visually assessed stem heights

Given that visually estimated stem heights may suffer from large errors, we estimated correction functions and applied them to our secondary and primary forest stem height data. These correction functions were derived from large datasets, collected in the Santarem region of the eastern Amazon, of 473 and 551 secondary and primary forest stems, respectively, for which stem height was initially estimated visually and then estimated using laser hypsometer. We fit polynomial functions of degree one to five to these data. We then selected the most parsimonious functional relationship as the polynomial fit with the lowest Bayesian Information criterion score. These data and the corresponding correction functions can be seen in Fig. S2, and they suggest that visually estimated heights tend to underestimate true heights. Consequently, they may underestimate plot-level carbon.

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Figures and tables

Table S1: General information of the study plots evaluated in the Bragantina region. This information is from the last census in 2017. Abbreviations are as follows: Plot code = codes according to the ForestPlots.net platform (www.forestplots.net); Classes = study-plot classes (SF = secondary forest; PF = primary forest); NC = number of censuses; Age = estimated from interviews with landowners; and RSR = rarefied species richness.

Plot	Classes	NC	Age	Municipality	RSR	Carbon (Mg ha^{-}
MHO-01	Long-term SF	10	48-58	Bragança	40.87	60.43
MHO-01	Long-term SF	10	48-58	Bragança	44.25	54.13
MHO-01	Long-term SF	10	48-58	Bragança	44.98	46.56
MHO-01	Long-term SF	10	48-58	Bragança	51.63	51.57
MHO-01	Long-term SF	10	48-58	Bragança	46.78	56.26
MHO-01	Long-term SF	10	48-58	Bragança	45.45	51.74
MHO-02	Long-term SF	10	48-58	Bragança	42.27	46.91
MHO-02	Long-term SF	10	48-58	Bragança	36.29	74.91
MHO-02	Long-term SF	10	48-58	Bragança	35.04	70.59
MHO-02	Long-term SF	10	48-58	Bragança	41.21	65.96
MHO-02	Long-term SF	10	48-58	Bragança	32.98	67.50
MHO-02	Long-term SF	10	48-58	Bragança	32.93	67.37
JSO-01	Extra SF plot	1	10	Bragança	10.83	5.2
PCE-01	Extra SF plot	1	15	Bragança	14.25	5.04
RUT-01	Extra SF plot	1	22	Bragança	17	2.76
JCO-01	Extra SF plot	1	6	Bragança	6.25	0.91
ALE-01	Primary forest	1	-	Bragança	52	113.63
VAV-01	Primary forest	1	-	Bragança	63.07	136.06
FRE-01	Primary forest	1	-	Viseu	65.09	162.1

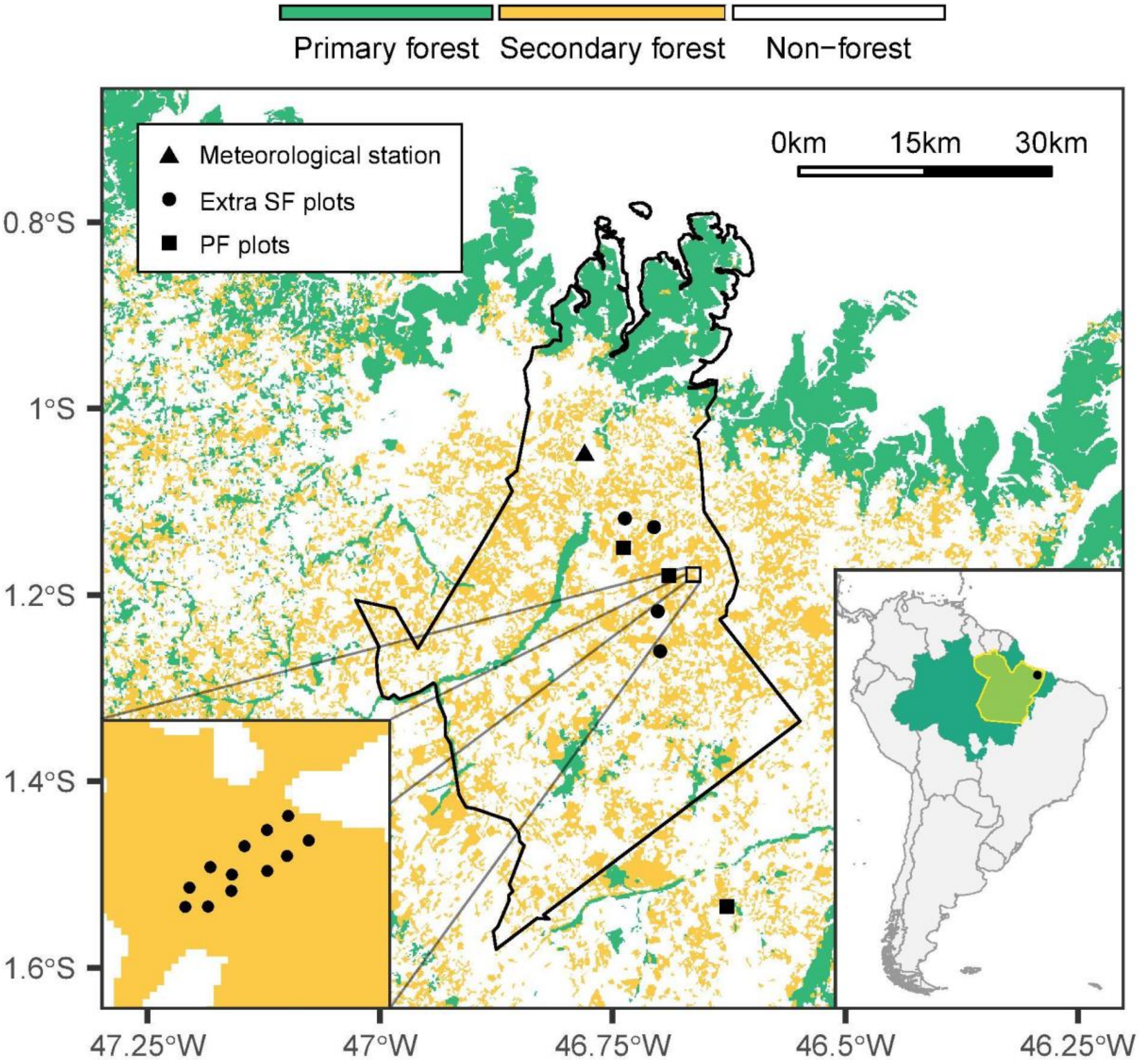

Figure S1: Study region and land-use context. The distribution of primary and secondary forest in the Bragantina region of the eastern Amazon. The unfilled square shows the location of the twelve long-term study plots, and this region is magnified in the left-hand inset. The Bragança municipality is shown in black outline. Also shown are the locations of the four extra secondary forest plots (circles), the three primary forest study plots (filled squares) and the local meteorological station from which the climate data used in the study were obtained (triangle). The right-hand inset shows the study location (black point) within the state of Pará (yellow) and the Brazilian Amazon (green).

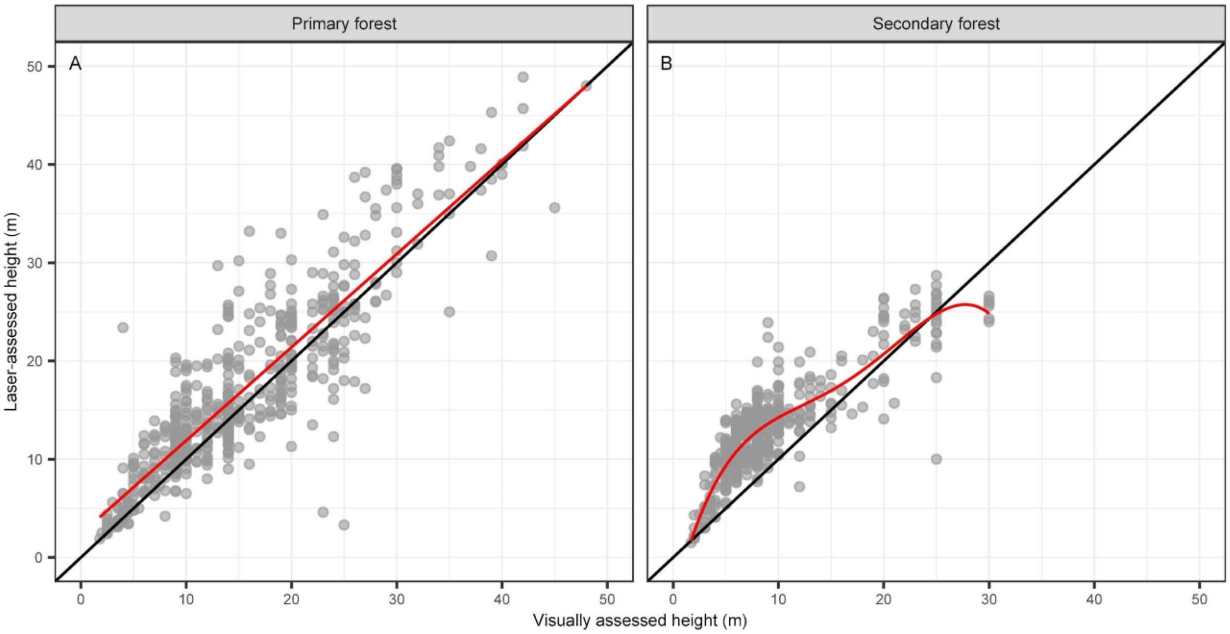

Figure S2: Correcting visually assessed stem height estimates. The relationship between visually assessed and laser-assessed stem height estimates from c. 500 primary forest (A) and c. 500 secondary forest (B) stems. This dataset was collected in the Santarém region of the eastern Amazon. The black line shows a one-to-one correspondence. The red lines show the most parsimonious polynomial relationships, which were used to correct the visually assessed stem heights used in this study.

