PEDRO MANUEL VILLA

ECOLOGICAL DRIVERS OF TREE DIVERSITY AND ECOSYSTEM FUNCTIONING DURING SUCCESSION IN AMAZON: FOREST RESILIENCE AFTER INDIGENOUS SHIFTING CULTIVATION

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

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APROVADA: 05 de abril de 2018.

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Dedico este trabalho à minha família.

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SUMÁRIO

PRÓLOGO

Esta tese faz parte de um projeto de pesquisa e desenvolvimento coordenado pela Fundação para a Conservação da Biodiversidade (PROBIODIVERSA) conjuntamente com comunidades indígenas Piaroa, diversos atores da sociedade civil e instituições públicas no Norte da região Amazônica. Além disso, este projeto foi apoiado por diferentes fontes de financiamento, principalmente pelo Fundo mundial ambiental (GEF) e Programa das Nações Unidas para o Desenvolvimento (PNUD).

O povo Piaroa é um dos grupos étnicos que vivem ao longo do rio Orinoco e vários dos seus afluentes no Norte da região Amazônica, que se caracterizam por serem muito dedicados à agrossilvicultura e ao uso de produtos florestais não-madeireiros como seus principais meios de subsistência sustentáveis. No entanto, uma grande parte das populações Piaroa tem uma forte influência da cultura ocidental (homem branco) que historicamente tem influenciado a perda de seus padrões culturais, bem como a sua linguagem. Nas proximidades dos rios Cuao e Guayapo, as populações monolíngues mais tradicionais ainda são relativamente isoladas, às vezes sem contato com populações crioulas devido ao difícil acesso às cabeceiras com uma topografia muito acidentada e densa cobertura florestal.

O projeto se inicia no ano 2008 frente à necessidade de propor alternativas de desenvolvimento sustentável em comunidades indígenas que apresentam uma forte influencia da cultura ocidental que promove mudanças nos padrões culturais no uso da terra (intensificação da agricultura de corte e queima). Estas mudanças no uso da terra têm induzido a um incremento das taxas de desmatamento para o estabelecimento de sistemas agrícolas itinerantes (coivaras) que tem permitido abastecer demandas locais e regionais de produtos agrícolas. A diminuição do tempo de descanso da terra (pousio) e o incremento dos ciclos de coivaras têm levado a uma evidente degradação florestal, que reduze a resiliencia das florestas (menor capacidade de recuperação), e em consequência perda de biodiversidade e funções ecosistémicas (ex., produção e estoque de biomassa e fontes de alimentos). As alterações de processos ecossistémicos têm graves implicações no equilíbrio global entre atmosfera e biosfera, especialmente das florestas da Amazônia que tem uma importante função no balanço hidrológico e climático da Terra.

Por este motivo, a partir do ano 2009 se inicio o trabalho de campo com a finalidade de analisar os processos ecológicos que determinam a dinâmica de uso da terra nestas comunidades indígenas e ecossistemas florestais, analisando o impacto da agricultura itinerante sobre a biodiversidade e processos ecosistémicos durante a sucessão secundaria. O proposito de entender estes processos ecológicos tem sido com o objetivo de definir estratégias de conservação e manejo de florestas secundarias assim como alternativas de produção agrícola sustentável (ex, Agroflorestal). Durante este período, se contou com o valioso apoio do Lic. Norman Mota Cancio, quem é técnico florestal nativo da etnia Piaroa, e que tem sido fundamental para superar barreiras culturais e comunicacionais no desenvolvimento de atividades do projeto dentro destas comunidades.

Neste contexto, eu tive a oportunidade de continuar esta pesquisa no Laboratório de restauração florestal da UFV como bolsista da Organização dos Estados Americanos (OEA) desde o ano 2014 a través do desenvolvimento desta tese de doutorado. Assim, o objetivo principal desta pesquisa foi avaliar os efeitos dos modeladores ecológicos sobre a diversidade taxonômica e funcional (alfa e beta) e sua relação com funcionamento ecossitêmico durante a sucessão secundária de uma floresta Amazônica, através de uma abordagem de cronosecuencias depois dos sistemas agrícolas indígenas itinerantes.

Esta pesquisa foi dividida em seis capítulos, dois capítulos para descrever os efeitos do padrão de uso da terra sobre a recuperação da diversidade e perda da resiliência florestal, dois capítulos para explicar os efeitos dos modeladores ambientais e antropogênicos sobre a diversidade taxonômica e funcional (alfa e beta) e os efeitos sobre o funcionamento ecossitêmico durante a sucessão, e tres capítulos como recomendações para o manejo e conservação de florestas da Amazônia.

Neste estudo, foi demostrado como a intensidade do uso da terra induz uma perda de resiliência florestal depois varios ciclos de coivaras. Os resultados deste primeiro capítulo foram aceitos para sua publicação na Revista *Forest ecology and Management*. Pelo contrario se evidencia que com disturbios intermediários depois de um único ciclo de coivara ocorre uma rápida recuperação da diversidade, atingindo aproximadamente um 70% da riqueza de uma floresta madura depois de 20 anos. No entanto, a recuperação da composição das espécies nesse mesmo período atingiu uma média de 25% em relação à floresta madura. Os resultados deste segundo capítulo foi aceito para publicação na revista *Ecological Indicator*.

Os resultados desta pesquisa proporcionam importantes evidências sobre a relação biodiversidade-função ecossistêmica durante a sucessão secundária de uma floresta tropical. Assim, neste estudo se indica que diferentes modeladores (idade de sucessão, solos, estrutura da floresta) podem ser bons preditores do funcionamento ecossistémico. Além disso, este estudo contribui no entendimento da relação BEF ao longo da sucessão secundária, e pode ajudar a predizer como as florestas tropicais respondarão aos cenários futuros de mudanças climáticas. Por esse motivo, discutimos que para aumentar a eficiência na implementação de estratégias REDD+ em florestas da Amazônia, é necessário compreender simultaneamente a relação de padrões e processos dos ecossistemas florestais com o sistema sócio-ecológico, através da análise de preditores biofísicos e antropogênicos, a partir de um nível local para uma escala regional. Estes dois últimos capítulos foram publicados na revista Bosque.

Espero que esta contribuição permita gerar novas perguntas e ideias para o desenvolvimento de projetos de pesquisa e gestão na área de ecologia de comunidades e ecossistemas florestais, especialmente orientadas ao manejo e conservação.

ABSTRACT

VILLA, Pedro Manuel, D.Sc., Universidade Federal de Viçosa, April, 2018. **Ecological drivers of tree diversity and ecosystem functioning during succession in amazon: forest resilience after indigenous shifting cultivation.** Advisor: Sebastião Venâncio Martins.

The Amazon forest is being threatened by land use changes for the agricultural expansion, causing a taxonomic and functional simplification, and consequently generating negative impacts on the relation of biodiversity and ecosystem functioning. Thus, the main objective of this research was to evaluate the effects of ecological drivers on taxonomic and functional diversity (alpha and beta) and their relationship with ecosystem functioning during the secondary succession of an Amazon forest, in Amazonas state, Venezuela. For this reason, this research was divided into seven chapters, two chapters to describe the effects of the land use pattern on the recovery of diversity and loss of forest resilience, two chapters to explain the effects of environmental and anthropogenic drivers on taxonomic diversity and functional (alpha and beta) and effects on ecosystem functioning during the succession, and three chapters as recommendations for the management and conservation of Amazonian forests. We used plant inventory data from 63 plots (1000 m^2, 20 x 50 m) at six sites with five and 10 year regeneration secondary forests after one to six cycles of shifting cultivation to evaluate the effect of different intensities of use land, as well as soil fertility in the recovery of forest diversity and structure. We also analyzed changes in the diversity and composition of tree species after a single cycle of shifting cultivation, using data from 45 plots distributed in four secondary forests (5, 10, 15, and 20 years old after cultivation) and a mature forest (> 100 years). Within each sampling area three plots of 1000 m2 (20 x 50 m for trees with DBH> 5 cm) were established. In each area a soil sample was collected at different depths (0-10 cm). Thus, we analyzed ecological and environmental drivers and patterns of taxonomic and functional diversity (alpha and beta), and the effects of stand age and soil quality (fertility and texture) on the storage of above-ground biomass through functional diversity and functional dominance during the secondary succession. We use different statistical methods and types of models to test these ecological relationships. In this study, we show how the intensity of land use induces a loss of forest resilience. On the contrary, it is evident that with intermediate disturbances after a single cycle of agriculture a rapid recovery of diversity occurs, reaching 70% of the richness of one mature forest after 20 years. However, the recovery of the species composition in the same period reached an average of 25% in relation to the mature forest. Our study shows that beta diversity accounts for up to 70% of the variation in total species richness among sites, probably because deforested patches are embedded within a mature forest matrix. This ecological context also justifies the high taxonomic turnover during the succession. Thus, the functional diversity was lower than the taxonomic beta diversity, probably due to a lower functional turnover in comparison to the taxonomic turnover. Our results provide important evidence on the relation between biodiversity and ecosystem function (BEF) during the secondary succession of a tropical forest. Thus, the structural equation models (SEM) tested on functional dominance and functional diversity allowed to explain variations in the above-ground biomass individually. The succession time was the best predictor to explain above-ground biomass variations in all SEM models, followed by soil texture that had significant positive effects on above-ground biomass compared to soil fertility that had negative effects and not significant. Our study contributes to the understanding of the BEF relationship throughout the secondary succession, and may help predict how tropical forests will respond to future scenarios of climate change. For this reason, we have argued that in order to increase the efficiency in the implementation of REDD+ strategies in Amazonian forests, it is necessary to simultaneously understand the relationship of patterns and processes of forest ecosystems with the socio-ecological system, through the analysis of biophysical and anthropogenic predictors, from a local level to a regional scale.

RESUMO

VILLA, Pedro Manuel, D.Sc., Universidade Federal de Viçosa, abril de 2018. **Ecological drivers of tree diversity and ecosystem functioning during succession in amazon: forest resilience after indigenous shifting cultivation.** Orientador: Sebastião Venâncio Martins.

A floresta Amazônica vem sendo ameaçada pelas mudanças no uso da terra para a expansão da fronteira agrícola, provocando uma simplificação taxonômica e funcional, e em consequência gerando impactos negativos na relação da biodiversidade e funcionamento dos ecossistemas. Assim, o objetivo principal desta pesquisa foi avaliar os efeitos dos modeladores ecológicos sobre a diversidade taxonômica e funcional (alfa e beta) e sua relação com funcionamento ecossitêmico durante a sucessão secundária de uma floresta Amazônica, no estado Amazonas, Venezuela. Por este motivo, esta pesquisa foi dividida em sete capítulos, dois capítulos para descrever os efeitos do padrão de uso da terra sobre a recuperação da diversidade e perda da resiliência florestal, dois capítulos para explicar os efeitos dos modeladores ambientais e antropogênicos sobre a diversidade taxonômica e funcional (alfa e beta) e os efeitos sobre o funcionamento ecossitêmico durante a sucessão, e três capítulos como recomendações para o manejo e conservação de florestas da Amazônia. Utilizamos dados de inventário de plantas de 63 parcelas (1000 m^2, 20 x 50 m) em seis locais com florestas secundárias de cinco e 10 anos de regeneração depois de um até seis ciclos de agricultura itinerante para avaliar o efeito de diferentes intensidades de uso da terra, bem como a fertilidade do solo na recuperação da diversidade e estrutura da floresta. Também analisamos as mudanças na diversidade e composição das espécies arbóreas após um único ciclo de agricultura itinerante, utilizando dados de 45 parcelas distribuidas em quatro florestas secundárias (5, 10, 15, e 20 anos de idade após do cultivo) e uma floresta madura (> 100 anos). Dentro de cada área de amostragem se estabeleceram três parcelas de 1000 m^2 (20 x 50 m para árvores com DAP > 5 cm). Em cada área foi coletada uma amostra de solo a diferentes profundidades (0-10 cm, 10-30 cm). Assim, analisamos padrões ecológicos e modeladores ambientais da diversidade taxonômica e funcional (alfa e beta), e os efeitos do tempo de sucessão e qualidade do solo (fertilidade e textura) sobre a estocagem de biomassa acima do solo através da diversidade funcional e dominância funcional durante a sucessão secundária. Usamos diferentes métodos estatísticos e tipos de modelos para testar estas relações ecológicas. Neste estudo, demostramos como a intensidade do uso da terra induz uma perda de resiliência florestal, de forma contrária se evidencia que com disturbios intermediários depois de um único ciclo de agricultura ocorre uma rápida recuperação da diversidade, atingindo aproximadamente um 70% da riqueza de uma floresta madura depois de 20 anos. No entanto, a recuperação da composição das espécies nesse mesmo período atingiu uma média de 25% em relação à floresta madura. Nosso estudo mostra que a diversidade beta explica até 70% da variação na riqueza total de espécies entre os sítios, provavelmente devido a que as manchas desmatadas estão inseridas dentro de uma matriz de floresta madura. Este contexto ecológico também justifica o elevado *turnover* taxonômico durante a sucessão. Assim, a diversidade funcional foi menor do que a diversidade beta taxonômica, provavelmente devido a um menor *turnover* funcional em comparação com o *turnover* taxonômico. Nossos resultados proporcionam importantes evidências sobre relação biodiversidade-função ecossistêmica durante a sucessão secundária de uma floresta tropical Assim, os modelos de equação estruturais testados sobre dominância funcional e diversidade funcional, permitiram explicar variações na biomassa acima do solo de forma individual. O tempo de sucessão foi o melhor preditor para explicar variações da biomassa acima do solo em todos os modelos SEM explorados, seguidamente da textura solo que teve afeitos significativos positivos sobre a biomassa acima do solo, em comparação à fertilidade do solo que apresentou efeitos negativos e não significativos. Nosso estudo contribui no entendimento da relação BEF ao longo da sucessão secundária, e pode ajudar a predizer como as florestas tropicais respondarão aos cenários futuros de mudanças climáticas. Por esse motivo, discutimos que para aumentar a eficiência na implementação de estratégias REDD+ em florestas da Amazônia, é necessário compreender simultaneamente a relação de padrões e processos dos ecossistemas florestais com o sistema sócio-ecológico, através da análise de preditores biofísicos e antropogênicos, a partir de um nível local para uma escala regional.