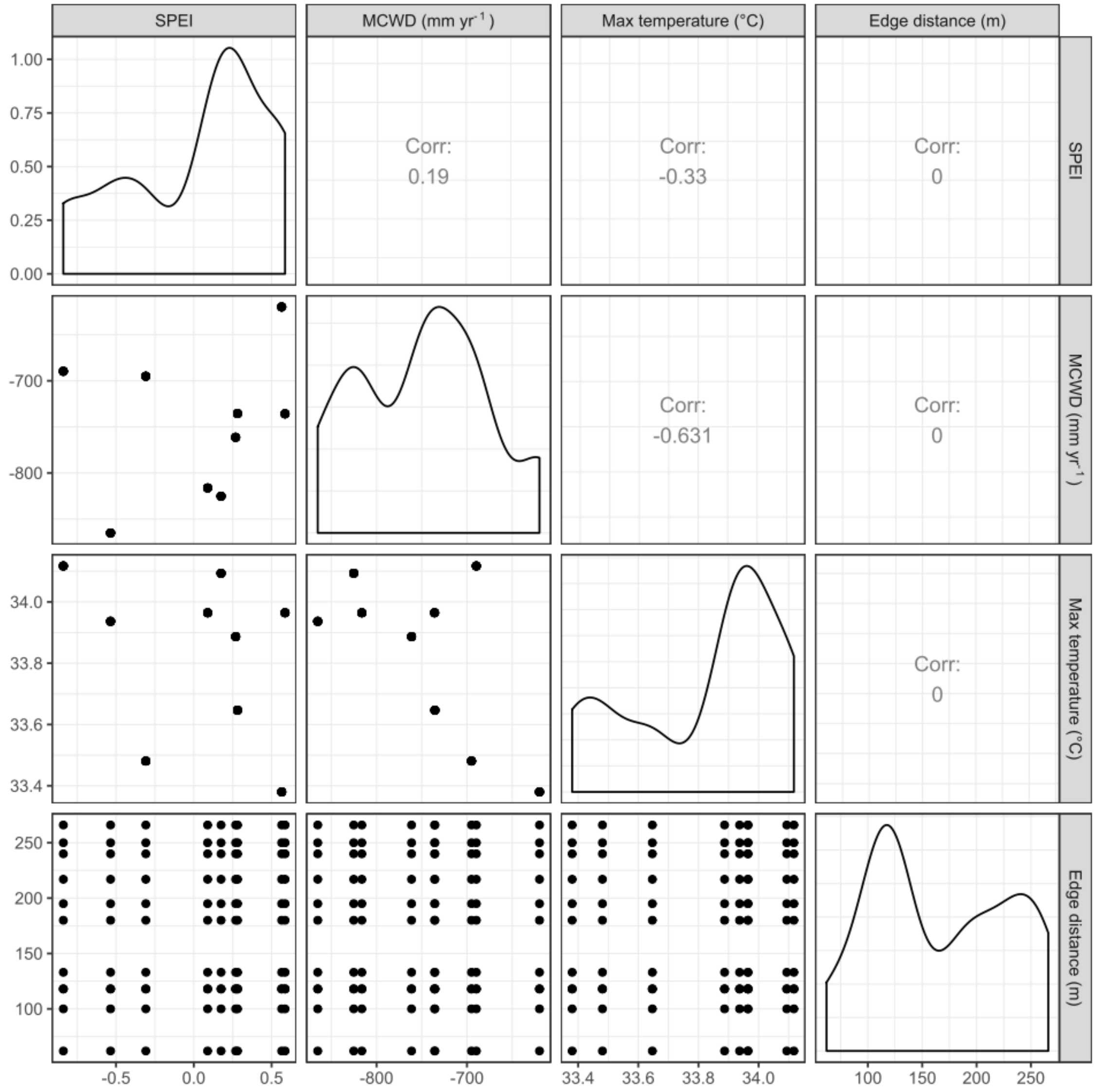

Figure S3: Climate and land-use context variables. The distribution of and relationships between the climatological (maximum cumulative water deficit (MCWD), standardized precipitation-evapotranspiration index (SPEI), and maximum dry season temperature (Max temperature)) and land use context (edge distance) variables.

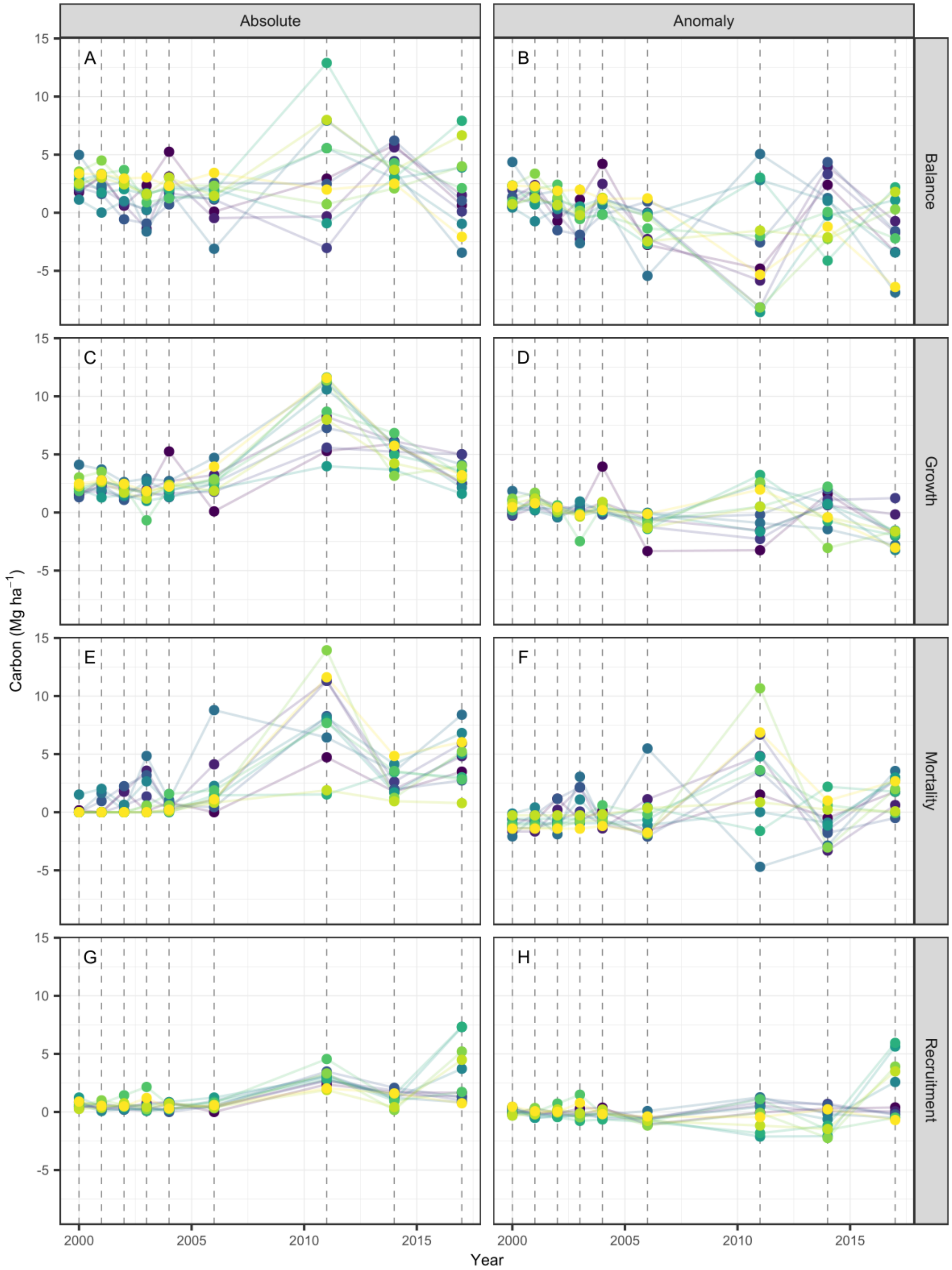

Figure S4: Carbon dynamics. Carbon balance (A-B), growth (C-D), mortality (E-F) and recruitment (G-H), expressed in absolute terms (A, C, E, F) and as anomalies (B, D, F,

H) between the 10 censuses (shown by dashed vertical lines). Points show results at each census. Points and lines are colour coded by plot.

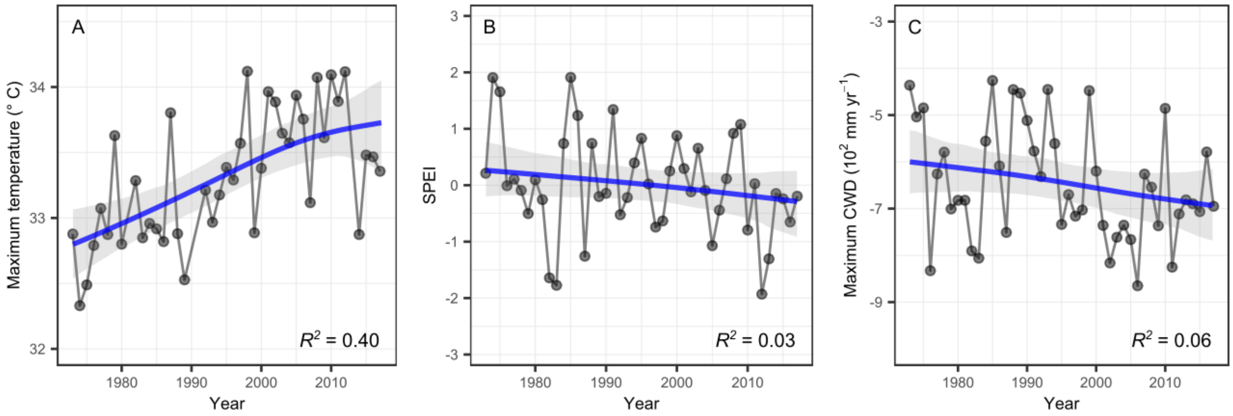

Figure S5: Climate change in Bragança. The maximum seasonal temperature (A), standardized precipitation-evapotranspiration index (SPEI; B) and cumulative water deficit (CWD) between 1973 and 2017. The blue line shows the median trend; the grey band shows the 95% credible interval.