INTRODUÇÃO GERAL

As florestas tropicais cobrem cerca de 10% da superfície da Terra e armazenam aproximadamente 25% do carbono terrestre acima e abaixo do solo, e são responsáveis por 34% da produtividade primária terrestre (Bonan, 2008). Além disso, as florestas tropicais contêm mais de metade da biodiversidade terrestre e têm uma influência importante na manutenção de funções ecossistêmicas (Lewis et al., 2015; Sullivan et al. 2017), como também no fornecimento de serviços ecossistêmicos na escala local, regional e global (Aerts and Honnay, 2011). No entanto, as florestas tropicais vêm sendo foretemente afetadas pela perturbação antrópica (Lewis, 2006; Lewis et al. 2015), principalmente pelas mudanças no uso da terra (Thompson et al. 2012; Laurance et al. 2014), induzindo impactos negativos sobre a biodiversidade e funcionamento dos ecossistemas (Hooper et al., 2012; Naeem et al., 2012), provocando assim alterações de processos climáticos em diferentes escalas (Lewis et al. 2015; Anderson-Teixeira et al., 2016). Apesar das mudanças no uso da terra em florestas tropicais, as florestas secundárias que regeneram após os distúrbios antropogênicos ainda representam um importante reservatório de biodiversidade (Chazdon, 2014, Gibson et al., 2011), já que essas florestas contêm mais de metade da área florestal global (FAO, 2010).

Neste contexto, a bacia amazônica contêm a floresta tropical mais extensa do mundo (Laurance et al., 2001), com cerca de 11% da biodiversidade arbórea mundial (Cardoso et al., 2017). Além disso, a Amazônia desempenha um papel fundamental na sustentação de populações indígenas por fornecer diferentes bens e serviços baseados na biodiversidade (Arroyo-Kalin, 2012). Por exemplo, a agricultura itinerante de corte e queima praticada durante séculos (Bush et al., 2015), ainda é o principal sistema agrícola que sustenta as populações humanas na Amazônia (Villa et al., 2017), produzindo alimentos não só para demandas domésticas, mas também para mercados locais ou nacionais (van Vliet et al., 2013; Jakovac et al., 2016b). O aumento do desmatamento das florestas amazônicas pela agricultura itinerante em comunidades indígenas e não indígenas ameaça seriamente as florestas maduras e sua biodiversidade (Barlow et al., 2016, Jakovac et al., 2016a), além de aumentar a pressão sobre a recuperação das florestas secundárias (Jakovac et al., 2015). Estas mudanças no uso da terra também estão induzindo uma perda de biodiversidade e funções ecossistêmicas (Olden and Rooney, 2006; Baiser et al. 2012; Solar et al. 2015).

Apesar de que recentes evidências demostram que existe uma relação positiva entre a biodiversidade e o funcionamento do ecossistema (BEF) nas florestas tropicais

(Poorter et al., 2017), ainda há pouca informação sobre como os modeladores ambientais e antropogênicos influem na estruturação das comunidades de árvores das florestas amazônicas e seu impacto na produção e estocagem de biomassa como importantes processos ecossistêmicos durante a sucessão secundária. A análise da relação BEF é muito importante para entender como a diversidade de espécies afeta a dinâmica de produção e armazenamento de biomassa acima do solo (e.x., Chisholm et al., 2013; Poorter et al., 2015) e, mais recentemente, tem sido utilizada no estudo de sucessão secundária em paisagens florestais sob modificação humana (Lohbeck et al, 2015; de Ávila et al., 2018). Assim, deve-se notar que a maioria dos estudos BEF em florestas tropicais tem sido desenvolvidos para analisar a produtividade e estocagem de biomassa acima do solo (Lasky et al., 2014), pois, fazem parte dos componentes mais importantes para o armazenamento de carbono e equilíbrio global com a atmosfera (e.x., Brienem et al., 2015).

Padrões e processos ecológicos durante a sucessão secundária em florestas tropicais se tem baseado principalmente na análise das mudanças da diversidade e composição das espécies depois dos distúrbios antropogênicos (Chazdon et al., 2014; Guariguata e Ostertag, 2001) com base na abordagem da cronosequência (Chazdon et al., 2007). Mais recentemente, novas pesquisas têm demostrado que os traços funcionais das plantas também permitem explicar BEF, analisando seus efeitos diretos ou indireitos sobre a estruturação das comunidades durante a sucessão de florestas tropicais (e.g., Lohbeck et al, 2015; van der Sande et al., 2017; de Avila et al., 2018). Esta abordagem baseada em traços funcionais (trait-based approach) é bastante prometedora nos estudos ecológicos, porque permite conectar mecanismos baseados na teoria de nicho com processos das comunidades através de gradientes ambientais, cenários de mudanças climáticas e mudanças no uso da terra. No entanto, existem limitados estudos que explicam qual é a importância relativa dos modeladores sobre as disimilidades espaciais e temporais na composição da espécie e traços (beta diversidade), assim como a relação da diversidade beta taxonômica e funcional baseada em traços funcionais ao longo da sucessão de florestas tropicais. A abordagem da diversidade beta tem sido amplamente usada como uma medida da variação na composição das espécies (traços) entre os sítios e parcelas (Tuomisto, 2010; Anderson et al., 2011).

Existem duas importantes hipóteses que permitem explicar parcialmente como os traços funcionais das espécies dentro das comunidades vegetais podem modelar diferentes processos ecossistêmicos simultaneamente, as hipóteses razão de massa (Grime, 1998) e complementaridade de nicho (Tilman et al. 1997). A hipótese de razão de massa (MRH, Mass ratio hypothesis) postula que os processos ecossistêmicos são conduzidos pelos traços funcionais das espécies mais abundantes das comunidades (Grime, 1998). Assim, existem importantes evidências que suportam esta hipótese onde traços conservativos (i.e. traços do caule) das espécies mais dominantes representam fortes modeladores da estocagem de biomassa e carbono (Finegan et al., 2015; Prado-Junior et al., 2016), enquanto traços ligados à aquisição de recursos (i.e., traços foliares) são importantes para o incremento de biomassa e sequestro de carbono (Poorter and Bongers, 2006; Finegan et al., 2015). A hipótese de complementaridade de nicho (NCH, Niche complementarity hypothesis) propõe que a amplitude de traços funcionais de uma comunidade afeta positivamente o funcionamento do ecossistema mediante a utilização complementar de recursos (Tilman et al., 1997; Tilman et al., 2014). A diversidade funcional pode ser quantificada através da amplitude de valores dos traços funcionais ponderado pela abundância relativa das espécies dentro do espaço multidimensional do nicho (Petchey and Gaston, 2006; Villéger et al., 2008). NCH explica que diferentes traços funcionais podem ter a mesma importância relativa através de efeitos simultâneos sobre uma função ecossistêmica (Laughlin et al., 2014). Essas hipóteses tem sido utilizadas de forma complementar para explicar o funcionamento ecossistêmico de floresta tropicais (e.g., Finegan et al. 2015; Prado-Junior et al. 2016) e durante a sucessão secundária (e.g., Lohbeck et al, 2015, 2016).

Uma abordagem recente propõe fazer comparações entre a diversidade taxonômica e funcional para testar até que ponto os processos estocásticos e filtragem ambiental são determinantes na estruturação das comunidades e BEF (Baraloto et al. 2012; Meiners et al. 2015). Com base no pressuposto de que os modeladores ambientais e antropogênicos geram padrões espaciais específicos nas comunidades (Diamond 1975; Pausas and Verdu 2010), estes tipos de análises comparativas avaliam as diferenças entre diversidade taxonômica e funcional dentro e entre comunidades (Chalmandrier et al. 2015). Se as espécies coexistentes nas comunidades locais são funcionalmente mais semelhantes do que o esperado, dados os níveis de diversidade taxonômica, isto sugeriria a ocorrência de uma filtragem ambiental ou limitação de dispersão à base de traços funcionais (Webb et al. 2002; Cavender-Bares et al. 2009; Meiners et al. 2015). Por outro lado, no caso que a similaridade funcional seja inferior ao esperado por acaso entre espécies coexistentes, seria uma consequência prevista da exclusão competitiva de espécies funcionalmente semelhantes (Webb et al. 2002; Schwilk and Ackerly et al. 2005; Violle et al. 2011).

O objetivo principal desta pesquisa foi avaliar padrões e modeladores ecológicos que moldam a diversidade taxonomica e funcional (alfa e beta) e seus efeitos conjuntos sobre o funcionamento ecossitêmico durante a sucessão secundária de uma floresta Amazônica. Por este motivo, esta pesquisa foi dividida em seis capítulos, dois capítulos para descrever os efeitos do padrão de uso da terra sobre a recuperação da diversidade e perda da resiliência florestal (Capitulo I-II), dois capítulos para explicar os efeitos dos modeladores ambientais e antropogênicos sobre a diversidade taxonômica e funcional (alfa e beta) e os efeitos sobre o funcionamento ecossitêmico durante a sucessão (Capitulo III-IV), e três capítulos como recomendações para o manejo e conservação de florestas da Amazônia (Capitulo V,VI,VII).

No **primeiro capítulo,** analisamos as mudanças na riqueza, composição de espécies de árvores e estrutura de florestas secundárias ao longo de um gradiente de intensificação do uso da terra e fertilidade do solo na floresta amazônica. Utilizamos dados de inventário de plantas de 63 parcelas em seis locais com florestas secundárias de cinco e 10 anos de regeneração depois de um até seis ciclos de agricultura itinerante para avaliar o efeito de diferentes intensidades de uso da terra, bem como a fertilidade do solo na recuperação da diversidade e estrutura da floresta. Nós propuzemos a hipótese de que o aumento da intensidade no uso da terra e a diminuição da fertilidade do solo promovem uma diminuição da riqueza e da estrutura florestal, bem como mudanças na composição de espécies. No **segundo capítulo**, analisamos as mudanças na diversidade e composição das espécies arbóreas após de um único ciclo de agricultura itinerante, utilizando dados de 45 parcelas distribuidas em quatro florestas secundárias (5, 10, 15, e 20 anos de idade após do cultivo) e uma floresta madura (> 100 anos). No primeiro capítulo demostramos como a intensidade do uso da terra induz uma perda de resiliência florestal, de forma contrária no segundo capítulo se evidencia que com disturbios intermediários depois de um único ciclo de agricultura ocorre uma rápida recuperação da diversidade.

No **terceiro capítulo**, avaliamos padrões ecológicos e modeladores ambientais da diversidade taxonômica e funcional de beta durante a sucessão secundária. Com este capítulo explicamos i) como as escalas espaciais e temporais determinam mudanças na partição da diversidade beta nas florestas secundárias em comparação com a floresta de crescimento antigo, ii) a relação da diversidade beta taxonômica e beta funcional, e 3) qual é importância relativa da idade da floresta e da fertilidade do solo na diversidade beta. No **quarto capítulo,** avaliamos os efeitos do tempo de sucessão e qualidade do solo (fertilidade e textura) sobre a estocagem de biomassa acima do solo através da diversidade funcional e dominância funcional. Neste capítulo explicamos os efeitos individuais e conjuntos da diversidade e dominância dos traços funcionais sobre a biomassa acima do solo, depois de considerar simultaneamente os efeitos do tempo de sucessão e qualidade do solo. Assim, foi possível avaliar os efeitos simultâneos das hipóteses de razão de massa e complementariedade do nicho como mecanismos complementares na estrutura funcional das comunidades de árvores e seu impacto sobre a relação biodiversidade-função ecossistêmica.

Os resultados indicados nos capítulos anteriores revelam padrões ecológicos determinantes para estabelcer critérios de manejo e conservação de florestas secundárias na Amazônia. Por este motivo, no **quinto capítulo**, discutimos sobre a importância da abordagem da relação biodiversidade-função ecossistêmica, com a finalidade de ii) analizar os possíveis impactos sinérgicos de preditores biofísicos e antropogênicos de desmatamento e degradação, e desta forma iii) propor a implementação integral de estratégias de redução de emissões de carbono à atmosfera (REDD+) na bacia amazônica. Discutimos a importancia de avaliar a magnitude dos efeitos multifatoriais dos preditores de desmatamento, e em consequência integrar as atividades REDD+, através da reabilitação de áreas degradadas com sistemas agroflorestais permanentes, bem como com a aplicação de diferentes métodos de restauração. No **sexto capítulo**, discutimos os impactos ambientais potenciais dos sistemas agroforestais como alternativa REDD+, i) para a reabilitação de áreas florestais degradadas pela intesificação no uso da terra, ii) a restauração passiva de florestas secundárias, e iii) implementação de pousio melhorado com a gestão de espécies agroflorestais. Assim, finalmente propomos que as futuras pesquisas em florestas tropicais devem começar a considerar uma abordagem que integre os múltiplos efeitos dos *drivers* ambientais e traços funcionais sobre BEF durante a sucessão secundaria. Finalmente destacamos a importancia da transferencia de conhecimento e mecanismos de informação na gestão agroflorestal (**sétimo capítulo**).

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CAPITULO I: Intensification of shifting cultivation reduces forest resilience in the northern Amazon

Aceito em Forest Ecology and Management

Abstract

Shifting cultivation systems are traditional land-use systems to ensure livelihood in the Northern Amazon. Here, we evaluated how intensification of shifting cultivation (SC) affects secondary forest recovery in the northern Amazon forest. To measure intensity of shifting cultivation, we used the number of previous SC cycles. We selected three study sites containing second-growth forest (SG) with different stand ages (5 and 10 years) after one, three or six SC cycles. Furthermore, we selected old-growth forest (OG) in each study site. In each selected SG and OG, three plots of 20 x 50 m were established, totalizing 63 plots in the study area. In each plot, all trees, palms and lianas with diameter at breast height ≥ 5 cm were tagged and identified to species level. We analyzed the effects of SC intensification and soil fertility on woody species richness, species composition and basal area using mixed effect models. Species richness and basal area, lower in SG than in OG, increased with regeneration time after abandonment, but reduced with intensification of SC. Community dissimilarities (Bray-Curtis distances) between OG and SG increased with the number of shifting cultivation cycles. Soil fertility differed between SG with different regeneration stages and reduced with number of SC cycles. We found that models including soil fertility and management intensity, i.e., number of previous SC cycles, consistently explained pattern observed in richness, species composition and basal area. As soil fertility is expected to reduce with SC intensity, our data indicate that intensification of SC reduces recovery of these vegetation characteristics, reducing overall forest resilience as well.

Keywords: basal area; land use intensification; land degradation; secondary forests; species composition; species richness

1. Introduction

The Amazon basin accommodates the largest tropical forest in the world (Laurance et al., 2001), holding about 11% of the world’s tree biodiversity (Cardoso et al., 2017). Moreover, the Amazon plays a fundamental role in sustaining indigenous and non-indigenous people providing different goods based on biodiversity by food gathering, hunting, and shifting cultivation (SC, Arroyo-Kalin, 2012). Also known as swidden agriculture, SC represents the logging of small forest areas (slash and burn) for short-time crop plantation (Aweto, 2013). After harvest and loss of soil fertility, areas become abandoned (D'Oliveira et al., 2011; Arroyo-Kalin, 2012), and regenerate naturally, forming second growth forests (SG, Chazdon, 2014). Practiced for centuries (Bush et al., 2015), shifting cultivation is still the main agricultural system sustaining peoples’ livelihoods in the Amazon (Villa et al., 2017), producing yields not only for domestic demands, but for local or national markets as well (van Vliet et al., 2013; Jakovac et al., 2016a). Increasing deforestation of Amazon forests due to SC by human communities seriously threatens old growth forests (OG) and their biodiversity (Barlow et al., 2016; Jakovac et al., 2016b). Furthermore, intensification of SC increases the pressure on the recovery of SG (Jakovac et al., 2015).

SC dynamics are characterized by three main processes. The initial perturbations are generated by the cutting and the burning of the forests. Then, the agricultural systems’ intensity and duration and the forest recovery by natural regeneration, considered as the fallow time until a new cycle takes place again, depend on crop management and available land (Piperno et al., 2009; Aweto, 2013; Delang and Li, 2013). The cycle’s length is variable; short cycles comprise 1-3 years of agriculture followed by fallow periods of 2-7 years, while long cycles comprise fallow periods of more than 15 years. However, these temporal dynamics of SC have changed considerably during the last decade due to increased demands for crops. As access of traditional communities to external inputs such as fertilizers, mechanization, or pesticides is extremely restricted, the intensification of SC generally occurs due to the reduction of fallow time between two cutting and burning events (Jakovac et al., 2015).

The intensification of SC has been recognized as an important driver for the loss of biodiversity in the Amazon (van Vliet et al., 2013), although SG regrowth after abandonment of SC may constitute important biodiversity reservoirs by harboring rare and endangered species, increasing furthermore connectivity among OGs (Gibson et al., 2011; Chazdon, 2014). The potential of SG as biodiversity reservoirs and for resilience in tropical forests depends on their frequency in the landscape and the relative importance of the land use history (Klanderud et al., 2010; Holl and Aide, 2011), intensity and duration of land use (Aweto, 2013; Delang and Li, 2013), as well as the time since abandonment (Pascarella et al., 2000; Mwampamba and Schwartz, 2011), that determine successional trajectories (Meiners et al., 2016).

Non-simultaneous cycles of SC induce spatial and temporal landscape heterogeneity, forming mosaics of cultivated areas with different successional stages within a forest matrix (Jakovac et al., 2017). Thus, understanding how intensification of SC affects the succession trajectories of second growth forests, i.e., the resilience of Amazonian forests, is essential to establish criteria for biodiversity restoration and conservation in these landscapes (Arroyo-Rodríguez et al., 2015, Wandelli and Fearnside, 2015). For instance, there are evidences that the biodiversity recovery in secondary forests may be high, because species richness can quickly recover to mature forest levels in up to two decades after a disturbance (e.g., Norden et al., 2009. Understanding the recovery pattern of species diversity, species composition and structural attributes during succession in SG from human-modified landscapes is an important challenge to improve forest conservation, restoration and management in the Amazon forest (Villa et al., 2017).

In this context, we analyzed the changes in woody species richness, species composition and stand structure of SG of different ages along a gradient of land use intensification and soil fertility in the northern Amazon forest. We used plant inventory data from 63 plots across three study sites containing OGs as well as SGs of different regeneration ages (5 and 10 years) after one, three or six SC cycles, in order to evaluate the effect of SC intensification on the recovery of forest diversity and structure. We hypothesize that increased land use intensity and decreased soil fertility decreases species richness and triggers changes in the species composition. Likewise, it is expected that these predictors generate a degradation gradient that causes a reduction in the recovery of structural attributes of the SG (i.e., basal area).

2. Materials and methods

2.1. *Selection of study sites*

This study was carried out in a semi-deciduous forest of the Cataniapo River basin in close proximity to the indigenous communities of Piaroa de Gavilán and Sardi (5°32´28 S, 67°24´13 E), in the municipality of Atures, Amazon State, Venezuela (Fig. 1), located approximately 60 km from Puerto Ayacucho city, capital of the State of

Amazonas. Both communities correspond to the Piaroa ethnic group that established 60 years ago in the Cataniapo basin, maintaining traditional SC systems for the production of *cassava* (*Manihot esculenta*) (Villa et al., 2012).

The climate of the study area corresponds to a rainy tropical system with a dry season of two months between December and January. The mean annual temperature and precipitation are 28°C and 2,700 mm, respectively. The predominant soil types are characterized as Oxisols (Latosols) and Ultisols (Argisols) with low cation exchange capacity and nutrient content, and with high levels of acidity (Villa et al., 2012).

We selected three sites within an area of 12 km^2 area between Piaroa de Gavilán and Sardi, where SG patches of different stand ages regenerating naturally after different number of SC cycles are inserted in an OG matrix. The information about the land use history of each study site was obtained by semi-structured interviews, with open and qualitative questions to the owners about different aspects related to forest management and SC dynamics. For that, a total of 63 people were interviewed (corresponding to 15% of people from each community).

Interviews were conducted primarily with the family member with direct responsibility for the selection and management of the land in each study site. Although in most cases it was necessary to interview other members of the family who also participated in the agricultural activities, we gave special emphasis to interviewing the oldest member responsible for the first SC cycles in the study sites.

During interviews, information was requested about site characteristics related to intensity of each shifting cultivation system (i.e., time of use, number of cycles, and type of crops) to outline the number of SC and the regeneration age of each SG. In some cases, first SC was dated back to 1960 (Venezuelan agrarian reform period); in the following, these areas have been cleared again. With fallow cycles of approximately 7-15 years, these areas reach three to six SC cycles. For our study, we selected SGs with regeneration times between 4-6 and 10-11 years, i.e., 5 and 10 years in the following, after one, three or six SC cycles and fallow periods between 10 and 12 years in each study site (Fig. 1D). Furthermore, we selected OGs in each study site. Patch size in the study areas varied between 0.5 and 2 ha, but for our surveys, we selected patches larger than one hectare with sufficient space for the establishment and distribution between the three plots in each patch.

2.3. *Vegetation sampling*

In each selected SG and OG patch, three plots of 20 x 50 m were established between January, 2009, and December, 2012 (Fig. 1C), totalizing 63 plots, i.e., nine plots for each SG type (stand age of 5 or 10 years after one, three or six SC cycles), and nine plots for OG distributed among the three study sites. The relative distance between plots varied between 15 and 30 meters within patches.

In each plot, all trees, palms and lianas with diameter at breast height (DBH) ≥ 5 cm were tagged and identified to species level. Species identification was carried out in the Julian Steyermark herbarium of Puerto Ayacucho (Ministry of the Environment, Amazonas State). The *Angiosperm Phylogeny Group* IV (APG IV 2016) was used to classify the taxa. For liana we did not consider DBH, but the diameter at 1.3 m after the last rooting point (Gerwing et al., 2006). Furthermore, non-native or ruderal herbaceous species occurring in abundances in understory layers were qualitatively registered, when dominating the understory; in the statistical analysis regarding species richness or community composition, their occurrence was not considered.

2.4. Soil parameter collection

In each plot, we collected three samples of surface soil (0-10 cm depth) evenly distributed within the plot to obtain one composite sample for chemical and physical analysis. Analyses were carried out in the Soil Analysis Laboratory of National Institute of Agricultural Research (Gilabert et al., 2015), following regular protocols (e.g., INIA, 2015). The following parameters were assessed: soil organic carbon (C), total N, available P, K, Ca, Mg, Fe, Zn, effective cation exchange capacity (ECEC), exchangeable acidity (H + Al), pH, organic matter (OM), and the soil texture (sand, clay and silt contents).

2.5. *Data analyses*

All analyses were carried out in R Environment (R Core Team 2017). For each plot, we calculated the stand total basal area (m^2 ha^{-1}). To compare species richness, basal area and soil properties between different SG and OG forest types, we tested normal distribution with the Shapiro-Wilk test and by evaluating the Q-Q plot. For non-normally distributed data, we used Kruskal-Wallis’s test followed by a posterior Dunn’s test performed with the ‘stats’ and ‘dunn.test’ packages (Dinno, 2017).

Non-metric multidimensional scaling (NMDS) was performed to illustrate differences in species composition among different SG types and OG (Clarke, 1993). For that, we calculated abundance-weighted Bray-Curtis dissimilarities. We then performed the NMDS using the metaMDS function of the ‘vegan’ package in R (Oksanen et al., 2016). We used the betadisper function in ‘vegan’ package to determine differences in species composition (9999 permutations), based on the PERMDISP2 method (Anderson 2006).

We furthermore used the abundance-weighted Bray-Curtis dissimilarity index between different SG plots and their nearest OG plot to assess species composition recovery (McNicol et al., 2015; Dent et al., 2013; McNicol et al., 2015). To assess the extent to which species composition has recovered across the succession, we examined whether the compositional similarity of SG to their nearest OG plots reached levels equal to, or greater than, the similarity between nearby pairs of OG plots (e.g., Dent et al., 2013). We employed Mantel tests (based on 9,999 permutations) to assess spatial autocorrelation of the sampling units within each area between the composition distance matrix and a matrix of spatial distances between plots. For that, we used the Mantel test function in the 'ade4' package (Dray et al., 2017).

Soil variables were summarized by a principal components analysis (PCA) on the correlation matrix, using the 'FactoMineR' package (Husson et al., 2017). For that, all variables were centered and standardized and correlation between individual variables and

PCA axes were presented. To investigate a possible relationship between the abiotic (soil and SC) and biotic (species) variables, a Canonical Correspondence Analysis (CCA) was used applying Monte Carlo randomizations (Monte Carlo test with 999 randomizations). The CCA were performed using PC-ORD software, version 6.0 (McCune and Mefford, 2006).

To explain main effects of potential predictor variables on species richness, species composition (i.e., extracting the scores on abundance-weighted NMDS axis 1, Oksanen, 2016; Dayananda et al., 2017) and basal area, we constructed linear mixed effect models. Predictor variables were SC management intensity, i.e., number of previous SC cycles for each stand age(e.g., Jakovac et al., 2015), soil fertility, defined as the first principal component from PCA considering all 15 analyzed parameters (see above), as well as further soil parameters such as sand, silt, clay, Al, pH, and CEC. We used both soil fertility as well as single soil parameters as explanatory variables for modelling, because soil fertility summarizes a significant portion of entire soil variance (see results section), although single soil parameter potentially show a direct effect on species richness, composition or stand structure. For predictors selection, we assessed collinearity between selected predictor variables using Spearman correlation analysis; when two variables were strongly correlated ($r \geq 0.6$), we selected the most compelling predictors which were included in separate models (e.g., Matos et al., 2016). Only SC and soil fertility had a strong correlation ($r = 0.89$), therefore we evaluated these parameters in separate models.

We used generalized linear mixed effects model with Poisson error distribution (GLMMs) to investigate the effect of soil parameters and management intensity on species richness and species composition, while log-transformed basal area was assessed using linear mixed effects models (LMMs) after checking for normality by the Shapiro-Wilk test and Q-Q graph (Crawley, 2012). In all models, study site was included as a random factor. All models were calculated using the packages ‘lme4’ and ‘MASS’ (Bates et al. 2014) in the platform R (R-Core-Team, 2015); for illustration, we used the package ‘ggplot2’ (Hadley, 2015).

To assess the best models (GLMMs and LMMs), we applied a multi model inference approach (Burnham and Anderson, 2002) with the ‘dredge’ function from the “MuMIn” package (Barton, 2015), which returns all possible combinations of the explanatory variables included in the global model. To determine which of these variables were the most decisive in explaining changes in richness, species composition, and basal area, we used an information theoretical approach based on the Akaike information criterion with a correction for finite sample sizes (AICc) and AIC weights (Burnham and Anderson, 2002). The model with the lowest AICc was considered as the best one, but all models that differ less than four units with the best model were considered as equally good models (Burnham, Anderson and Huyvaert, 2011).

3. Results

3.1. *Richness and stand structural attributes*

Species richness increased with regeneration time, i.e., was higher in 10 year-old stands than in 5 year old stands, but increasing number of SC cycles reduced species richness (Fig. A.1. Appendix/from Electronic Supplementary Material, ESM hereafter). Species richness decreases between 40 and 47% during early succession after six SC cycles compared to forests SGs with a single SC cycle. Thus, species richness clearly showed consistent decreasing patterns over land-use intensification in comparison to OG, being up to five times higher in OG than in 10 year-old SG after six SC cycles (Table 1). Although basal area increased with regeneration time, we furthermore observed that the basal area decreased considerably with the number of SC cycles; for instance, after the six SC there is a reduction of basal area greater than 90% in comparison to SC after one cycle only (Table 1).

3.2. *Species composition among communities*

The NMDS showed that woody species composition varied considerably among successional stages and OG (Fig. 2). The NMDS ordination of species composition distinguished seven different groups with significant differences between them (Anova-Permdisp, $F_{6,56} = 2.67$, $p < 0.01$). The differences between successional stages (5 and 10 year old SG as well as OG) are determined by the first axis, while the number of SC cycles separates floristic composition along the second axis (Fig. 2). The NMDS showed furthermore that basal area varied with the stand age and the SC intensity. Thus, basal area is higher in OG than in SG, but longer regeneration times contribute to higher basal area.