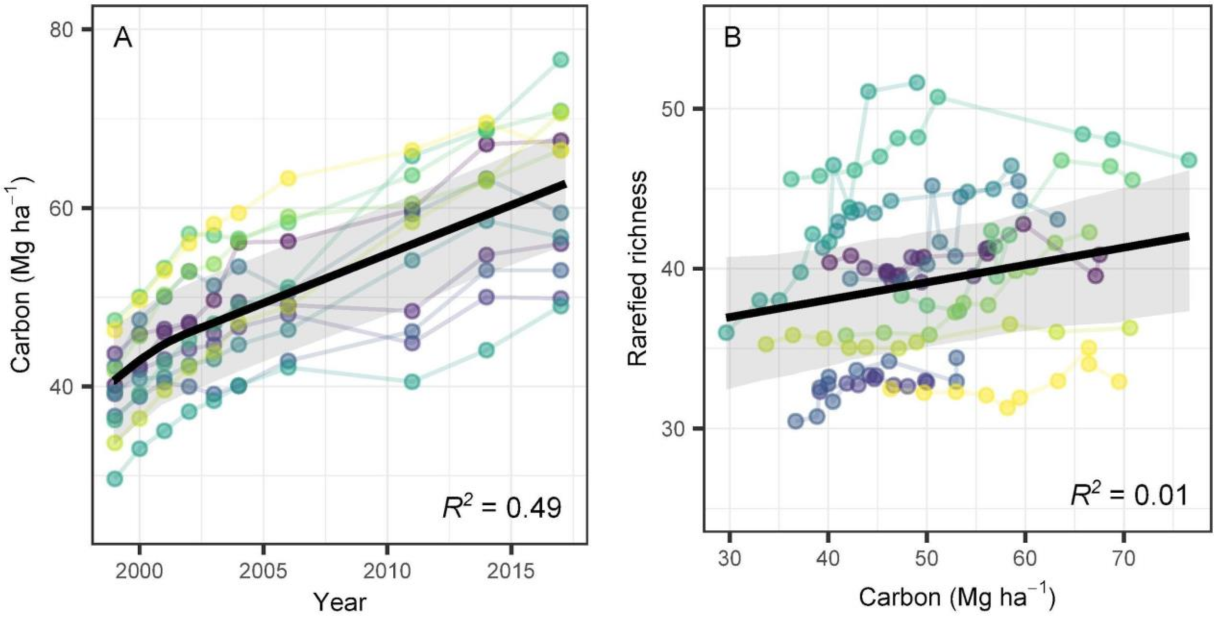

Figure S6: Carbon recovery estimated without using stem heights. The recovery of carbon (A) and the relationship between carbon and rarefied richness (C) between 1999 and 2017 in the twelve long-term study plots. These carbon estimates were derived using an allometric equation that does not include a height parameter (see Eq. (1)). Points show results at each census. Points and lines are colour coded by plot. The black line shows the median trend. The grey band shows the 95% credible interval.

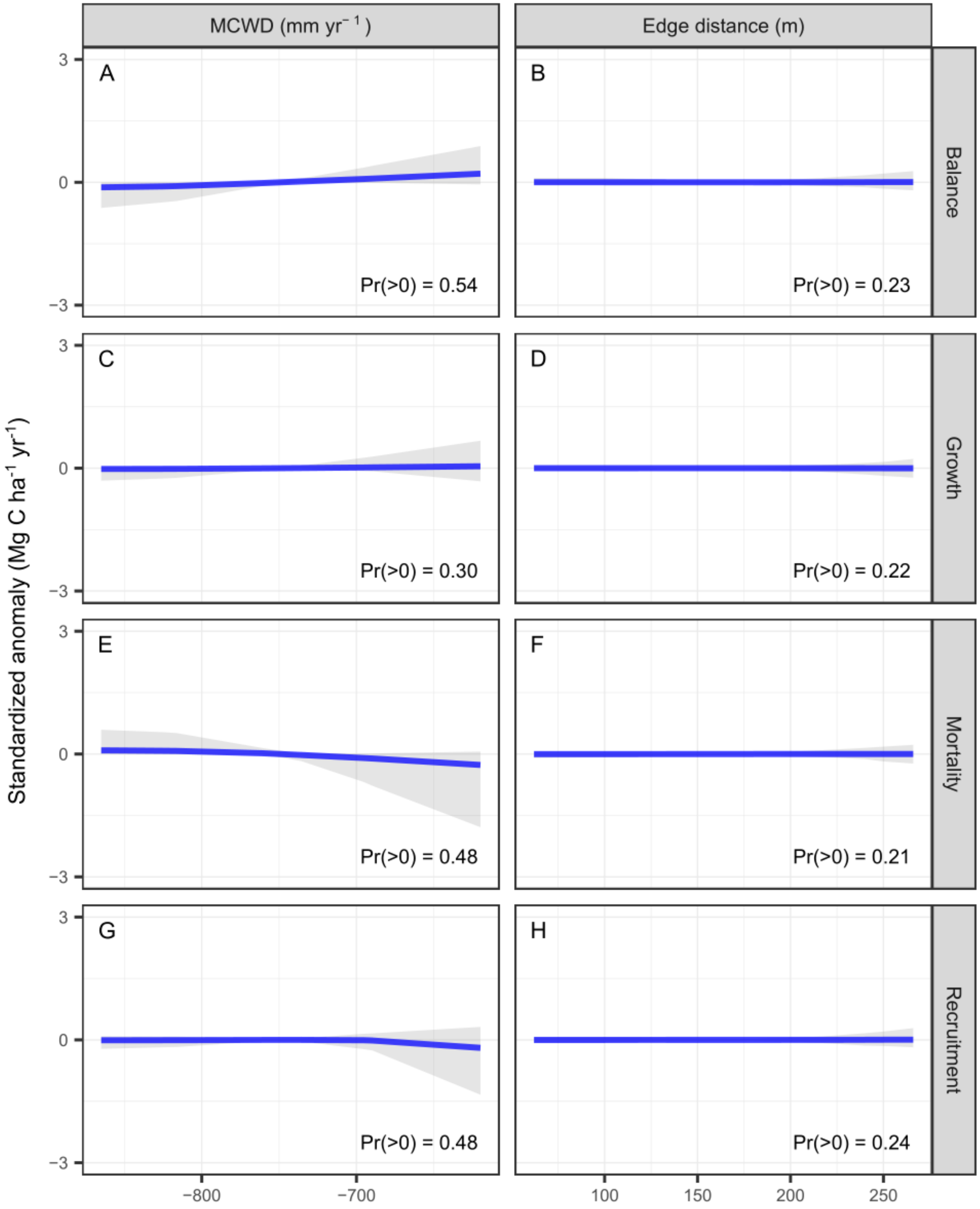

Figure S7: The relationship between land-use context and secondary forest carbon dynamics. The marginal effect of the maximum cumulative water deficit (MCWD: A, C, E,

G) and distance to forest edge (edge distance: B, D, F, H) on carbon balance, growth, mortality and recruitment in the twelve long-term secondary forest study plots. Lines show the median relationship. Bands show the 95% credible interval. An association was assumed for posterior probabilities of a non-zero effect (*Pr(>0)*) > 0.75.

CAPÍTULO 2

ASSESSING THE FUNCTIONAL RECOVERY OF AMAZONIAN SECONDARY FORESTS

O segundo capítulo dessa tese está formatado conforme as normas da revista Ecology disponível em: https://esajournals.onlinelibrary.wiley.com/journal/.

Abstract

Functional traits can provide important insights about succession mechanisms and recovery of ecosystem services and their understanding from the perspective of current global changes is essential for a comprehensive analysis of the future of tropical forests resilience. We used a set of functional data from 24,924 individuals from 43 permanent plots, covering 10.5 ha of forest in the Bragantina, Marabá, Parauapebas and Santarém regions to investigate the changes and recovery of functional traits (specific leaf area, SLA; wood density, WD; seed size and endozoochoric dispersion) and its relationships with soil and climate predictors. Bragantina region showed lower recovery for SLA and seed size and greater recovery for wood density relative to primary forest, while endozoochoric dispersion was similar between all regions. The recovery of seed size and WD in relation to adjacent primary forests was positively related to age of abandonment, while the recovery of SLA was related to less annual precipitation and higher fertility and clay content. These results reflect the differences in species composition between the succession stages and functional variation in the landscape context between the evaluated regions. The differential influence of predictors between functional traits is evidence of the complexity of the recovery process in secondary forests. In addition, these differences show that each trait has a successional trajectory, such as the seed size and WD, that were related to the age of abandonment and can be indicators of the succession stages during the recovery of these areas.

Keywords: Amazon, restoration, secondary vegetation, heterogeneity, functional traits.

Introduction

Tropical forests are important repositories of global biodiversity and mitigators of climate change (Ellison et al. 2017). The unprecedented conversion of these areas to other types of human land-use has substantially reduced the amount of old-growth primary forests in the last decades, while secondary forests — areas regenerating after land clearance — have proportionally increased (Wang et al. 2020). Research on forest recovery needs to be constantly updated due to ongoing and accelerating global environmental change (Chang and Turner 2019) and the desire to speed up restoration (Chazdon and Guariguata 2016).

Secondary forests are not ecologically equivalent to primary forests (Gibson et al. 2011), but can play an important role in maintaining biodiversity and biogeochemical cycles (Houghton and Nassikas 2018, Rozendaal et al. 2019, Matos et al. 2019). Currently these forests represent a large portion of the world's tropical forests, and could become the predominant forest type in the future (Chazdon 2017a). At the same time, secondary forests themselves will be affected by climate change: severe droughts and higher temperatures negatively affect their recovery (Elias et al. 2019), threatening tropical forests and the ecological services provided by them (Allen et al. 2010, Duffy et al. 2015, Ellison et al. 2017).

Functional traits can provide important insights about succession mechanisms and recovery of ecosystem services (Chazdon 2017b, Berenguer et al. 2018, Chua and Potts 2018, Poorter et al. 2019), and their understanding from the perspective of current climate change is essential for a comprehensive analysis of the future of tropical forests resilience. Some traits such as dispersal type and seed size demonstrate the limiting factors for forest recovery due to their strong relationship with the colonization and establishment of species (Wijdeven and Kuzee 2000, Reid et al. 2015). In this case, trees with larger seeds and zoochoric dispersion tend to have larger dispersal distance and most successful colonization of new areas (Russo and Augspurger 2004, Clark et al. 2005, Lozada et al. 2007). In contrast, other traits like specific leaf area may provide insights on water use efficiency and plant performance (Wright et al. 2004, Poorter and Bongers 2006); and wood density is directly related to the carbon cycle and drought and fire resistance (Brando et al. 2012, Berenguer et al. 2018, Phillips et al. 2019). Many of these traits are linked by trade-offs in plant life history strategies. For example, fast-growing species tend to have lower wood density, many smaller seeds as opposed to fewer large ones, and larger specific leaf area due to low tissue investment, accelerated metabolism, and need to colonise large areas quickly - whereas for long-lived species it is the opposite (Poorter and Bongers 2006).