We observed that community dissimilarity between SG and nearest OG plots was greater than the dissimilarity among pairs of OG plots. OGs among themselves are similar, but dissimilarity increases between SG and OG with intensification of SC (Fig. 3). This result was also corroborated by two ways cluster dendrogram generated based on Bray-Curtis dissimilarities (Fig. A.2. from ESM). Non-native or ruderal species were recorded only in SFs after three or six cycles (Fig. A.2. and Table A.2. from ESM). No significant correlation between species composition and spatial distance was found according to a Mantel test ($r = 0.15$, $p = 0.64$).

3.3. *Descriptors of soil fertility*

The first two axes of the PCA explained 80.9% of the variation in the soil data (Fig. 4). The first axis explained 66.5% of variance and was negatively correlated with sand ($R = -0.55$, $p < 0.001$) and pH ($R = -0.82$, $p < 0.001$) (Table A.3. from ESM). Furthermore, the first axis was positively correlated with silt, cation exchange capacity, soil organic carbon, and nutrients, separating SG from OG (Fig. 4, Table A.3. from ESM). Furthermore, position of SG on axis one varied according to their intensity (number of SC cycles). The second axis explained 14.4% of the variation in soil data and was positively correlated with Al and clay and negatively with sand. In SGs after three or six cycles, the second axis separated between 5 and 10-year SGs (PERMANOVA, $F_{6,56} = 20.48$, $p <0.001$).

The first axis of the CCA biplot explained 21.4% of the species composition with differences in soil fertility, while the second axis explained 15.8% (Fig. 5). The CCA separated species characterizing SG after 6 SC cycles from that ones from SG after one or three cycles or OG, that formed a continuum along a pH and OM gradient. Factor separating both groups is soil’s sand content (Fig. 5). On the other hand, species from OGs are linked to higher contents of nutrients, CEC, and soil organic matter (Fig. 5).

3.4. *Effects of management intensity and soil fertility on diversity and basal area*

A marked gradient of soil fertility was observed along the SG gradient with different regeneration stages and numbers of SC cycles. Soils of SG had in general lower CEC, lower nutrient availability (i.e., lower soil fertility) higher sand contents and higher pH values than OG (Table 1). In the multi-model comparison applied between sites and forest type, we found that models including management intensity determined by number of previous SC cycles or soil fertility (PCA axis 1) consistently explained more variation in richness and species composition than those with multivariate effects of soil fertility descriptors (Table A.4. from ESM). According to our best model, richness was best explained by effects of soil fertility (GLMM: $z = -5.72$, $p < 0.001$) and management intensity (GLMM: $z = -3.35$, $p < 0.001$) in the study area. Richness was also significantly affected by cation exchange capacity (GLMM: $z = 4.09$, $p < 0.001$) and sand (GLMM: $z = -4.08$, $p < 0.001$) between sites (Table 2).

The linear mixed-effects models showed that species composition was explained by soil fertility, management intensity, and predictor of soil fertility through six potential models (Table 2). The linear mixed-effects models revealed significant shifts of species composition across the soil fertility (LMM, $t = 5.62$; $p < 0.001$) and management intensity gradient (LMM, $t = 7.45$, $p < 0.001$). Species composition of both sites was furthermore significantly associated with pH and CEC considering our best models (Table 2). For basal area, our best model was composed of soil fertility (LMM, $t = - 6.28$, $P < 0.001$) and the number of previous cycles (LMM, $t = - 2.01$, $P < 0.01$).

4. Discussion

4.1. Intensification of shifting cultivation reduces forest resilience

Our results showed that species richness and basal area, a proxy for above-ground biomass (i.e., Torres and Lovett, 2013), increased with regeneration time, but reduced with the number of SC cycles, while community dissimilarity to OGs increased with number of cycles. Similar relationships were detected between species richness, basal area and community similarity to OGs and soil fertility. Community composition differed strongly between OG, SGs with low and high intensities of SC, indicating that species colonizing SGs after a single SC are different from that colonizing SGs after three or more SC cycles and that from mature forests (OGs). Species colonizing after a single SC may be considered light-demanding pioneer species such as *Cecropia* sp., while species from OG might be shade-tolerant species (Chazdon, 2014). Species colonizing SGs after more than one SC are stress-tolerant, invasive, or liana species, i.e., *Imperata* sp. occurring in SGs after 6 SC cycles (data not shown), a species that is considered an indicator for land degradation (Styger et al., 2007; Holl, 2017).

Our analysis showed richness losses up to 47% during early succession after six SC cycles compared to forests with a single SC cycle. Thus, we showed that increasing number of SC cycles caused significant losses in richness and species composition in early successional stages, confirming previous results (Ding et al., 2012; Jakovac et al., 2015). Furthermore, we found that the basal area recovery reaches up to 30% of OG levels after 10 years of succession, but after the six SC cycles there was a reduction of basal area greater than 90%. These results allow us to infer that both the increase in fallow time and the reduction in the number of SC cycles are decisive for both recovery and loss of forest structure (i.e., basal area) through a gradient of intensity of land use. Therefore, both mechanisms can be considered as base lines for the planning of restoration and management of secondary forests.

The recovery of structural parameters such as basal area, species richness and community composition depends on the intrinsic resilience of the ecosystem, landscape context and the land-use history (Holl and Aide, 2011). As landscape context and ecosystems do not change within our study, differences may be related to differences in land-use history, i.e., intensity of SC. Thus, SC may explain the observed pattern of species richness, community similarity and basal area. Nevertheless, soil fertility or sand content are statistically equally good candidates to explain pattern in species richness, community composition and basal area. As we analyzed chronosequences (i.e., patches differing in stand age and number of previous SC cycles), but no true time-series, we are unable to disentangle the influence of SC intensity and eventual intrinsic differences, e.g., soil fertility or soil texture, between study sites. High correlation between SC and soil fertility indicates that SC may influence soil fertility, which may influence species richness directly or indirectly, or SC may influence directly species richness, for instance. Higher sand contents in SG after three and six SCs reduce water and nutrient availability, able to reduce plant growth. This might explain decreasing recovery of basal area in sandier soils, i.e., SGs with more than one SC cycle (Lu et al., 2002; Robinson et al., 2015) nevertheless a straightforward evidence that soil texture itself reduces species richness or diversity during recovery of SG is still lacking.

Although we conclude that probably there is a synergistic effect of both variables on the vegetation, influencing species richness, species composition and structural parameters such as basal area, it seems plausible that soil seed banks may become impoverished with intensification of SC due to seed predation, loss of viability, or loss of dispersers (Holl, 1999, Randriamalala et al., 2015, Markl et al., 2012), which by itself may lead to impoverishment of regenerating communities after more than one SC as observed in similar studies (Lawrance, 2004; Styger et al., 2007; Jakovac et al., 2015). Furthermore, reduced richness after the first SC cycle in comparison to OG may reduce seed bank diversity for further cycles. Likewise, mutualists may become limited with time (Zobel and Öpik, 2014), reducing seed germination and survival of seedlings of some species. Soil fertility is expected to reduce with SC intensification due to nutrient export with crops (e.g., Jakovac et al., 2016a). Furthermore, increasing disturbance levels with intensification of SC may increase the vulnerability of sites for liana infestation and biological invasion (e.g., Hogan et al., 2017) due to lower seed bank diversity, fertility and mutualist losses. Thus, our data are consistent with a scenario in which intensification of SC reduces the recovery of species richness, composition and basal area of SGs following productive periods, thus impacting forest resilience negatively. As a low number of SC cycles affect forest resilience less than large numbers of SC cycles, we may furthermore conclude that sustainability of this ancient land-use form is restricted to low intense systems. Contrasted by increasing needs for crops by local population to achieve an adequate income, this puts limits on the amount of crop production for this form of land-use, and requires immediate action to guarantee protection of the outstanding biodiversity of the forests from the northern Amazon basin as well as livelihood for people of the region.

4.2. Implications for conservation and forest management

Different intensities of SC increase the heterogeneity at landscape level, increasing the diversity in the region. This is provided by beta-diversity, which shows that the different forest types show differences in species composition. Nevertheless, our results regarding plant diversity loss and stand structure changes indicate that forest resilience in landscapes under human modification is affected by land-use intensification of SC in the northern Amazon forest. We show that SC affects not only species richness negatively, but also generates changes in species composition and basal area with the intensity of SC. As losses of biodiversity and forest structure result in reductions of ecosystem functions (e.g., carbon and biomass stocks and their dynamics, nutrient cycling and many others), our results are alarming and indicate the non-sustainability of intense SC in the northern Amazon.

In this context, taking into account that OG are essential for the conservation of ecosystem functioning (Gibson et al., 2011), we propose that degraded forests should be managed so that they can return to a stable, self-sustained SG condition. In such a scenario, SGs should play an important focus of conservation actions due to their fundamental roles in the resilience of biomass, carbon sequestration and storage and restoration of biodiversity at local and regional scales (Poorter et al., 2016). To avoid the permanent loss of forest resilience, repeated SC in the same patch should only take place when structural and diversity parameters of SG reached OG or near OG levels (e.g., Villa et al., 2015). Our data indicate that species richness and basal area increase with regeneration time, so that OG levels may be achieved with time, if this tendency is ongoing; nevertheless, ten years of fallow periods are not enough to achieve OG levels. Although necessary for conservation planning, our data do not permit a more accurate estimation of the duration of fallow periods.

The suggested reduction of crop production in low-intense SC systems to maintain forest resilience is contrasted by growing indigenous and non-indigenous communities in combination with crop production for commercial purposes, increasing the need for more intense land use systems. Thus, alternative managing systems such as agroforestry systems should be considered as alternative for indigenous communities where there was a strong influence of western culture on sedentary populations with intensified agricultural systems through deforestation.

The switch from SC to permanent agroforestry systems may limit the demand for new forests burned and slashed for SC, reducing deforestation and forest degradation on the long term, thus contributing to the conservation of primary forests or OGs with larger carbon reservoirs and biodiversity. Thus, with the installation of permanent agroforestry systems, primary forests with larger carbon reservoirs and biodiversity can be conserved. Additional benefits arise from such agroforestry ecosystems as these systems provide a fundamental ecological basis for establishing criteria for SG management during early successional stages, after a SC area has been abandoned, which are also known as improved fallows or successional agroforestry systems.

Finally, two complementary actions are necessary to maintain forest resilience and increase carbon sequestration and biodiversity in Amazonian forests, guaranteeing livelihood for traditional communities: First, the rehabilitation of areas degraded by SC of high intensities; and second, sustainable management of secondary forests as agroforestry systems such as improved fallows or forests gardens, Taungyas or agro-successional systems. The first action should ensure that degraded SGs should be managed so that they return to OG levels. Then, SGs may play an important role for biodiversity conservation and the performance of ecosystem services, as they might be able to harbor significant portions of biomass, sequestered carbon and biodiversity at local and regional scales (Poorter et al., 2016). The latter, increases the planting density of long-cycle agroforestry tree species (e.g., Vieira et al., 2009; Villa et al., 2015), which by itself contributes to the protection of biodiversity and ecosystem services. Thus, our results provide important insight to establish critical points of forest management based on intensification and ecological indicators (soil fertility, richness and species composition), which may be key for forest restoration activities.

5. Conclusions

Our data indicate that intensification of shifting cultivation, i.e., reducing fallow time by increasing the number of SC cycles, reduces the recovery of species richness, composition and basal area of SGs following productive periods. Thus, the intensification of SC cycles reduces the resilience of SG and this ancient form of land-use becomes less sustainable. Due to positive effects for SG resilience, environmental sustainability of SC may be achieved by reducing the number of swidden cycles and extending fallow periods, although this limits the maximum yield that may be produced within a region. To attend growing demands of indigenous and non-indigenous communities in combination with crop production for commercial purposes, we propose other alternatives of land-use such as permanent agroforestry systems.

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Table 1. Woody species diversity, structural attributes, and soil variables (mean ± SD) of old growth (OG), 5 and 10 year-old second-growth forests (SG) after different numbers of shifting cultivation (SC) cycles in Venezuelan Amazon State. For each SG type (combination of number of previous cycles and stand age) and OG, nine plots were sampled, totalizing 63 plots.