The evaluation of the dynamics of functional traits may indicate different strategies of species during recovery and successional trends, although these mechanisms are still poorly understood (Stan and Sanchez-Azofeifa 2019). Early stages of succession in secondary forests generally are dominated by fast-growing species (Chazdon et al. 2010, Chazdon 2017b), however, the succession trajectory is variable and driven by a mix of different stochastic and deterministic processes (Nuñez et al. 2019). Environmental factors such as climate, soil and disturbance severity may account for variation in plant functional traits recovery over time (Boukili and Chazdon 2017, Pinho et al. 2018, Chua and Potts 2018, Estrada-Villegas et al. 2019). For example, there is evidence that aboveground biomass recovery is extremely slow in highly fragmented landscapes devoid of primary forests compared to regions with greater forest cover (Elias et al. 2019). Likewise, wetter sites recover faster than driers sites (Poorter et al. 2016). Thereby, different trajectories for the succession of functional traits can be found across regions, which may help to clarify the role of this component in the assessment of tropic forest resilience.

Here, we seek investigate the changes and recovery of functional traits (specific leaf area, wood density, seed size and dispersal type) in secondary forests of different regions in the eastern Amazon. We addressed three questions: 1) Are functional traits recovering at the same rate across different regions? 2) What is the successional trajectory in functional traits over time? 3) Does variation in climate, soils and age influence the recovery rates of functional traits?

Material and methods

Study area and landscape context

Our study was developed in 43 permanent plots covering 10.5 ha of forest in the Bragantina, Marabá, Parauapebas and Santarém regions of the state of Pará, Brazil (Table S1). Twenty-nine of these plots were established in secondary forests (SF), and fourteen in old-growth primary forests (PF). The landscape context in the four regions is very different. Bragantina region (Appendix S1: Fig. S1) is the oldest agricultural frontier in the Amazon, whereas Marabá (Appendix S1: Fig. S2), Parauapebas (Appendix S1: Fig. S3) and Santarém (Appendix S1: Fig. S4) are more recent agricultural frontiers with ongoing deforestation since 1970s. The majority of the SF plots evaluated across regions were abandoned by smallholders after successive cycles of slash-and-burn agriculture (for manioc, maize, and rice cultivation) or pasture.

Tree censuses

In the Bragantina region, we established 12 SF plots in 1999, with repeated surveys taking place in 2000, 2001, 2002, 2003, 2004, 2006, 2011, 2014 and 2017; three SF and three PF plots with a single sampling in 2017. In Marabá and Parauapebas, we established five and three SF plots in 2014 respectively, with single resampling in 2017. Additionally, we established three PF plots for each region in 2017, whereas in Santarém region we sampled five plots for SF and PF plots (for each) in 2010, resampling in 2014 and 2016 (Appendix S1: Table S1). Primary forest plots were used as a regional baseline for recovery. In these plots we measured trees ≥ 10 cm diameter at breast height (DBH) and we estimated stem height by visual assessment. Plant identification was conducted in the field and when necessary we collect samples for comparison with collection from the Herbarium IAN-Embrapa Amazônia Oriental. The data from all plots are available on the digital platform ForestPlots.net (Lopez-Gonzalez et al. 2011).

Age of secondary forests

We were unable to determine the age of the secondary forest plots by satellite imagery due to the resolution limitations (e.g., Landsat 1 and MapBiomas) that do not allow the identification of nuances along the 250-m long plots. Most of the SF areas in these regions are created by family farmers from the cleaning and rotational abandonment of small areas < 0.5 hectares (e.g., *'roça de toco'*;) using slash-and-burn techniques (Perz and Walker 2002). In this case, a single SF plot evaluated in this study, with a length of 250 m, may have various abandonment ages. Thereby, we used estimates based in interviews with landowners conducted at the time of establishment of the SF plot (Appendix S1: Table S1).

Functional attributes

We compiled traits data for 24,924 individuals among the plots evaluated. The traits database compiled by the Sustainable Amazon Network-RAS (Gardner et al. 2013) were the main trait input data for seed size, specific leaf area (SLA) and dispersal type, and when necessary was complemented with Botanical Information and Ecology Network database (Maitner et al. 2018). Tree wood density was obtained from the Global Wood Density Database to South America tropical regions estimates (Zanne et al. 2009). For all traits, we prioritize to use data at the species level, and when necessary we use the values at the genus, family, plot and region levels, respectively. The selected traits are related to important ecological functions such as dispersion syndromes, leaf and wood economics spectrum (Appendix S1: Table S2).

Climatic and soil variables

Climate variation between plots was represented by annual precipitation extracted from the WordClim 2 database (Fick and Hijmans 2017). Soil properties were determined in each plot by five random and composite samples along the transect at depths of 0-10, 10-20 and 20-30 cm. Each composite sample consists of a mix of three random samples for each depth. The chemical parameters evaluated were: phosphorus (P), potassium (K) contents (Mehlich-I method); total nitrogen (N) (Kjeldahl); soil carbon (C; Walkey-Black) and textural contents (sand, clay and silt; Bouyoucos). The soil analyses were carried out in the Laboratório de Análises de Solos of Embrapa Amazônia Oriental following the Embrapa Soil Analysis Manual (Teixeira et al. 2017).

Statistical analysis

We calculated for each trait between censuses the community-level weighted mean (CWM) based in the abundance performed in the 'FD' package (Laliberté and Legendre 2010). We calculated the CWM recovery in relation to PF levels; and the annual net changes for each functional trait. Soil fertility was determined by the N, P, K and C contents, and summarized in the first axis of the Principal Coordinate Analysis (PCoA) based in the Bray Curtis distance using the 'vegan' package (Oksanen et al. 2018). To standardize the scale of the variables, we use the Box-Cox transformation in the matrices using the 'car' package (Fox and Weisberg 2019).

We classify SF plots evaluated at two age classes, i.e., younger (≤ 24 years of abandonment) and older plots (>24 years). To evaluate the differences in CWM recovery and net changes between age classes, we used Bayesian models comparisons estimated from Markov Chain Monte Carlo simulations performed in the 'BEST' package (Read et al. 2013).

To assess the influence of soil fertility, texture (clay content), annual precipitation and stand age fixed factors) on CWM recovery and net changes of the traits SLA, seed size, endozoochoric dispersion and wood density, we used Linear Mixed Effects Models (Zuur et al. 2009) performed in the ‘lme4’ package (Bates et al. 2013). The random effect was represented by plot regions (i.e., Bragança, Marabá, Parauapebas and Santarém). The variation explained by the global model was defined by the coefficient of marginal determination (R2m) performed in the ‘MuMin’ package (Nakagawa and Schielzeth 2013). All statistical analysis were performed in software R 3.6.1 (R Core 2019).

Results

The recovery of evaluated traits was variable between regions and age classes. Bragantina region showed lower recovery for SLA and seed size and greater recovery for wood density to primary forest levels than the other regions. The recovery of endozoochoric dispersion was similar between all regions (Fig. 1). Among the age classes, average SLA and seed size recovery in younger plots was 8.6% and 7.5% higher than in older plots, while in older plots the recovery of endozoochoric dispersion and wood density was 18% and 23.7% higher than in the younger plots, respectively (Fig. 2, Table 1).

Changes in functional traits occurred between censuses, except for SLA; and between age classes for wood density and endozoochoric dispersion (Fig. 2; Table 1). For example, older plots showed greater changes between censuses for wood density (Pr_{diff}=77%) than younger plots, while changes in endozoochoric dispersion (Pr_{diff}=80%) were significant only in the older plots. Seed size changes were positive in both age classes, but were not different from each other (Fig. 2, Table 1).

The recovery of seed size and wood density in relation to adjacent primary forests was positively related to age of abandonment, while the recovery of SLA was related to less annual precipitation and higher fertility and clay content (Table 2). Changes in wood density between censuses were negatively associated with fertility and clay content (Table 3). In contrast, changes in endozoochoric dispersion were positively associated with fertility, while changes in seed size were negatively associated with annual precipitation and clay content and positively with age of abandonment (Table 3). Global models explained 61, 62 and 30% of the SLA, wood density and seed size recovery (Table 2); and 62, 33 and 22% of the wood density, endozoocoric dispersion and seed size changes, respectively (Table 3).

Discussion

Our results show that the changes between censuses and the recovery of functional traits at the level of primary forests are subject to variations in the age of abandonment, annual precipitation, fertility and clay content among the fragments in the different regions evaluated, highlighting the importance of habitat characteristics during the successional trajectory of the functional traits. Besides, the age of abandonment was a good predictor of recovery and changes in wood density and seed size, which shows the importance of these traits as indicators of successive changes in secondary forests.

Recovery and changes in functional traits across regions and age classes

Differences in the recovery of functional traits between regions may be related to the environmental variations between the evaluated plots. This is because environmental characteristics such as land-use, climate and edaphic conditions are generally convergent in regional scale (Nepstad et al. 2008, Reis et al. 2018), leading similar successional trajectories. For example, the higher recovery of wood density in the Bragantina region may be related to the advanced stage of succession of the evaluated forests (Appendix S1: Table S1). Floristic composition in secondary forests is mutable over time, with fast-growing, acquisitive species dominating the early stages and later replaced by conservative and slow-growing species in the intermediate and advanced stages of succession (Chazdon et al. 2010, Siminski et al. 2011, Chazdon 2017b). Conservative species generally have higher wood density compared to acquisitive species (Poorter and Bongers 2006, Reid et al. 2015, Macera et al. 2017), which may explain the differences observed between regions and age classes.

On the other hand, the low recovery of SLA and seed size in the Bragantina region shows that the dynamics are variable between functional traits and may indicate a delay in the recovery of secondary forests in this region related to the persistence of long-lived pioneer species. Long-lived pioneer species (> 50 yr) are taller and their established adult individuals may occupy the canopy and persist for long periods, although they still share morphological characteristics with short-lived pioneer species (<50 yr) from the early stages of succession (Tabarelli et al. 2008, Santos et al. 2012, Chua et al. 2013). The persistence of these species in secondary forests has been related to the negative effects of habitat fragmentation (e.g. edge effects, small fragments, lower connectivity) that reduce species turnover over time and lead to slow recovery in these areas (Chazdon 2017b).

The similar recovery of endozoochoric dispersion between regions, even with differences in abandonment ages among the evaluated plots, is surprising. This is because the variation in the floristic composition between the succession stages ensures greater similarity of dispersion between older secondary forests and primary forests (Hammond and Brown 1995, Hawes et al. 2020). A possible explanation for dispersion convergence and lower recovery of seed size and SLA may be related to the shifted baseline in the Bragantina region. Disturbance alters the quantity and quality of seed dispersal effectiveness by animals (de Melo et al. 2006, McConkey and O’Farrill 2016), and the very few remnants of primary forests in this region are certainly not free from disturbances. In the broad context, Bragantina region is the oldest colonization region in the Amazon and is extremely devastated (Almeida et al. 2010). Degraded primary forests in fragmented landscapes tend to present generalized simplification of the floristic composition due to the edge effects and the continuous persistence of pioneer species (Tabarelli et al. 1999), which makes these forests have functional redundancy with early (<25 years old) and intermediate (25-45 years) secondary forests (Santos et al. 2008).

The greater SLA and seed size recovery in younger plots may be related to environmental conditions such as increased light availability, seed bank and resprouts, which favors the recovery of tree diversity (Wijdeven and Kuzee 2000, Chazdon 2017b). In addition, the younger plots evaluated in this study are in the Marabá, Parauapebas and Santarém regions, where the remaining forest cover is high (Berenguer et al. 2014, Souza-Filho et al. 2016, Lennox et al. 2018, Santos et al. 2019). The presence of primary forests in the landscape increases the chances of colonization and establishment of new species due to the supply of propagules and dispersers (Chazdon 2017b), which justifies the greater recovery of these traits in younger plots in this study.

Our results also indicate that older plots show greater changes in wood density and endozoochoric dispersion than younger plots. These changes between age classes evidence the dynamics of floristic composition over time and different functional strategies between succession stages. For example, species in the advanced stages of succession usually are taller and with larger fruits and therefore require greater tissue resistance and biotic dispersers while the opposite is observed in the early stages (Lohbeck et al. 2013, 2015, Jimenez-Rodríguez et al. 2018). Finally, the canopy formed by these species does not favor wind dispersion at this stage (Hammond and Brown 1995), which justifies our results.

Drivers of recovery and changes in functional traits

The influence of the age of abandonment on the recovery of seed size and wood density at the level of primary forest coincides with changes in plant strategies during recovery, demonstrating the importance of these functional traits as indicators of succession stages when compared to the others. On the other hand, the biggest changes in seed size associated with drier and less clayey plots may be related to the selection of tolerant species to water stress during drought periods in these habitats. This is because the size of the seed is positively related to the available energy reserves and the root mass in the early stages of development (Larson et al. 2016). Thus, germination and the establishment of species with large seeds are more effective during forest recovery, especially in unfavourable habitats (Muller-Landau 2010, Macera et al. 2017).

Likewise, changes in wood density between censuses related with lower fertility evidence the species strategies in the face of the trade-off between growth and survival in limited resource soils. In poor soils, mortality is lower due to the dominance of conservative species in the use of limited resources (Wright et al. 2004, De Toledo et al. 2011). These species persist under conditions of nutrient hypo-sufficiency, even in the early stages of succession, and have greater resistance in leaf and wood tissues, which gives them better performance in the face of disturbances such as trunk breakage and severe droughts (Poorter et al. 2010, Larjavaara and Muller-Landau 2010). Thus, the persistence and lower mortality of these species in poor soils may justify the largest changes in wood density in this study.

The variable relationships between drivers and recovery at the level of primary forests and the temporal changes in functional traits help us to understand the succession process in more detail, as well as the gaps in the literature. For example, SLA is a functional trait that responds directly to plant growth and a good predictor of response to variations in soil resource availability (Ordoñez et al. 2009, Jager et al. 2015). Thus, the variations in this characteristic between the plots evaluated were easier to capture due to its direct relationship with growth and availability of resources such as water, fertility and clay content in the soil (Table 2 and 3). In contrast, the relationship of recovery of seed size, endozoochoric dispersion and wood density is more difficult to capture by the predictors evaluated in this study since they are related to several axes of explanation, such as biotic relationships (pollinators and dispersers), fragmentation of the landscape (edge effects and connectivity), etc. This shows that the succession process is extremely complex and constantly changing and, therefore, for an efficient prediction of functional, compositional and structural models, it is necessary to incorporate different axes of explanation under different aspects of the niche.

Conclusion

Successional pathways of tropical secondary forests are complex, but their understanding is extremely necessary in the present times of global climate and land-use changes. Our study provides evidence that functional traits, especially wood density and seed size, respond to variations in climate and soils during secondary forest recovery. Our results help to understand the resilience of forests as a whole and may be useful in restoration actions related to the conservation of these areas.

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Figures

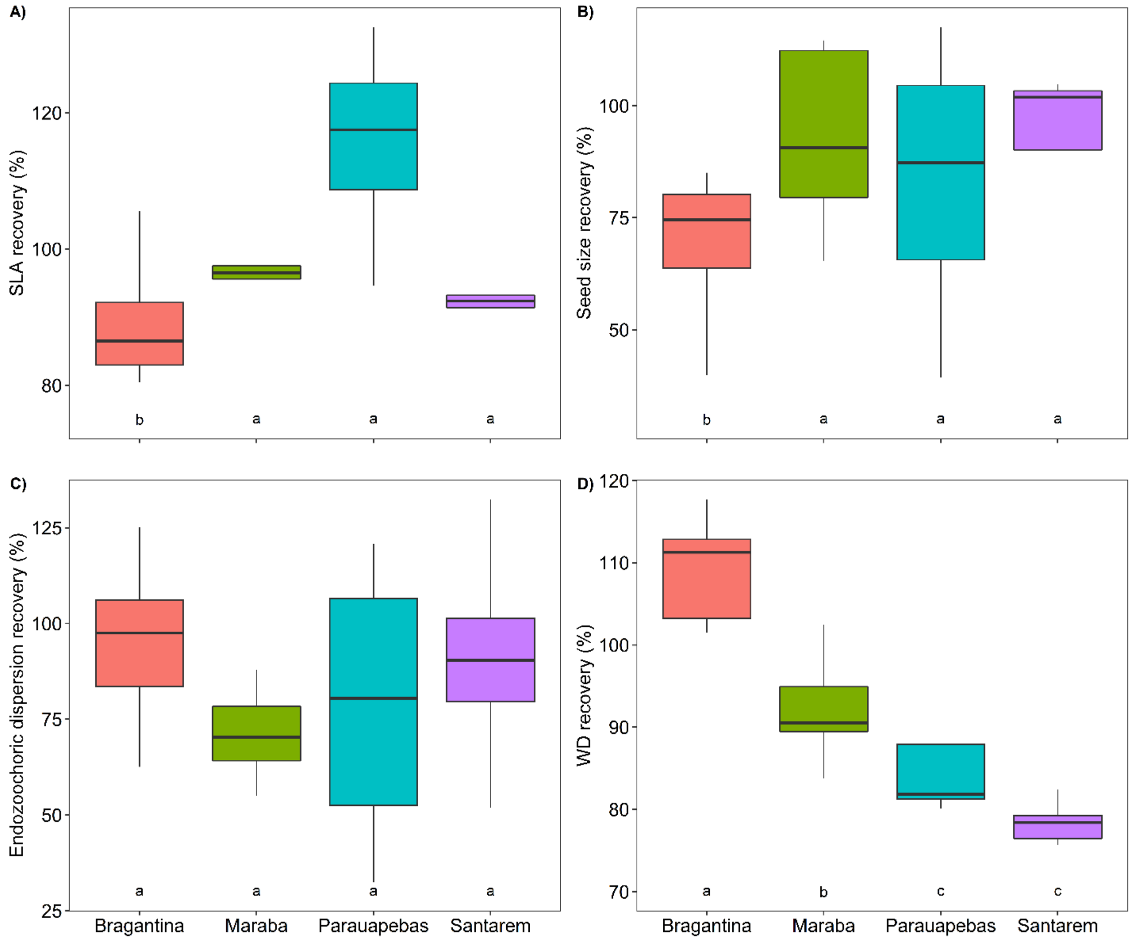

Figure 1: Recovery of CWM of functional traits specific leaf area – SLA (A), seed size (B), % endozoochoric dispersion (C) and wood density - WD (D) of secondary forest in the regions of Bragantina, Marabá, Parauapebas and Santarém. Comparisons were made using pairwise permutation t-tests and represented by letters.