Previous cycles	**One SC cycle**		**Three SC cycles**		**Six SC cycles**		**OG**
Code plot age	SG1_5yr	SG1_10yr	SG2_5yr	SG2_10yr	SG3_5yr	SG3_10yr	OG
Site parameter							
Diversity							
Species richness	19	39	13	27	9	15	75
Structural attributes							
Basal area (m^2 ha^{-1})	2.83 (0.34)^{c}	10.81 (1.12)^{b}	1.53 (0.92)^{c}	2.54 (0.41)^{c}	0.22 (0.34)^{d}	0.51 (1.03)^{d}	35.03 (2.50)^{a}
Soil parameters							
Sand (%)	59.77 (1.39)^{e}	54.22 (0.66)^{ef}	78.07 (1.58)^{c}	69.55 (1.43)^{d}	91.35 (1.17)^{a}	85.95 (2.61)^{b}	50.22 (1.39)^{f}
Clay (%)	24.44 (1.13)^{c}	27.11 (0.78)^{b}	15.15 (0.81)^{d}	25.01 (0.73)^{c}	5.99 (1.12)^{f}	10.83 (1.98)^{e}	41.77 (1.22)^{a}
Silt (%)	15.77 (1.78)^{b}	18.66 (0.5)^{a}	6.78 (0.26)^{d}	5.43 (0.62)^{e}	2.65 (0.16)^{g}	3.20 (0.94)^{f}	8.0 (1.87)^{c}
pH	4.94 (0.18)^{c}	4.60 (0.06)^{d}	5.37 (0.13)^{ab}	5.19 (0.28)^{b}	5.85 (0.53)^{a}	5.46 (0.27)^{a}	3.60 (0.16)^{e}
OM (g kg^{-1})	17.24(2.12)^{b}	19.02 (1.57)^{b}	12.09 (1.63)^{d}	15.17 (1.86)^{c}	2.33 (0.57)^{e}	3.51 (1.26)^{e}	37.9 (1.05)^{a}
Al (cmol Kg^{-1})	3.65 (0.13)^{b}	3.09 (0.03)^{c}	3.11 (0.12)^{c}	3.03 (0.39)^{c}	4.09 (0.09)^{a}	4.01 (0.14)^{a}	3.01 (0.07)^{d}
CEC (cmol Kg^{-1})	3.54 (1.22)^{b}	4.17 (1.09)^{b}	2.50 (0.95)^{c}	2.76 (0.43)^{c}	2.17 (0.12)^{c}	2.28 (0.37)^{c}	8.61 (0.28)^{a}
C (g kg^{-1})	10.03 (2.96)^{b}	10.72 (0.48)^{b}	7.37 (1.71)^{c}	8.41 (0.87)^{c}	4.75 (2.71)^{d}	5.10 (1.64)^{d}	21.01 (0.54)^{a}
N (g kg^{-1})	1.44 (0.04)^{c}	1.58 (0.04)^{b}	1.13 (0.14)^{d}	1.23 (0.23)^{d}	0.82 (0.31)^{e}	0.94 (0.18)^{e}	1.95 (0.08)^{a}
P (mg Kg^{-1})	2.30 (0.11)^{b}	1.89 (0.16)^{c}	1.50 (0.09)^{e}	1.76 (0.11)^{d}	1.30 (0.54)^{f}	1.48 (0.19)^{e}	3.38 (0.06)^{a}
K (cmol Kg^{-1})	0.08 (0.02)^{b}	0.08 (0.01)^{b}	0.06 (0.02)^{c}	0.07 (0.03)^{c}	0.05 (0.01)^{d}	0.05 (0.01)^{d}	0.14 (0.10)^{a}
Mg (cmol Kg^{-1})	0.24 (0.07)^{b}	0.27 (0.05)^{b}	0.17 (0.08)^{c}	0.19 (0.05)^{c}	0.12 (0.03)^{d}	0.14 (0.02)^{d}	0.46 (0.02)^{a}
Ca (cmol Kg^{-1})	0.10 (0.02)^{b}	0.13 (0.12)^{b}	0.08 (0.03)^{c}	0.09 (0.02)^{c}	0.04 (0.01)^{e}	0.06 (0.01)^{d}	0.25 (0.12)^{a}
Fe (mg Kg^{-1})	94.68 (8.22)^{c}	130.3 (12.4)^{b}	65.51 (1.72)^{e}	74.19 (9.59)^{d}	26.72 (7.65)^{f}	35.3 (6.38)^{f}	233.77 (25.2)^{a}
Zn (mg Kg^{-1})	0.91 (0.06)^{b}	0.96 (0.21)^{b}	0.54 (0.31)^{c}	0.64 (0.03)^{c}	0.25 (0.16)^{d}	0.38 (0.09)^{d}	1.21 (0.39)^{a}

Different letters indicate significant differences at posteriori analyses (Dunn's test, $P < 0.05$) between forest types.

Table 2. Candidate mixed effect models predicting the species richness with Poisson error distribution (generalized linear mixed effects model - glmer), species composition and basal area with Gaussian error distribution (linear mixed effects model - lme) from different second -growth and old-growth forests from Venezuelan Amazon State. Predictors are soil fertility (PCA1), management intensity expressed as number of previous shifting cultivation cycles (Cycle), cation exchange capacity (CEC). Result of information-theoretic–based model selection is indicated (Akaike criterion corrected for small samples). We present only the models with values of ΔAICc < 4.

Response variable	Model	AICc	ΔAICc	AICcwt
Richness	~ Soil fertility	340.20	0	0.38
Poisson glmer	~ Cycle	340.47	0.27	0.18
	~ Sand	340.90	0.70	0.14
	~ Cycle + CEC	341.43	1.23	0.11
	~ CEC	342.60	2.40	0.10
	~ pH	343.73	3.53	0.08
Species composition	~ Cycle	350.32	0	0.41
Gaussian lme	~ Soil fertility	350.71	0.39	0.22
	~ pH	351.20	0.88	0.14
	~ CEC	352.23	1.91	0.11
	~ pH + CEC	352.41	2.09	0.10
	~ Cycle + pH	352.72	2.40	0.09
Basal area	~ Soil fertility	231.40	0	0.62
Gaussian lme	~ Cycle	231.72	0.32	0.17
	~ pH	232.26	0.86	0.14
	~ CEC	234.41	3.01	0.10

Figure captions

Fig. 1. Localization and general aspects of the study area. Localization of the study area in relation to South America (A), the Cataniapo basin from northern Amazonas State, Venezuela (B), and the Gavilán and Sardi villages in the Cataniapo basin (C). Satellite image of the study area (D), points indicate sampled patches. Illustrations of an old-growth forest (E), slash and burn (F), shifting cultivation with cassava (G), early second growth forest after shifting cultivation with 1-2 years (H), second growth forest with 5 years (I), and second growth forest after six SC cycles with *Imperata brasiliensis* (J).

Fig. 2. Non metric multidimensional scaling (NMDS) based on species composition from different second growth (SG) and old-growth (OG) forests from Venezuelan Amazon State

. SG1-5yr are SG after one shifting cultivation (SC) cycle and five years of natural regeneration, SG1-10yr are SG after one SC cycle and 10 years of natural regeneration, SG2-5yr are SG after three SC cycles and five years of natural regeneration, SG2-10yr is SG after three SC cycles and 10 years of natural regeneration, SG3-5yr are SG after six SC cycles and five years of natural regeneration, and SG3-10yr are SG after six SC cycles and 10 years of natural regeneration. Dot size of indicates basal area in m^2ha^{-1}.

Fig. 3. Plant community dissimilarity (Bray-Curtis) along a land-use intensification gradient by shifting cultivation (SC). Each point represents the similarity between each plot and its nearest old-growth plot sampled in the same area. SG1-5yr are SG after one shifting cultivation (SC) cycle and five years of natural regeneration, SG1-10yr are SG after one SC cycle and 10 years of natural regeneration, SG2-5yr are SG after three SC cycles and five years of natural regeneration, SG2-10yr is SG after three SC cycles and 10 years of natural regeneration, SG3-5yr are SG after six SC cycles and five years of natural regeneration, and SG3-10yr are SG after six SC cycles and 10 years of natural regeneration.

Fig. 4. Biplot of the Principal Component Analysis (PCA) for the soil parameters of different types of second growth forests (SG) after shifting cultivation (SC) along land use intensification gradient and old growth forest (OG). SG1-5yr are SG after one shifting cultivation (SC) cycle and five years of natural regeneration, SG1-10yr are SG after one SC cycle and 10 years of natural regeneration, SG2-5yr are SG after three SC cycles and five years of natural regeneration, SG2-10yr is SG after three SC cycles and

10 years of natural regeneration, SG3-5yr are SG after six SC cycles and five years of natural regeneration, and SG3-10yr are SG after six SC cycles and 10 years of natural regeneration. For analysis, soil organic carbon (C), total N, available Zn, effective cation exchange capacity (ECEC), exchangeable acidity (H^+Al), pH, organic matter (OM), and the soil texture (sand, clay and silt contents) were included.

Fig. 5. Canonical correspondence analysis (CCA) biplot showing species and plot scores in function of soil properties and land-use intensity sampled within different types of secondary (SG) and old growth forest (OG). SG1-5yr are SG after one shifting cultivation (SC) cycle and five years of natural regeneration, SG1-10yr are SG after one SC cycle and 10 years of natural regeneration, SG2-5yr are SG after three SC cycles and five years of natural regeneration, SG2-10yr are SG after three SC cycles and 10 years of natural regeneration, SG3-5yr are SG after six SC cycles and five years of natural regeneration, and SG3-10yr are SG after six SC cycles and 10 years of natural regeneration.

Figure 1.

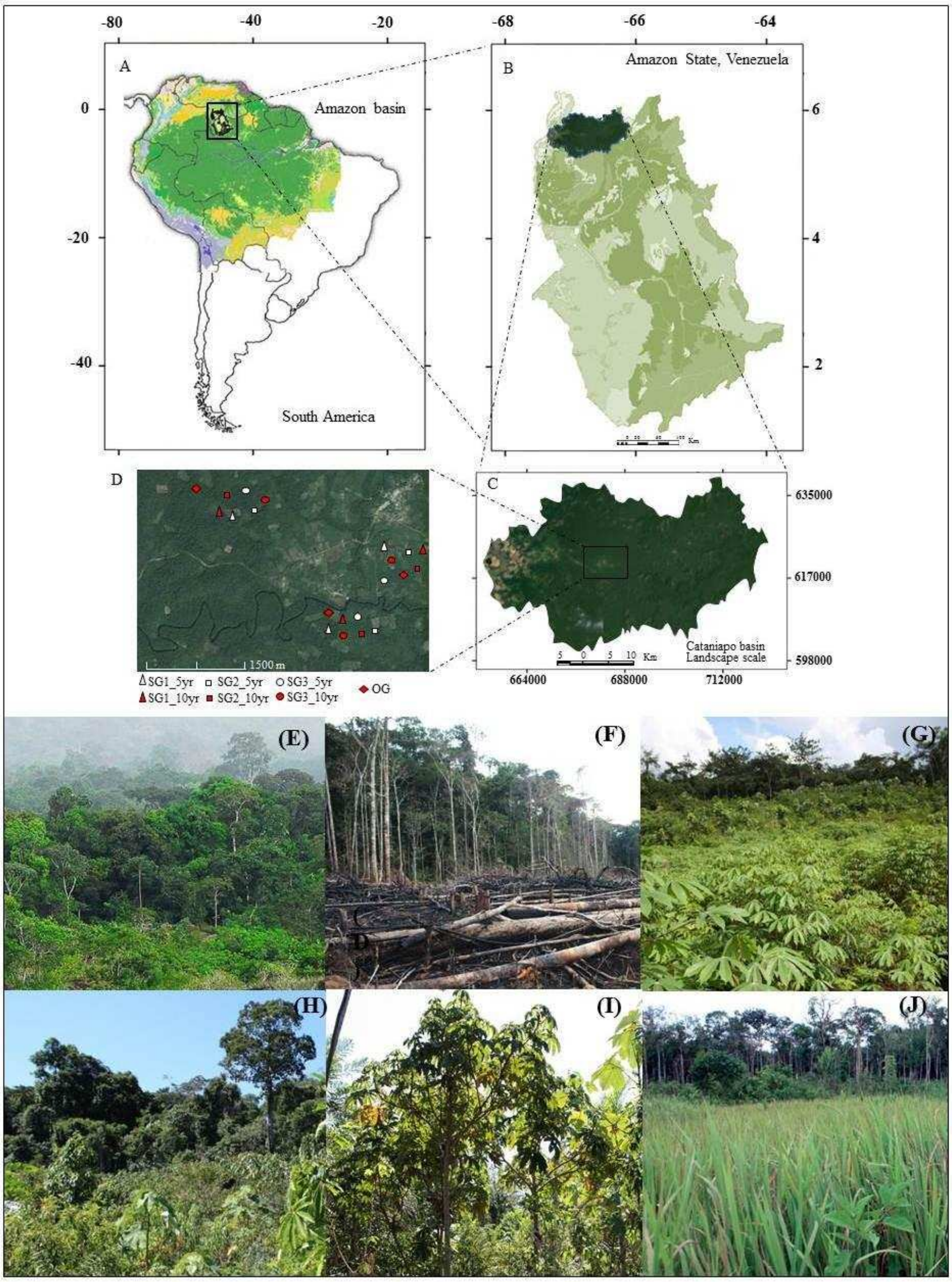

-80
-40
-20
0
-20
-40
A
Amazon basin
South America
-68
-66
-64
B
Amazon State, Venezuela
6
4
2
Km
D
1500 m
△ SG1_5yr
□ SG2_5yr
○ SG3_5yr
▲ SG1_10yr
■ SG2_10yr
● SG3_10yr
◆ OG
C
635000
617000
598000
664000
688000
712000
5 0 5 10 Km
Cataniapo basin
Landscape scale
(E)
(F)
(G)
(H)
(I)
(J)

Figure 2.

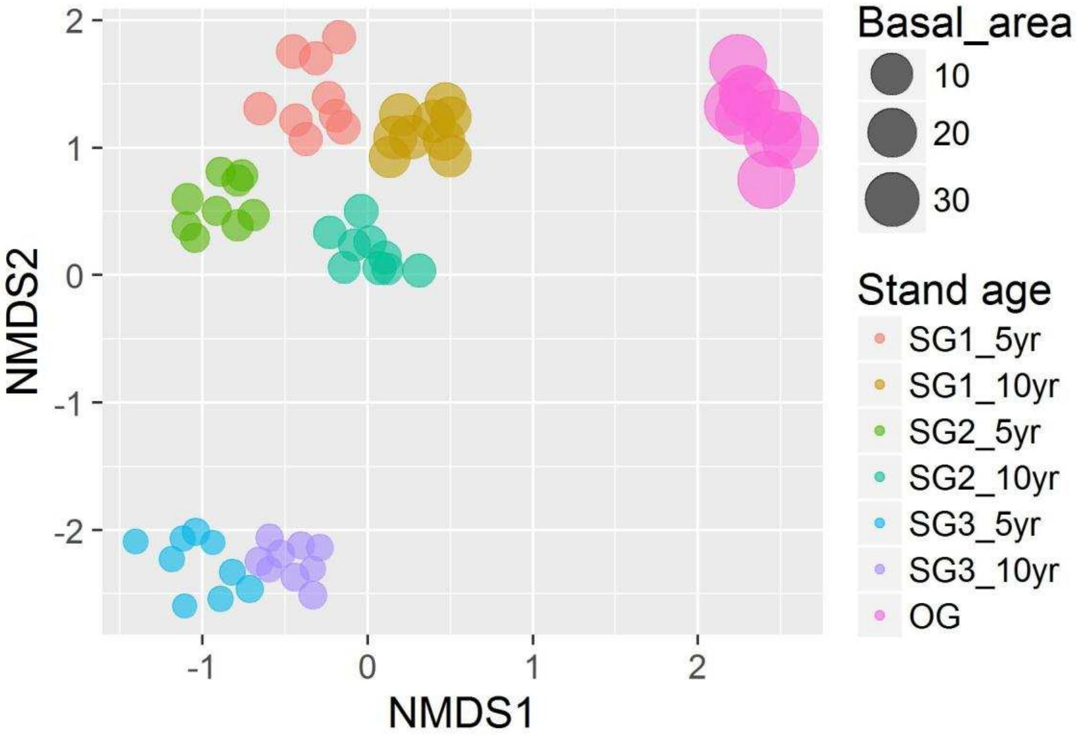
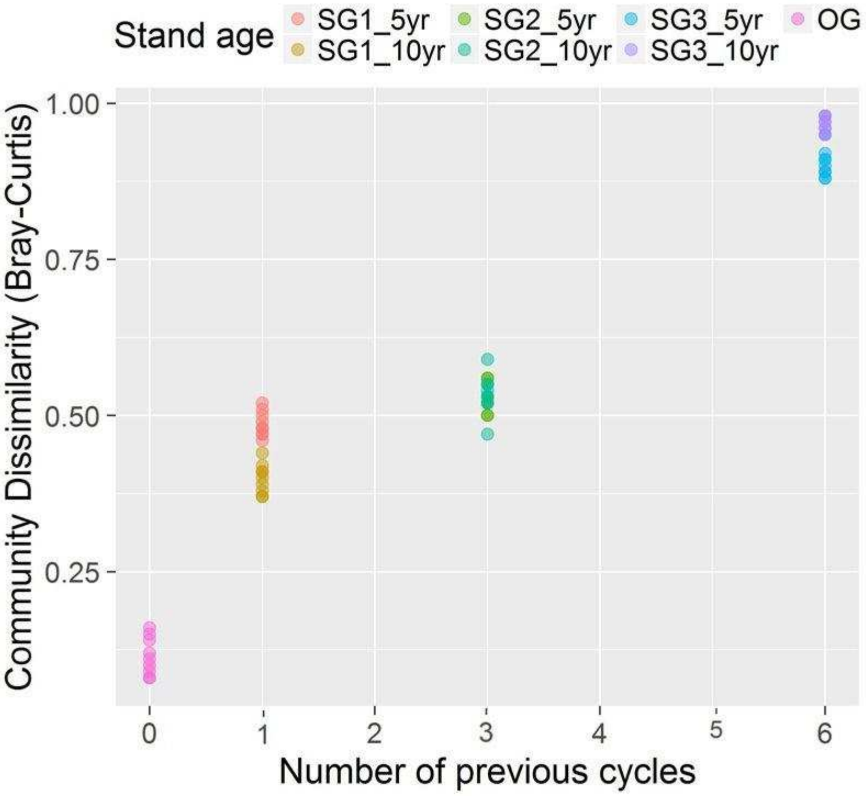

Basal_area
10
20
30
Stand age
SG1_5yr
SG1_10yr
SG2_5yr
SG2_10yr
SG3_5yr
SG3_10yr
OG
NMDS2
2
1
0
-1
-2
NMDS1
-1
0
1
2

Figure 3.



Stand age
SG1_5yr
SG1_10yr
SG2_5yr
SG2_10yr
SG3_5yr
SG3_10yr
OG
Community Dissimilarity (Bray-Curtis)
1.00
0.75
0.50
0.25
0
1
2
3
4
5
6
Number of previous cycles

Appendix A: Supplementary data

Table A.1. Results of the mantel test among the woody sample plots. Observed correlation value and p-value are indicated

Stand age	Observation	P
Plots	0.15	0.064

```
data(dados_amaz)

gen <- quasieuclid(as.dist(dados_amaz $gen))

geo <- quasieuclid(as.dist(dados_amaz $geo))

r1 <- mantel.rtest(geo,gen), main = "Mantel's test"

r1
```

geo is a matrix of geographical distances

gen is a matrix of floristic distances

Table A.2. List of woody species identified in different types of secondary forests (SG) along a land-use intensification gradient and old growth forest (OG) from Cataniapo River basin, Amazonas state, Venezuela.

Specie	Common name	Family
Justicia_sp	Palo (24)	Acanthaceae
Lindackeria_paludosa	Cuyubi	Achariaceae
Annona_rigida	Majagua tierra firme	Annonaceae
Duguetia_lucida	Majagua anoncillo1	Annonaceae
Duguetia_cauliflora	Majagua negra	Annonaceae
Annona_exsucca	Majagua babosa	Annonaceae
Unonopsis_velutina	Majagua de montana	Annonaceae
Xylopia_emarginata	Majagua anoncillo2	Annonaceae
Aspidosperma_cuspa	Cunaguaro	Apocynaceae
Himatanthus_sucuuba	Platanote	Apocynaceae
Tabernaemontana_attenuata	Gallineta	Apocynaceae
Schefflera_sp	Palo de garza	Araliaceae
Attalea_racemosa	Mavaco	Arecaceae
Bactris_sp	Cubarro	Arecaceae
Euterpe_precatoria	Manaca	Arecaceae
Astrocaryum_acaule	Macanilla	Arecaceae
Jacaranda_copaia	Cedrillo	Bignoniaceae
Adenocalymma_sp1	Bejuco 1	Bignoniaceae
Adenocalymma_flaviflorum	Tua tua	Bignoniaceae
Bignoniaceae	liana	Bignoniaceae
Dacryodes_chimantensis	Carana	Burseraceae
Protium_ferrugineum	Catamajaco	Burseraceae
Bauhinia_guianensis	Bejuco mariposo	Fabaceae
Caryocar_glabrum	Jigua	Caryocaraceae
Cuervea_kappleriana	Naranjo	Celastraceae
Trema_micrantha	Carrasposo	Cannabaceae
Licania_canescens	Guarray	Chrysobalanaceae
Tovomita_sp	Naranjillo	Clusiaceae
Croton_cajucara	Palo blanco	Euphorbiaceae

Hevea_benthamiana	Caucho	Euphorbiaceae
Albizia_pedicellaris	Palo de gavilan	Fabaceae
Brownea_similis	Rosa de montana	Fabaceae
Sclerolobium_dwyeri	Canache	Fabaceae
Dalbergia_monetaria	Sangrito	Fabaceae
Dioclea_holtiana	Bejuco 2	Fabaceae
Dipteryx_odorata	Sarrapia	Fabaceae
Machaerium_acuminatum	Arepillo	Fabaceae
Ormosia_sp	Peonia	Fabaceae
Pterocarpus_rohrii	Congrio	Fabaceae
Swartzia_macrophylla	Barbasco	Fabaceae
Banara_sp	Onotillo	Salicaceae
Casearia_ulmifolia	Palo_de_piapoco	Salicaceae
Goupia_glabra	Pilon	Goupiaceae
Vismia_cayennensis	Lacre 1	Hypericaceae
Vismia_sp1	Lacre 2	Hypericaceae
Vismia_baccifera	Sangre de toro	Hypericaceae
Aegiphila_intermedia	Tabaquillo1	Lamiaceae
Vitex_compressa	Teton	Lamiaceae
Nectandra_globosa	Laurel blanco	Lauraceae
Nectandra_cuspidata	Laurel amarillo	Lauraceae
Nectandra_sp1	Majagua hoja ancha	Lauraceae
Nectandra_sp2	Aguacatico	Lauraceae
Ocotea_sp	Palo de viudita	Lauraceae
Eschweilera_subglandulosa	Coco e mono 1	Lecythidaceae
Eschweilera_laevicarpa	Coco e mono 2	Lecythidaceae
Gustavia_pulchra	Rabipelao	Lecythidaceae
Couratari_guianensis	Tabari	Lecythidaceae
Miconia_affinis	Boyo boyo	Melastomataceae
Mouriri_nigra	Guayabo de danto	Melastomataceae
Guarea_sp	Tapaculo	Meliaceae
Guarea_macrophylla	Trompillo	Meliaceae
Abuta_grandiflora	Temblador	Menispermaceae

Inga_edulis	Guama conuquera	Fabaceae
Inga_rubiginosa	Guama hoja ancha	Fabaceae
Inga_thibaudiana	Guama rastrojera	Fabaceae
Parkia_pendula	Palo de murcielago	Fabaceae
Mascagnia Surinamensis	Trepadera	Malpighiaceae
Heteropterys_siderosa	Trepadera	Malpighiaceae
Heteropterys_sp	Mata hormiguera	Malpighiaceae
Malpighiaceae_sp1	Trepadera	Malpighiaceae
Sorocea_pubivena	Yuco	Moraceae
Brosimum_rubescens	Marima	Moraceae
Ficus_matiziana	Ficus	Moraceae
Virola_sp	Cuajo	Myristicaceae
Eugenia_cuaoensis	Ereyo	Myrtaceae
Myrcia_lucida	Curamen	Myrtaceae
Quiina_macrophylla	Salado blanco	Ochnaceae
Minquartia_guianensis	Majagua	Olacaceae
Picramnia_magnifolia	Chamanare	Picramniaceae
Piper_peltatum	Palo de raya	Piperaceae
Duroia_sp	Temare de montana	Rubiaceae
Palicourea_triphylla	Palo de picure	Rubiaceae
Palicourea_grandiflora	Palicourea	Rubiaceae
Casearia_spruceana	Palo de pava	Salicaceae
Toulicia_pulvinata	Palo amarillo	Sapindaceae
Simaba_sp1	Curayaga	Simaroubaceae
Siparuna_guianensis	Palo de bachaco	Siparunaceae
Cecropia_ficifolia	Yagrumo hoja ancha	Urticaceae
Cecropia_sciadophylla	Yagrumo hoja larga	Urticaceae
Cecropia_peltata	Yagrumo	Urticaceae
Lantana_trifolia	Cariaquito	Verbenaceae
Aegiphila sp	Moraito	Verbenaceae
Petrea sp	Flor de verano	Verbenaceae
Rinorea_racemosa	Palo de loro	Violaceae

Table A.3. Significance levels are based on Pearson's correlation coefficients between soil parameters and principal components from 63 different types of secondary forests along a land-use intensification gradient and old growth forests from Cataniapo River basin, Amazonas state, Venezuela.

Soil parameters	**PCA1**	**PCA2**
Sand (%)	-0.55	-0.67
Clay (%)	-0.38	0.52
Silt (%)	0.75	0.48
pH	-0.82	-0.39
OM (g kg^{-1})	0.82	0.39
Al (cmol Kg^{-1})	-0.11	-0.02
CEC (cmol Kg^{-1})	0.93	0.21
C (g kg^{-1})	0.88	0.20
N (g kg^{-1})	0.72	0.53
P (mg Kg^{-1})	0.82	0.21
K (cmol Kg^{-1})	0.86	0.25
Mg (cmol Kg^{-1})	0.81	0.35
Ca (cmol Kg^{-1})	0.74	0.26
Fe (mg Kg^{-1})	0.85	0.37
Zn (mg Kg^{-1})	0.21	0.18

Table A.4. Candidate mixed effect models predicting the species richness with Poisson error distribution (generalized linear mixed effects model - glmer), species composition and basal area with Gaussian error distribution (linear mixed effects model - lme). Result of information-theoretic–based model selection is indicated.

Response variable	Model	AICc	ΔAICc	AICcwt
Richness	~ Soil fertility	340.20	0	0.38
Poisson glmer	~ Cycle	340.47	0.27	0.28
	~ Sand	340.90	0.70	0.10
	~ Cycle + CEC	341.43	1.23	0.08
	~ CEC	342.60	2.40	0.08
	~ pH	343.73	3.53	0.06
	~ Cycle + pH	347.41	7.21	0.01
	~ pH + CEC	350.93	10.73	0.01
Species composition	~ Cycle	350.32	0	0.41
Gaussian lme	~ Soil fertility	350.71	0.39	0.22
	~ pH	351.20	0.88	0.14
	~ CEC	352.23	1.91	0.08
	~ pH + CEC	352.41	2.09	0.06
	~ Cycle + pH	352.72	2.40	0.06
	~ Sand	365.62	15.30	0.02
	~ Sand + cycle	368.83	18.51	0.01
Basal area	~ Soil fertility	231.40	0	0.62
Gaussian lme	~ Cycle	231.72	0.32	0.17
	~ pH	232.26	0.86	0.08
	~ CEC	234.41	3.01	0.06
	~ Cycle + CEC	235.57	4.17	0.03
	~ Cycle + pH	237.19	5.79	0.02
	~Sand	241.82	10.42	0.02

Predictors are soil fertility (PCA1), management intensity expressed as number of previous shifting cultivation cycles (Cycle), cation exchange capacity (CEC). The Akaike information criterion corrected for small samples (AICc), difference between one estimated AICc and the lowest AICc the best model (ΔAICc), and model weights (AICcwt).

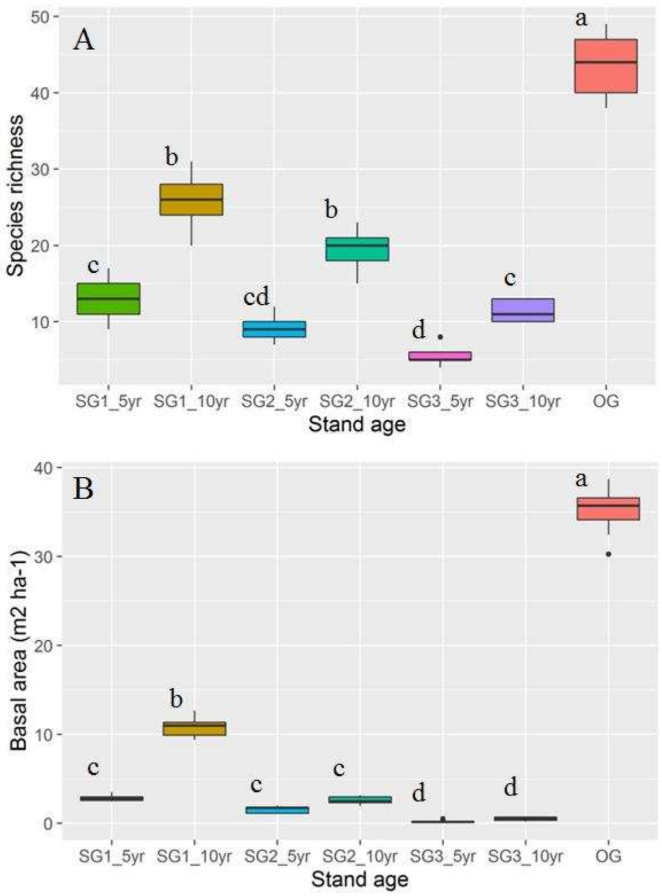


Fig. A.1. Differences in tree species richness (A) and basal area (B) in different types of secondary forests (SG) along a land-use intensification gradient and old growth forest (OG). SG1-5yr are SG after one shifting cultivation (SC) cycle and five years of natural regeneration, SG1-10yr are SG after one SC cycle and 10 years of natural regeneration, SG2-5yr are SG after three SC cycles and five years of natural regeneration, SG2-10yr is SG after three SC cycles and 10 years of natural regeneration, SG3-5yr are SG after six SC cycles and five years of natural regeneration, and SG3-10yr are SG after six SC cycles and 10 years of natural regeneration. Different letters indicate significant differences (Dunn's tests, $P \leq 0.05$) among the sampled forest areas.