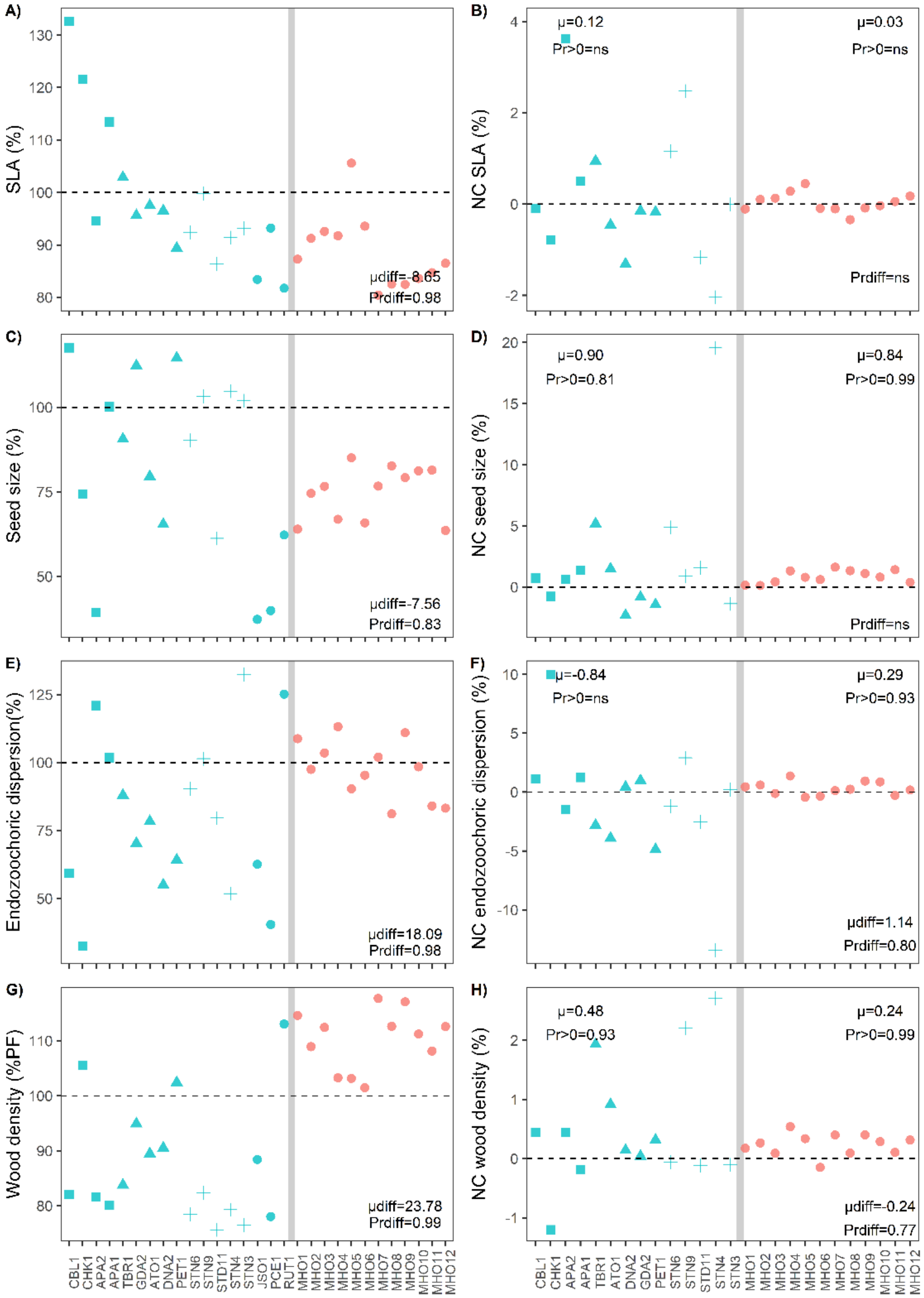

Figure 2. Recovery and changes in CWM of functional traits specific leaf area – SLA (A, B), seed size (C, D), % endozoochoric dispersion (E, F) and wood density - WD (G, H) between secondary forest in the regions of Bragantina (●), Marabá (▲), Parauapebas (■) and Santarém (+). The plots were separated by a grey vertical line into two age classes

(younger plots = blue; older plots = red) and ranked on the X-axis from smallest to largest annual precipitation. Posterior probabilities (*Pr*>0) greater than 0.75 were assumed to show strong evidence of a non-zero effect.

Table 1. Bayesian posterior distribution results of models testing for important (significant) changes in CWM trait values across time and recovery to primary forest levels between two age classes (Younger ≤ 24 years of abandonment; Older plots >24 years). Posterior probabilities/importance of changes (%; *Pr*) greater than 0.75 were assumed to show strong evidence of a non-zero effect. Important changes are highlighted in bold. Acronyms: HPDI = Highest posterior density interval; SLA = specific leaf area.

	Traits	**Groups**	**μ**	**$\text{HPDI}_{\text{lower}}$**	**$\text{HPDI}_{\text{upper}}$**	**Pr>0**	**μ_{diff}**	**Pr_{diff}**
Net change	SLA	Younger	0.12	-0.77	1.00	0.59	-	-
		Older	0.03	-0.10	0.17	0.69	-0.08	0.57
	Seed size	Younger	**0.90**	**-1.10**	**3.55**	**0.81**	-	-
		Older	**0.84**	**0.48**	**1.21**	**0.99**	-0.06	0.52
	Endozoochoric dispersion	Younger	-0.84	-3.64	2.10	0.25		
		Older	**0.29**	**-0.10**	**0.67**	**0.93**	**1.14**	**0.80**
	Wood density	Younger	**0.48**	**-0.15**	**1.12**	**0.93**		
		Older	**0.24**	**0.11**	**0.36**	**0.99**	**-0.24**	**0.77**
Recovery to PF levels	SLA	Younger	96.67	90.09	103.54	-		
		Older	88.02	83.59	92.48	-	**-8.65**	**0.98**
	Seed size	Younger	82.47	69.59	80.25	-		
		Older	74.91	67.68	97.19	-	**-7.56**	**0.83**
	Endozoochoric dispersion	Younger	97.38	89.81	104.77	-		
		Older	79.29	63.79	95.73	-	**18.09**	**0.98**
	Wood density	Younger	110.36	106.69	114.04	-		
		Older	86.59	80.88	92.59	-	**23.78**	**0.99**

Table 2. Linear Mixed Effects Models (LMM) assessing the influence of age of abandonment, soil fertility (PCoA Axis 1), annual precipitation and texture (fixed effect) on recovery of the traits at level of primary forests for specific leaf area (SLA), seed size, endozoochoric dispersion and wood density in secondary forests, Eastern Amazon. The random effect was represented by transect regions (Bragança, Marabá, Parauapebas and Santarém).

Response variables	**Fixed effects**	**Est.**	**Std. Er.**	**t**	***p***	**R2m**
SLA	*(Intercept)*	831.8	154.9	5.36	<0.001	-
	Age of abandonment	3.4	2.8	1.19	ns	-
	Soil fertility	140.7	41.5	3.39	0.002	-
	Annual precipitation	-105.4	20.6	-5.10	<0.001	-
	Clay content	11.27	3.71	3.03	0.005	-
	Global model	-	-	-	-	0.61
Seed size	*(Intercept)*	-115.8	643.8	-0.18	ns	-
	Age of abandonment	25.6	6.4	4.00	<0.001	-
	Soil fertility	211	156.5	1.34	ns	-
	Annual precipitation	16.1	84.9	0.19	ns	-
	Clay content	0.4	10.9	0.03	ns	-
	Global model	-	-	-	-	0.30
Endozoochoric dispersion	*(Intercept)*	-657.8	413.2	-1.59	ns	-
	Age of abandonment	12.7	7.6	1.67	ns	-
	Soil fertility	-158	110.7	-1.42	ns	-
	Annual precipitation	88.5	55.1	1.60	ns	-
	Clay content	4.9	9.9	0.50	ns	-
	Global model	-	-	-	-	0.39
Wood density	*(Intercept)*	-69.1	187.8	-0.36	ns	-
	Age of abandonment	10.1	3.4	2.92	0.007	-
	Soil fertility	102.6	50.3	2.03	ns	-

	Annual precipitation	17.5	25	0.70	ns	-
	Clay content	-0.4	4.5	-0.09	ns	-
	Global model	-	-	-	-	0.62

Table 3. Linear Mixed Effects Models (LMM) assessing the influence of age of abandonment, soil fertility (PCoA Axis 1), annual precipitation and texture (fixed effect) on net changes of the traits specific leaf area (SLA), seed size, endozoochoric dispersion and wood density in secondary forests, Eastern Amazon. The random effect was represented by transect regions (Bragança, Marabá, Parauapebas and Santarém). ns=non-significant.

Response variables	**Fixed effects**	**Est.**	**Std. Er.**	**t**	***p***	**R2m**
SLA	*(Intercept)*	-2.6	14.1	-0.18	ns	-
	Age of abandonment	-0.03	0.3	-0.09	ns	-
	Soil fertility	1.0	2.9	0.35	ns	-
	Annual precipitation	0.1	1.9	0.08	ns	-
	Clay content	0.3	0.2	1.19	ns	-
	Global model	-	-	-	-	0.10
Seed size	*(Intercept)*	59.6	22.9	2.59	0.020	-
	Age of abandonment	1.2	0.5	2.29	0.032	-
	Soil fertility	-5.7	5.9	-0.97	ns	-
	Annual precipitation	-7.6	3.0	-2.48	0.024	-
	Clay content	-0.9	0.4	-2.21	0.040	-
	Global model	-	-	-	-	0.22
	(Intercept)	-13.2	24.9	-0.53	ns	-

Endozoochoric dispersion	Age of abandonment	0.07	0.6	0.11	ns	-
	Soil fertility	13.2	5.1	2.55	0.018	-
	Annual precipitation	0.7	3.3	0.22	ns	-
	Clay content	1.4	0.4	3.11	ns	-
	Global model	-	-	-	-	0.33
Wood density	*(Intercept)*	14.5	9.3	1.55	ns	-
	Age of abandonment	0.2	0.2	1.10	ns	-
	Soil fertility	-5.3	1.9	-2.79	0.010	-
	Annual precipitation	-1.6	1.2	-1.31	ns	-
	Clay content	-0.5	0.1	-2.99	0.006	-
	Global model	-	-	-	-	0.62