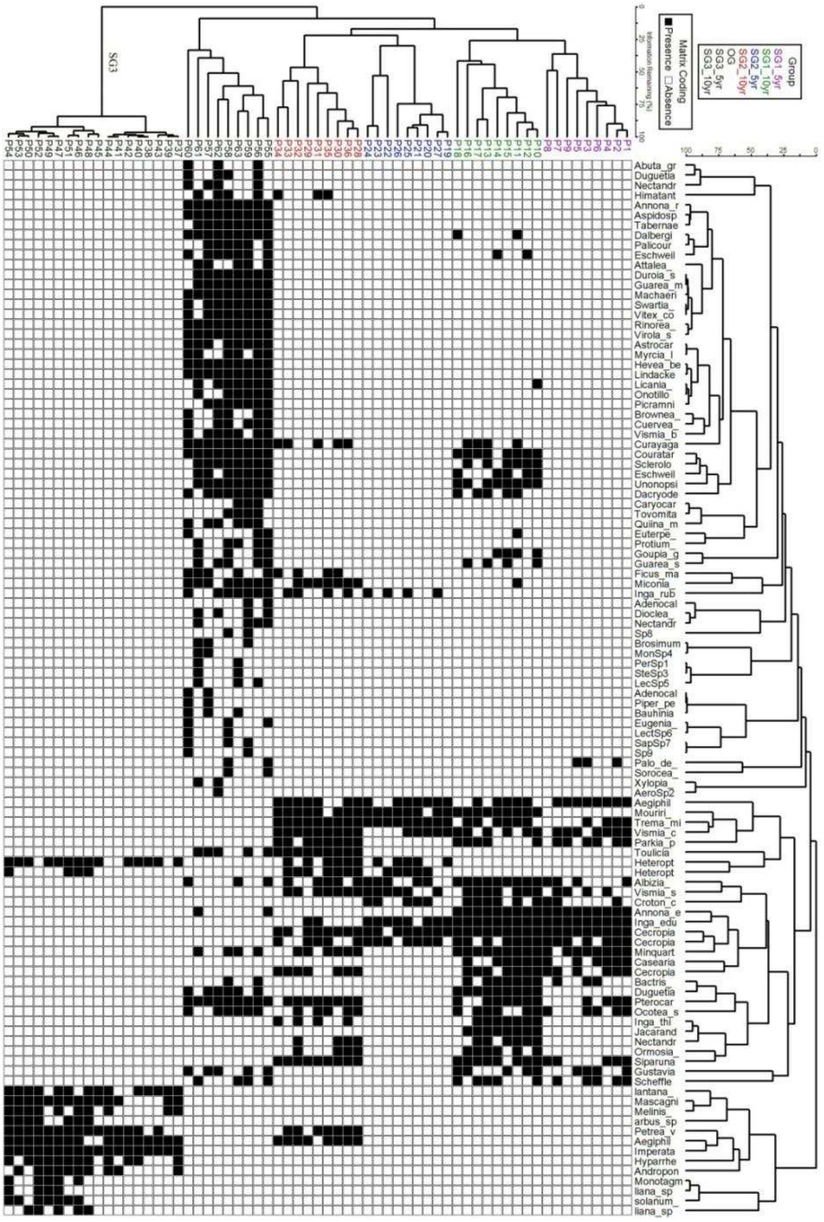


Fig. A.2. Distribution of 110 plant species within 63 plots installed along a land-use intensification gradient of shifting cultivation by a two way cluster dendrogram based on Bray-Curtis dissimilarities. SG1-5yr are SG after one shifting cultivation (SC) cycle and five years of natural regeneration, SG1-10yr are SG after one SC cycle and 10 years of natural regeneration, SG2-5yr are SG after three SC cycles and five years of natural regeneration, SG2-10yr are SG after three SC cycles and 10 years of natural regeneration, SG3-5yr are SG after six SC cycles and five years of natural regeneration, SG3-10yr are SG after six SC cycles and 10 years of natural regeneration, and OG is old-growth forest.

CAPITULO II: Woody species diversity after shifting cultivation in the northern Amazon basin: a chronosequence of diversity recovery

Aceito em Ecological Indicator

Abstract

The Amazon region harbors the most important tropical forest in the world. However, its biodiversity is seriously threatened due to land-use change. Here, we evaluated changes in tree species diversity and composition after shifting cultivation in the northern Amazon forest, Amazon state, Venezuela, through a chronosequence approach. We selected three sites over a 12 km^2 extension of an old-growth forest matrix with secondary forest patches of different stand ages. A total 45 plots (each having 20 × 50 m = 1000 m^2) were established. At each site, woody plant diversity and the composition of trees having diameter ≥ 5 cm were assessed in four secondary forests (5, 10, 15, and 20 years old stands after shifting cultivation) and in one old-growth forest (> 100 years old), and three plots were established in each forest type. Species richness and dissimilarity pairwise beta-diversity metric were calculated for paired plots among different forest types. We analyzed differences in diversity among the four successional stages and the old-growth forest using individual-based approach. Additionally, multivariate analyses were performed to examine differences among the sampled forest areas in terms of species composition along soil gradient. Species richness showed consistently increasing pattern along the succession to old-growth forest. Species richness in the old-growth forest was up to three times higher than in forests at early successional stages. Richness recovery rate in the 20-years old secondary forest two decades after the abandonment of shifting cultivation was on average equal to 70% of the species richness in the old-growth forest. In contrast, the recovery of species composition reached an average 25% in relation to the old-growth forest during the same period. Our results show that the effect of stand age and environmental drivers (i.e., soil properties) determine species diversity along succession. The environmental heterogeneity between successional stages can be analyzed by the differences in floristic composition and beta diversity observed among the analyzed plots. For that reason, we presume that beta diversity is the major determinant of species richness in secondary forests. The proposed approach contributes to the sustainable management of forest communities because it allows estimating the woody species diversity recovering after shifting cultivation disturbance across successional stages.

Keywords: natural regeneration; plant succession; secondary forests; species composition; species richness

1. Introduction

The Amazon basin is one of the most extension of continuous tropical forests, harboring about 11% of the global tree species (Cardoso et al., 2017). However, the biodiversity of Amazon old-growth forest (OG) is seriously threatened due to land-use changes such as agricultural expansion (Barlow et al., 2016; Lewis et al., 2015). Shifting cultivation is a type of agricultural system which consists of deforesting small areas (through slash-and-burn) of OG or secondary (growth) forest (SG) to establish agricultural crops for short periods of time (i.e., 2 to 3 years), and the subsequent abandonment of the land usually leads to the reduction of soil fertility (Arroyo-Kalin, 2012; D'Oliveira et al., 2011). Shifting cultivation is also one of the most common forms of land use that contribute to the loss of biodiversity in Amazonas (Jakovac et al., 2015; Villa et al., 2017). Despite that, SG re-growing after the abandonment of agricultural systems (e.g., shifting cultivation) still represent a reservoir of biodiversity (Chazdon, 2014; Gibson et al., 2011), as these forests contain more than half of the global forest area (FAO, 2010). In fact, secondary succession has been demonstrated to be a feasible method of great importance to restore forests with high floristic diversity, especially when compared with other methods with which a limited number of woody species can be employed (e.g., Palomeque et al., 2017).

The process of diversity recovery during secondary succession depends on several environmental drivers, which may largely determine its trajectory (Arroyo-Rodríguez et al., 2015; Meiners et al., 2015). However, in human-modified landscapes, the land-use history (Klanderud et al., 2010; Zermeño-Hernández et al., 2015), intensity and duration (Guariguata and Ostertag, 2001), and the time since abandonment (Pascarella et al., 2000) are some of the most important anthropogenic drivers in tropical forests (Chazdon, 2014). For instance, the changes in land use (e.g., agricultural expansion) may have significant impacts on ecological drivers (e.g., dispersal limitation, biotic homogenization), which consequently have direct effects on species diversity (Barlow et al., 2016). In this context, understanding how the species diversity and composition of SG recover along different chronosequences of succession in human-modified landscapes represents an important challenge to improve the methods of forest conservation, restoration and management in the Amazon basin (Villa et al., 2017).

Most of the previous studies on the secondary succession in tropical forests have addressed the changes in species diversity and composition after shifting cultivation (Chazdon et al., 2014; Guariguata and Ostertag, 2001) based on the chronosequence approach, aiming to establish comparisons between plots with different regeneration times (Chazdon et al., 2007). Studies comparing SG and OG have suggested that areas undergoing regeneration may harbor a higher diversity of tree species due to the maximized coexistence of fast-growing pioneer species and more competitive canopy species (Bongers et al., 2009; Mwampamba and Schwartz, 2011). The ecological theory on the mechanisms of maintenance of species diversity in relation to the disturbance intensities (e.g., Intermediate Disturbance Hypothesis: Connell, 1978) supports this observation. Indeed, the constant species turnover that takes place along succession (beta diversity) is one of the most important mechanisms that maintain local species diversity (Arroyo-Rodríguez et al., 2015; Meiners et al., 2015). There is also some evidence that the biodiversity resilience in SG may be high because species richness can quickly recover to mature forests during succession (e.g., Norden et al., 2009). On the other hand, recovering species composition might take centuries depending on the local environmental conditions (Dent et al., 2013; Finegan, 1996). It is noteworthy that after the seminal research by Saldarriaga et al. (1988), the present study represents a new contribution through the chronosequence approach for the better understanding of the diversity patterns in forests from the northern Amazon forest, where ecological processes remain largely unknown.

In this study, we analyzed the changes in woody species diversity and composition through a chronosequence approach after shifting cultivation in the Northern Amazon forest, using forest inventory data from 45 plots across four SG (5, 10, 15, and 20 years old stand after shifting cultivation) and one OG (> 100 years old). In order to evaluate the ecological patterns of woody species diversity along forest succession, we asked the following three research questions: 1) How does species diversity change during SG recovery following shifting cultivation in comparison with an OG? 2) What are the changes for beta diversity (β-diversity) and species composition between SG and OG? 3) What is the relative importance of forest stand age and soil fertility on species richness and β-diversity ? We hypothesize that species diversity recovery is highest and fastest during earlier successional stages whereas species composition recovery thereat is lower compared with late successional stage and OG. Our proposed hypothesis led to the following two key predictions: 1) the disturbance that follows shifting cultivation can cause high environmental heterogeneity, which in turn may promote the beta diversity in SG compared with OG, and it might be the main determinant of species richness; and 2) high environmental heterogeneity during succession promotes a high β-diversity due to a high turnover rate, while decreasing in stable OG.

2. Material and methods

2.1. Study area

The study was conducted in a semi-deciduous forest on the Cataniapo river basin, around and close to the indigenous communities of Piaroa de Gavilán and Sardi (5°32´28 S, 67°24´13 E) in the Northern Amazon region (Fig. 1A), at the municipality of Atures, Amazon state, Venezuela (Fig. 1B). Climate in the study area is tropical rainy with a two-month dry season in December and January. Mean annual temperature and mean annual precipitation are 28 °C and 2700 mm, respectively. The predominant soil types are characterized as Oxisols (Latosols) and Ultisols (red clay soils), with low cation exchange capacity, low nutrient content and high acidity levels (Villa et al., 2012).

The Amazon is recognized as the largest area inhabited by indigenous populations in the tropics. These populations live in and around the forests that provide them with different goods and services, which are mainly obtained from small-scale farming practices, food gathering and hunting (Arroyo-Kalin, 2012). Thus, the ecosystems in the area play a key role in the preservation of numerous indigenous civilizations that remain using the same ancestral patterns of land use, even if many of those human groups have already been strongly influenced by western civilization (Porro et al., 2012). Consequently, deforestation of Amazonian forests through the ever-growing implementation of agricultural systems in both indigenous and non-indigenous areas has been posing increasing pressure over forests and biodiversity, given the enlargement of the agricultural frontier and the increased yield serving not only domestic demands but also local and national markets (Porro et al., 2012; Villa et al., 2017). This same pattern of land use is observed on the three selected sites around the Gavilán and Sardi communities.

2.2. Forest inventory

We selected three sites over a 12 km^2 extension of land in an OG matrix with secondary-forest patches, of different stand ages, that had been abandoned after a single cycle of traditional shifting cultivation and were left to regenerate naturally. Sampling sites were systematically selected according to their successional stages, being identified with the assistance of local farmers and experts. A total of 45 plots (20 m ×

50 m = 1000 m^2, each) were established from January 2009 to December 2012 (Fig. 1C). At each site, we selected four SG at different successional stages: 5, 10, 15, and 20 years of succession, and one OG (> 100 years old) (Fig. 1D). Three plots were established within each SG as well as within the OG, at each site.

In each plot, all trees having a diameter at breast height (DBH) ≥ 5 cm were identified to the species level and tagged for measurement. Marked specimens were identified at the Julian Steyermark herbarium of Puerto Ayacucho (Ministry of the Environment, Amazonas state, Venezuela). The *Angiosperm Phylogeny Group* IV (APG IV, 2016) was used to classify taxa. Overall, 95 tree species belonging to 76 genera and 48 families were sampled across all 45 plots. Most species belonged to the Fabaceae (14 species), followed by the Annonaceae (6 species), Lauraceae (5 species), and Lecythidaceae (5 species). The 30 plots from the secondary forests contained 86 species belonging to 45 genera and 38 families, whereas the nine plots from the old-growth forest contained 74 species belonging to 52 genera and 46 families.