Supporting Information

Assessing the functional recovery of Amazonian secondary forests

Ecology

Appendix S1

Figure and tables

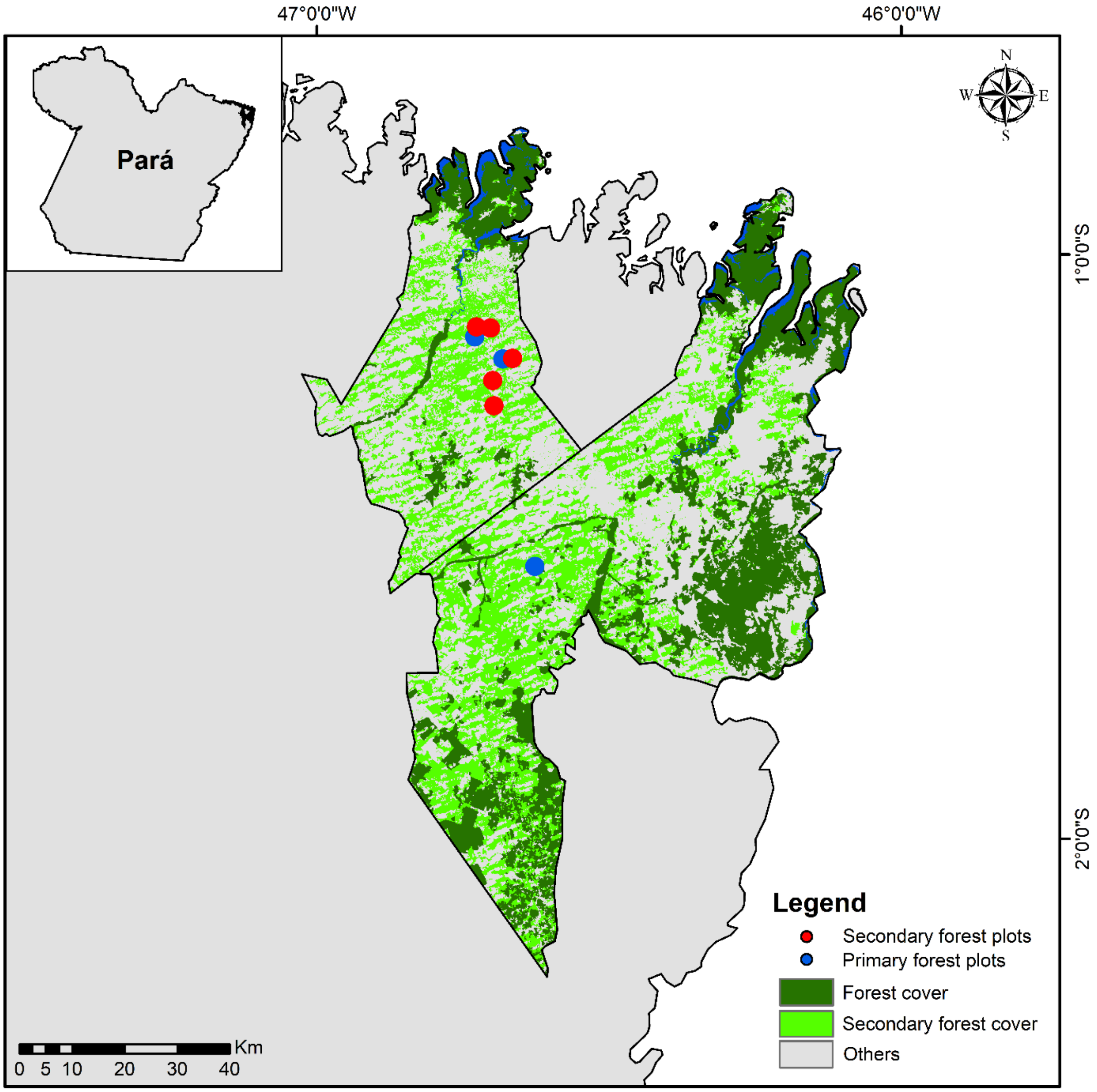

Figure S1: Map of forest cover of the Bragantina region in the eastern Amazon.

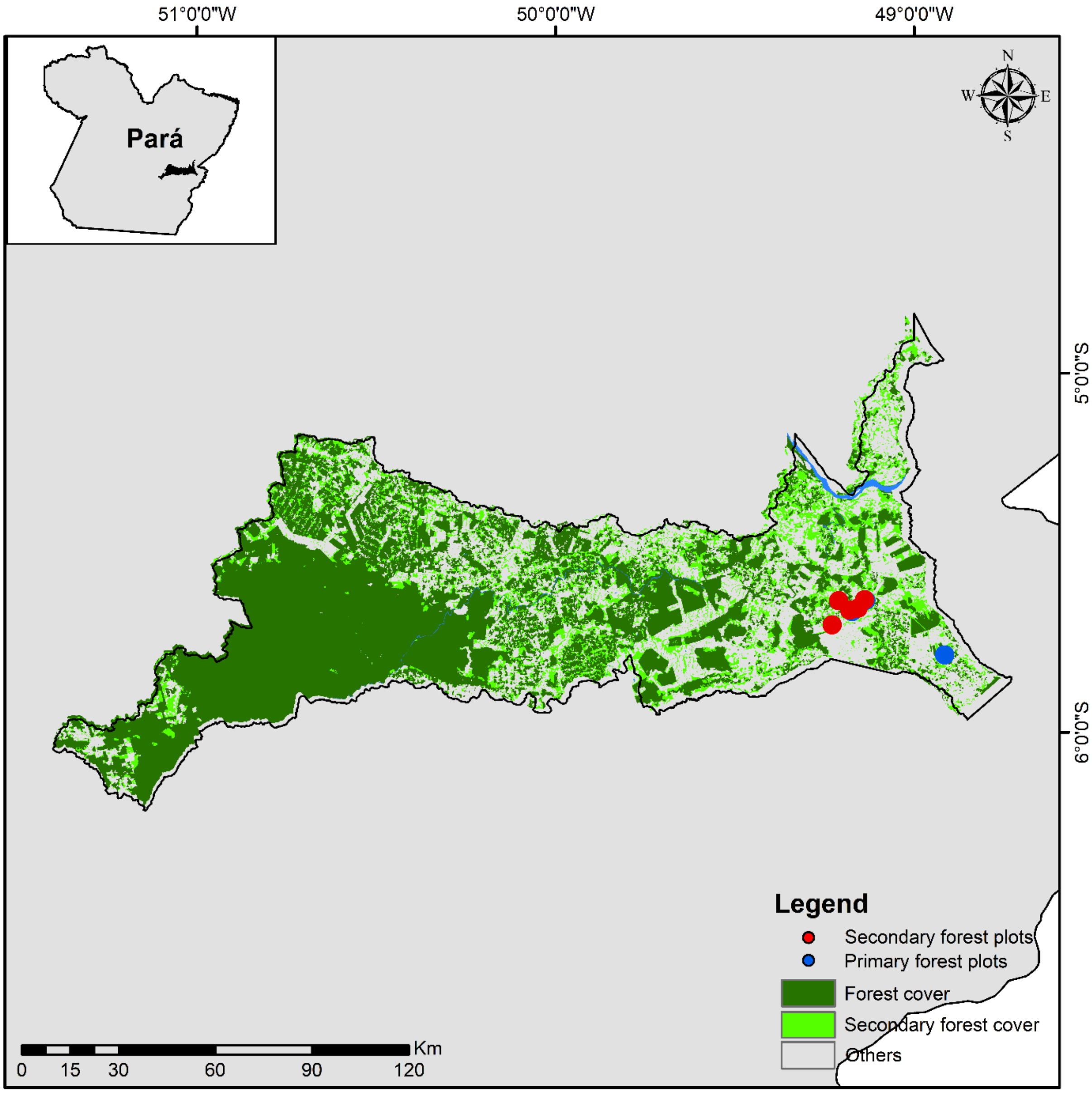

Figure S2: Map of forest cover of the Marabá region in the eastern Amazon.

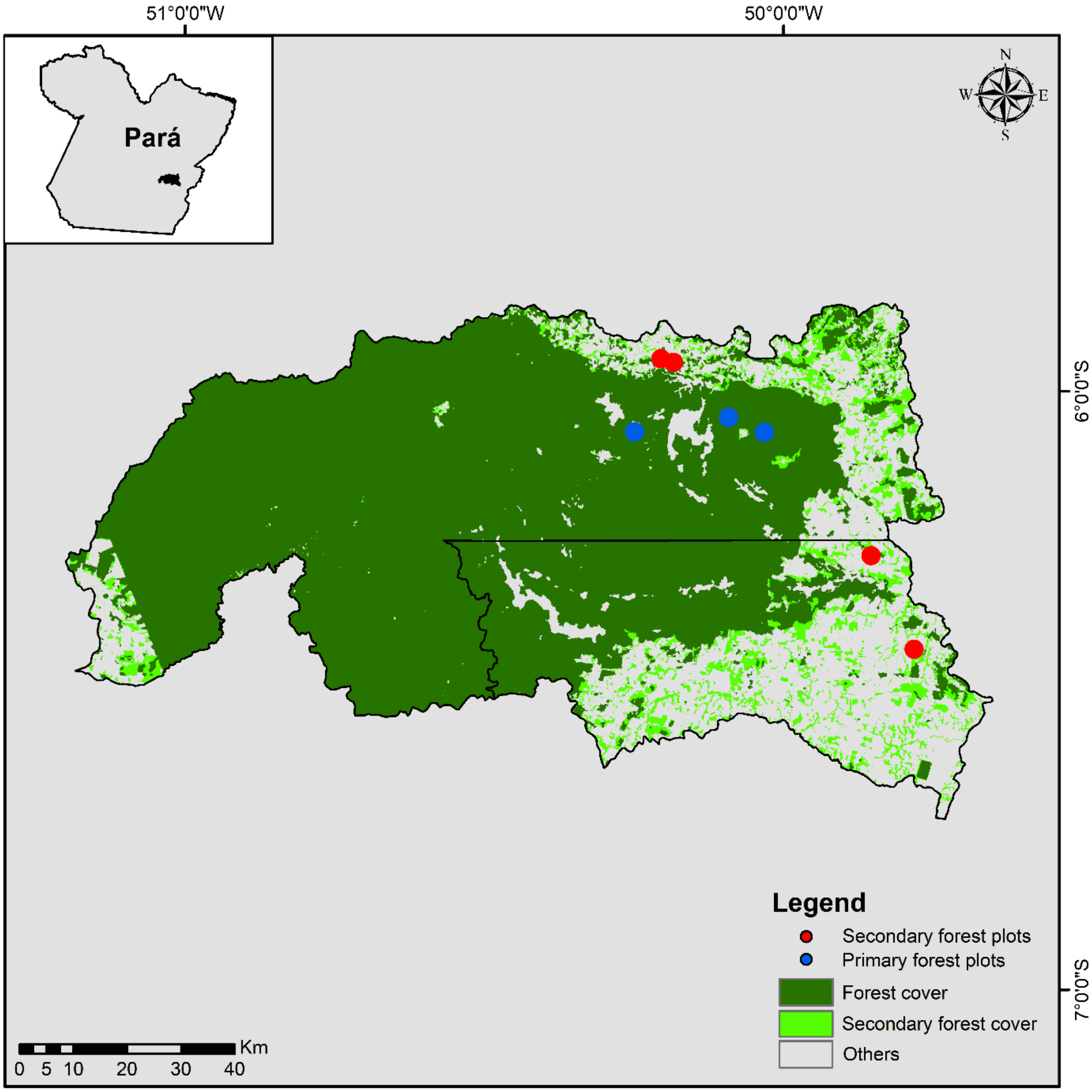

Figure S3: Map of forest cover of the Parauapebas region in the eastern Amazon.

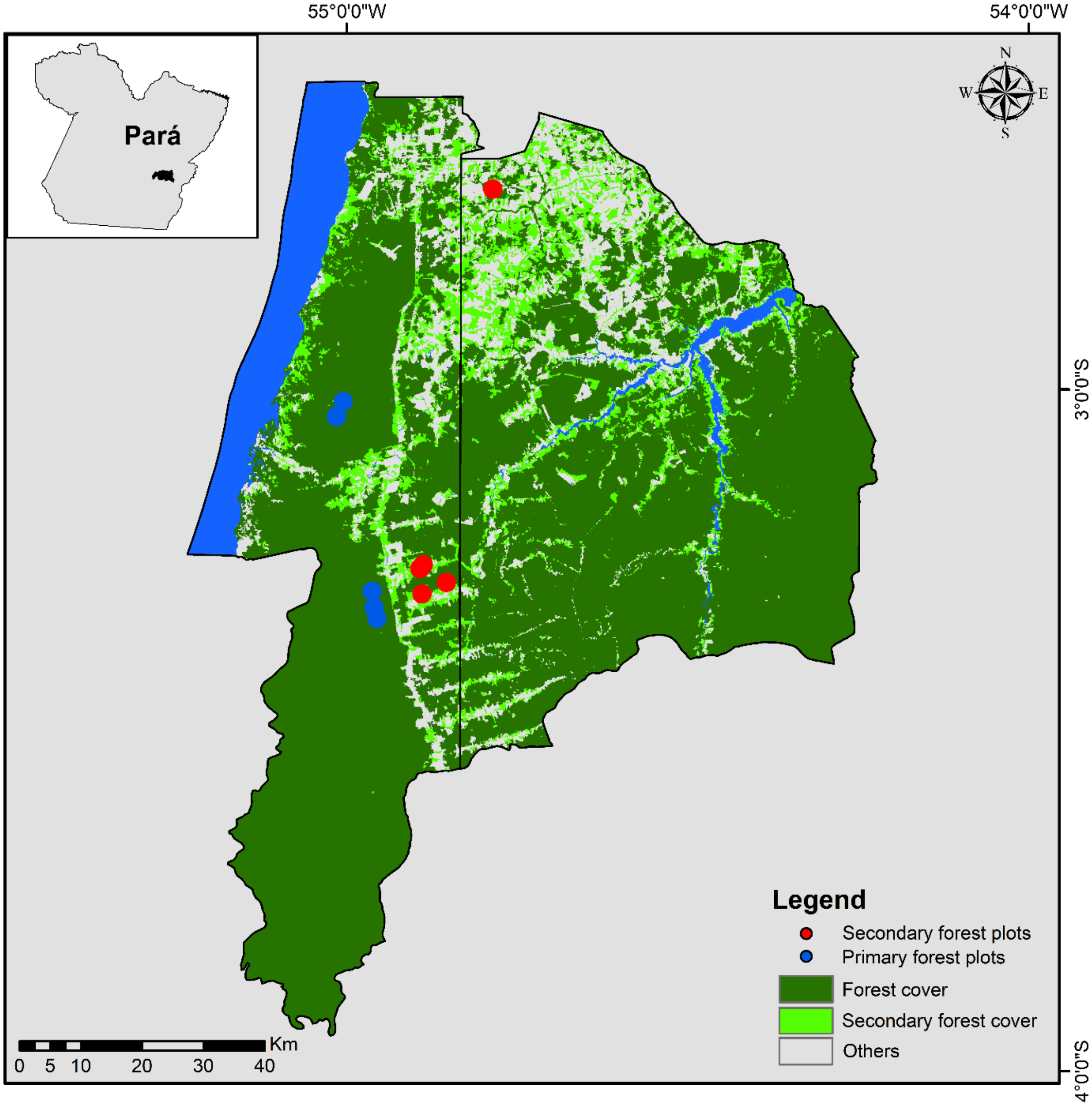

Figure S4: Map of forest cover of the Santarém region in the eastern Amazon.

Table S1: General information of the study plots evaluated in the eastern Amazon. Abbreviations are as follows: SF = secondary forest; PF = primary forest; NC = number of censuses.

Plot code	**Type**	**NC**	**Age (yrs)**	**Region**	**Latitude**	**Longitude**
ALE-01	PF	1	-	Bragança	-1.141	-46.730
FRE-01	PF	1	-	Bragança	-1.534	-46.627
VAV-01	PF	1	-	Bragança	-1.179	-46.682
JSO-01	SF	1	10	Bragança	-1.126	-46.703
PCE-01	SF	1	15	Bragança	-1.216	-46.699
RUT-01	SF	1	22	Bragança	-1.124	-46.727
MHO-01	SF	10	58	Bragança	-1.259	-46.697
MHO-01	SF	10	58	Bragança	-1.178	-46.665
MHO-01	SF	10	58	Bragança	-1.178	-46.665
MHO-01	SF	10	58	Bragança	-1.178	-46.665
MHO-01	SF	10	58	Bragança	-1.178	-46.665
MHO-01	SF	10	58	Bragança	-1.178	-46.665
MHO-02	SF	10	58	Bragança	-1.178	-46.665
MHO-02	SF	10	58	Bragança	-1.178	-46.665
MHO-02	SF	10	58	Bragança	-1.178	-46.665
MHO-02	SF	10	58	Bragança	-1.178	-46.665
MHO-02	SF	10	58	Bragança	-1.178	-46.665
MHO-02	SF	10	58	Bragança	-1.178	-46.665
DNA-01	PF	1	-	Marabá	-5.664	-49.174
GDA-01	PF	1	-	Marabá	-5.633	-49.135
JBI-01	PF	1	-	Marabá	-5.785	-48.915
DNA-02	SF	2	10	Marabá	-5.660	-49.180
ATO-01	SF	2	16	Marabá	-5.701	-49.229
GDA-02	SF	2	22	Marabá	-5.631	-49.138
PET-01	SF	2	22	Marabá	-5.634	-49.211
TBR-01	SF	2	23	Marabá	-5.655	-49.157
CAJ-01	PF	1	-	Parauapebas	-6.069	-50.032

CAJ-02	PF	1	-	Parauapebas	-6.044	-50.092
CAJ-03	PF	1	-	Parauapebas	-6.068	-50.249
CHK-01	SF	2	11	Parauapebas	-6.275	-49.854
APA-02	SF	2	12	Parauapebas	-5.952	-50.184
APA-01	SF	2	23	Parauapebas	-5.946	-50.205
CBL-01	SF	2	23	Parauapebas	-6.431	-49.782
STL-09	PF	2	-	Santárem	-3.040	-55.015
STL-10	PF	3	-	Santárem	-3.018	-55.005
STO-03	PF	3	-	Santárem	-3.296	-54.963
STO-06	PF	3	-	Santárem	-3.336	-54.956
STO-07	PF	3		Santárem	-3.320	-54.960
STN-03	SF	2	17	Santárem	-3.300	-54.890
STN-04	SF	3	17	Santárem	-3.283	-54.854
STN-06	SF	3	17	Santárem	-3.257	-54.888
STN-09	SF	3	17	Santárem	-3.263	-54.893
STD-11	SF	3	22	Santárem	-2.706	-54.786

Table S2: List of traits used in this study and their ecological functions.

Traits	Units	Main function	Others ecological functions	References
Specific leaf area (SLA)	$m^2.k g^{-1}$	Productivity	Relative growth rate, acclimation of light regime, leaf life span, photosynthetic capacity, water loss	(Wright et al. 2004, Poorter and Bongers 2006, Díaz et al. 2016)
Wood density	g/cm^3	Mechanical resistance	Provision of timber stocks, biomechanics safety, acts in the biogeochemical carbon cycle (i.e., regulating carbon storage)	(King et al. 2006, Chao et al. 2008, Brienen et al. 2015, Berenguer et al. 2018, Phillips et al. 2019, Poorter et al. 2019)
Seed size	cm	Dispersion limitation	Persistence, migration	(Hyatt et al. 2003, Clark et al. 2005, Thomson et al. 2011, 2018, Reid et al. 2015, Hawes et al. 2020)
Endozoochoric dispersion	-	Dispersion limitation	Competition, migration and seedling recruitment	(Holl 1999, Russo and Augspurger 2004, Clark et al. 2005, Seidler and Plotkin 2006, Giehl et al. 2007)

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Considerações finais

Florestas secundárias são ecossistemas com elevada importância socioecológica na paisagem e sua recuperação é dependente de diversos fatores idiossincráticos e variáveis ao longo do tempo. A compreensão da recuperação dessas áreas é essencial na elaboração de estratégias de manejo e restauração florestal, especialmente diante dos compromissos firmados pelo Brasil sob a perspectiva do Acordo de Paris e o Desafio de Bonn. Ambos os acordos preveem ações diretas do governo brasileiro em fomentar pesquisas e gerar políticas de restauração em todo o território nacional.

Nossos resultados fornecem evidências de que a recuperação em florestas secundárias em paisagens altamente fragmentadas e desprovidas de florestas primárias remanescentes é lenta - cerca de 150 anos -, e vulnerável diante de eventos intensos de seca. A implementação de políticas de restauração, incluindo métodos ativos, é fundamental para que o tempo de recuperação seja reduzido, principalmente diante da eminência de aumento da intensidade e frequência de eventos intensos de secas na região amazônica nas próximas décadas. Adicionalmente, demonstramos que as variações no clima, solos e idade de abandono influenciam as características funcionais de plantas entre diferentes regiões da Amazônia Oriental, destacando o papel do hábitat na recuperação e a importância desse componente como indicador de mudanças sucessionais em florestas secundárias.

Essa tese apresenta alguns aspectos inovadores, tais como a avaliação longitudinal ao longo de 18 anos, uma vez que a maioria dos estudos substituem o tempo pelo espaço nas estimativas de recuperação; acompanhamento e comparação da dinâmica de florestas secundárias antigas e jovens; avaliação da recuperação do carbono, diversidade arbórea e funcional entre regiões com diferentes contextos de paisagem na Amazônia Oriental; e o uso de extrapolações de cenários futuros de recuperação do carbono em uma das regiões mais degradadas da Amazônia – região Bragantina.

Consideramos que novos estudos devem ser realizados para preencher as lacunas sobre a recuperação de florestas secundárias, incluindo especialmente : 1) estudos de longa duração em diferentes regiões da Amazônia para aumentar a compreensão sobre o papel dos variados contextos da paisagem sobre a recuperação florestal; 2) estudos com maior esforço amostral em paisagens altamente desflorestadas e fragmentadas na Amazônia, que são particularmente importantes para direcionar os esforços de restauração nas regiões que mais necessitam e permitir a compreensão de cenários futuros, uma vez que a extensão dessas áreas poderá aumentar em médio e longo prazo sob as taxas de desflorestamento atuais; e 3) por fim, pesquisas ecológicas que forneçam as evidências necessárias para a elaboração e implementação de políticas públicas para proteção e manutenção de florestas secundárias – ecossistemas de extrema importância socioecológica, mas, ainda desprotegidos pela legislação.