2.3. Measurement of soil properties

In each plot, we collected three samples of surface soil (0-10 cm depth) evenly distributed within the plot to obtain one composite sample for chemical and physical analyses. Measurements of soil properties were carried out in the Soil Analysis Laboratory of National Institute of Agricultural Research (Gilabert et al., 2015), following regular protocols (INIA, 2015). The following properties were assessed: soil organic carbon (C), total nitrogen (N), available phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), zinc (Zn), effective cation exchange capacity (ECEC), exchangeable acidity (H^+Al), pH, organic matter (OM), and the soil textural contents (sand, clay and silt).

2.4. Decomposition of taxonomic Beta-diversity

The decomposition of taxonomic beta diversity proposed by Baselga (2010) was used to evaluate the differences of taxonomic compositions among tree communities and sites using three pairwise beta-diversity: i) βsor accounts for the total compositional variation between assemblages (including both turnover and nestedness patterns), ii) βsim captures only compositional changes due to species turnover, and iii) βsne represents the losses from site to site (Baselga et al. 2010; Cardoso et al. 2014). βsne is a resultant dissimilarity and was calculated as the difference between βsor and βsim (Baselga, 2010, 2012). The Sørensen dissimilarity index (β_{sor}), accounts for the total compositional variation between assemblages, including both turnover and nestedness patterns (Eq. 1, 2, 3).

$$\beta sor = \beta\mathrm{sim} + \beta\mathrm{sne} \quad (1)$$

$$\beta sor = \frac{b+c}{2a+b+c} \quad (2)$$

$$\beta sor = \frac{b}{b+a} + (\frac{c-b}{2a+b+c})(\frac{a}{b+a}) \quad (3)$$

where βsor is Sørensen dissimilarity, βsim is Simpson dissimilarity (i.e., turnover component of Sørensen dissimilarity), βsne is the nestedness component of Sørensen dissimilarity, a is the number of species common to both sites; b is the number of species that occur in the first site but not in the second; and c is the number of species that occur in the second site but not in the first (Baselga, 2010, 2012).

2.4. Statistical analyses

We analyzed differences in species richness among the four successional stages and the OG by using individual-based approach (Colwell et al., 2012). Species richness curves were constructed with Hill numbers: species richness ($q = 0$), for individual-based rarefaction and extrapolation curves (Chao et al., 2014; Colwell et al., 2012; Jost, 2007). Extrapolations were made from presence/absence data (Hill numbers of order 0), being higher than thrice the sample size (Colwell et al., 2012). Sample-based rarefaction/extrapolations with 95% confidence intervals were computed using the ‘iNEXT’ package (Hsieh et al., 2016). Rarefaction was estimated as the mean of 100 replicate bootstrapping runs to estimate 95% confidence intervals. Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $P < 0.05$ (Colwell et al., 2012). Recovery of species richness was expressed as percentage of the mean rarefied richness in old-growth forest plots at the same site.

We then compared the variation in species richness and beta diversity components (βsor, βsim, βsne) among sampled areas with a one-way ANOVA followed by a post hoc Tukey’s test (HSD = 0.05) for normally distributed data. Data were tested for normal distribution with Shapiro-Wilk test and a Q-Q plot (Crawley, 2012). All these basic statistical analyses were performed using the ‘car’ and ‘dunn.test’ packages in software R (Dinno, 2017; Fox et al., 2017). We employed Mantel tests (based on 9,999 permutations) to assess spatial autocorrelation of the sampling units within each area between the composition distance matrix and a matrix of geographical distances between plots. We performed partial Mantel tests using the ‘Mantel test’ function on the ‘ade4’ package (Dray et al., 2017).

We performed principal coordinate analysis (PCoA) based in Bray–Curtis dissimilarity matrix among sites, to explore the effects of soil variables on the patterns of woody species along the successional gradient (Dufrene and Legendre, 1997). PCoA is run on distance matrix (Monte–Carlo 999 permutations) and can directly represent the relationships among samples to determine differences in species composition. The PCoA was performed using the vegan package in R (Oksanen et al., 2016). We used the betadisper function in ‘vegan’ package to determine differences in species composition (9999 permutations), based on the PERMDISP2 method (Anderson, 2006). Soil variables were summarized by a principal components analysis (PCA) on the correlation matrix, using the ‘FactoMineR’ package (Husson et al., 2017). For that, all variables were centered and standardized. To investigate a possible relationship between the abiotic (soil parameters) and biotic (species) variables, a Canonical Correspondence Analysis (CCA) was used applying Monte Carlo randomizations (Monte Carlo test with 999 randomizations). The CCA was performed using the vegan package in R (Oksanen et al., 2016).

We constructed a series of linear models to find the most parsimonious models for explaining the main effect of potential predictor variables on the response of richness and β-diversity components across a soil fertility and stand age gradient. We used a generalized linear mixed effects model (GLMMs) to investigate the effect of soil fertility and stand age on richness and β-diversity components assuming Gaussian error distributions. In all models, each site was included as a random factor. Soil fertility was defined as the first principal component from PCA considering all 15 analyzed parameters (see above).

To assess the best models, we applied a multi-model inference approach (Burnham and Anderson, 2002) with the ‘dredge’ function from the “MuMIn” package (Barton, 2015), which returns all possible combinations of the explanatory variables included in the global model (Barton, 2015). To determine which of these variables were the most decisive in explaining changes in richness and β-diversity components we used an information theoretical approach based on the Akaike information criterion with a correction for finite sample sizes (AICc) and AIC weights (Burnham and Anderson, 2002). We selected the best model with the lowest AICc, but all models whose difference in AICc with the best model was less than two units are considered equally good (Burnham, Anderson and Huyvaert, 2011). All models were calculated in

R using the packages 'glmer' (Bates et al. 2014). All ecological and statistical analyses were conducted in R 3.4.2 (R-Core-Team, 2017).

3. Results

3.1. Woody species diversity pattern

The species richness curves showed a clear trend of change over time after shifting cultivation (Fig. 2A). Individual-based rarefaction and extrapolation curves showed higher tree species richness in the OG than in forests at early and intermediary successional stages (Fig. 2A). We observed differences in species richness among SG (Fig. 2B). Species richness clearly showed consistently increasing patterns over the succession to OG. Species richness in the OG was up to three times higher than in the forest at the earliest successional stage and twice as high as in forests at intermediary successional stages (Fig. 2B). No significant correlation between species composition and spatial distance was found according to a Mantel test ($r = 0.12$, $p = 0.72$; Table A.2. from ESM).

3.2. Vegetation–soil properties relationships

The PCoA revealed that woody species composition varied considerably among SG and the OG (Fig. 3, Fig. A.1. Appendix/from Electronic Supplement Material, ESM hereafter). The PCoA ordination of woody species composition allowed for the distinction of five different groups, with the two principal dimensions explaining most of the variance among plots (44.91%). Along the soil gradients, axis 1 of PCoA was positively correlated with sand ($r = 0.87$) and pH ($r = 0.91$), but negatively with silt ($r = -0.97$) and CEC ($r = -0.95$). The strongest predictors were soil pH, sand, CEC explaining 75.3% of the total variance in the species composition ($P < 0.001$).

The CCA separates species among SG and OG (Table A.1. from ESM), which form a continuum along a pH and CEC gradient (Fig. 4). Factor separating both groups mainly is soil fertility (Fig. 4). On the other hand, species from OGs are linked to higher contents of nutrients, CEC, and soil organic matter. The first axis CCA explains 39.21% of the species composition with differences in soil fertility, while the second axis explains 14.35% (Fig. 4).

3.3. *Descriptors of soil fertility*

The first two axes of the soil fertility PCA explained 84.8% of the variation in the data soils (Fig. A.2. from ESM). The biplot scores descriptors of the soil fertility were significantly correlated with the first axis and explained 57.6% of the variation. The first axis was positively correlated with cation exchange capacity, soil organic carbon, and nutrients, separating SG from OG (Fig. A.2. from ESM). The second axis explained 27.2% of the variation and was positively correlated with Al.

3.3. Taxonomic Beta-diversity components along the successional stages

Both components of taxonomic and functional β-diversity were higher in the different SG than in the OG (Fig. 5). Taxonomic β-diversity (BetaSOR) ranged from 0.60 during early successional stages (5-20 years) to 0.40 in OG (Fig. A.3. from ESM). Taxonomic turnover as well as β-diversity was higher at 20 years old stands than in further secondary or old growth forest. The taxonomic turnover was higher than nestedness-resultant component (Fig. 5).

3.4. Effects of stand age and soil fertility on taxonomic richness and beta-diversity components

In the multi-model comparison applied between sites and forest type, we found that models including single soil fertility and stand age explained more variation in taxonomic turnover and β-diversity (Table 1). According to the best model, stand age was the best predictor for richness (GLMM: $z = -5.72$, $p < 0.001$) and taxonomic β-diversity (GLMM: $z = -2.68$, $p < 0.001$), and taxonomic turnover (GLMM: $z = -1.59$, $p < 0.001$) in the study area. Taxonomic turnover and β-diversity declined linearly with increasing soil fertility, whereas that these beta components presented a peak at intermediate stand age before declining for old growth forest (Fig. 5).

4. Discussion

Our results demonstrate a rapid recovery of diversity during succession, with disturbed forests reaching diversity levels equivalent to the old-growth forests in which shifting cultivation had been abandoned at two decades earlier. In some cases, for example, an average 70% of species richness was recovered. The chronosequence approach allowed for observing the high regeneration capacity of forests after a single cycle of shifting cultivation. This relatively rapid increase in diversity of tree species after occurrence of the disturbance is consistent with the reports of similar studies carried out in other tropical forests (Dent et al., 2013; Guariguata and Ostertag, 2001; Norden et al., 2009). Analogously, Peña-Claros (2003), reported a similar pattern, whereby species richness increased with stand age and stabilized after 20 to 25 years. In other tropical forests, recovering diversity may take twice as long or even more (e.g., Powers et al., 2009; Xu et al., 2015). Nevertheless, such recovery capacity depends on different environmental drivers (Poorter et al., 2016) as well as on anthropogenic factors such as land use history (Chazdon, 2014; Jakovac et al., 2017). Such pattern of increased diversity has been associated with the probability of coexistence of fast-growing pioneer species that favor the establishment of shade-tolerant species during succession (McNicol et al., 2015; Mwampamba et al., 2011). Generally, the initial light-demanding pioneer species colonize these areas after the disturbance. Their short life cycles last between 10 and 15 years (Chazdon et al., 2007; Guariguata et al., 1997). Then, long-lived pioneer species (50-100 years) begin to dominate the canopy, enabling the recruitment of old-growth specialists that become dominant in late stages of succession (Finegan, 1996; Rozendaal and Chazdon, 2015).

An important implication of this study is that shifting cultivation not only affects species richness, but may also lead to changes in species composition. In contrast to the rapid recovery of richness in up to two decades after the disturbance, the species composition recovery reached only as much as 25% of the value found in the old-growth forest in the same period. This has been previously reported in different tropical forests, which could take centuries for their species composition to reach the levels of a mature forest (Finegan, 1996; Chazdon, 2014). Additionally, it has already been discussed that species composition may vary considerably between secondary and mature forests due to the influence of different determinant drivers (Pascarella et al., 2000). In fact, even the dominance of a few species can affect the floristic composition of the whole community during succession (Grime and Pierce, 2012). On the other hand, it may possible that the composition cannot be fully recovered, as some species can only persist in old-growth forests (e.g., Lugo and Helmer, 2004). Still, secondary forests are deemed highly important, as they contribute to maintaining local and regional biodiversity (Scales and Marsden, 2008; Gibson et al., 2011).

Species compositions in the SG at the evaluated successional stages were more similar among each other (60% to 90%) than to the one of the OG. Composition similarity between plots among different successional stages decreased from early to intermediary forests (from 90% to 25%), the highest value being found in the forest with 20 years of succession. These trends had also been previously observed in different investigations, which reported a decrease in such similarity along succession. According to these reports, even after 50 years of natural succession the species composition can differ considerably from that of mature forests (McNicol et al., 2015; Xu et al., 2015).

In our study, we found marked differences in β-diversity among the sampled forest areas. Despite the lower richness in SGs after shifting cultivation in relation to those in the OGs, we observed that the disturbance led to higher β-diversity. We cannot safely state that this pattern responds to the intermediate disturbance hypothesis, due to the need to prove this empirically as well as to the possible variation in the effects of intensity, frequency and duration of the land use. We argue that shifting cultivation disturbances generate higher environmental heterogeneity (expressed in resource availability), which in turn promotes species turnover at the local scale. Other researchers argue that the intermediate disturbance hypothesis predicts that species diversity would be maximized under the traditional low-impact management practices, which pose an intermediate level of disturbance to agricultural lands (Kleijn et al., 2011). As several empirical studies have demonstrated, tropical forests with natural disturbance regimes have also higher environmental variability, which leads to an increased species richness (Peña-Claros, 2003; Dent et al., 2013). Nonetheless, other studies have shown that an increase in the intensity of the disturbance can cause a significant decrease in diversity (Styger et al., 2007; Jakovac et al., 2016).

The aforementioned environmental heterogeneity between successional stages can be analyzed by the differences in floristic composition and β-diversity observed among the analyzed plots. In our study, we found that β-diversity was generally higher in secondary forests than in primary forests, the former showing a higher species turnover among plots during succession. For that reason, we presume that β-diversity may be the major determinant of species richness in SG. In that sense, the high β-diversity of the forest with 20 years of succession compared to the ones of the other sampled forest areas may be due to the high proportion of pioneer and shade-tolerant species coexisting therein (Table A.1. from ESM), both of which contributes significantly to diversity recovery.

Recent studies have shown that disturbed ecosystems present more related species than undisturbed ones (e.g., Ding et al., 2012). In this sense, presumably after land use for agricultural systems, β-diversity between plots, as well as between patches in the same forest landscape, declines along the succession gradient, from the early stages dominated by generalist species (e.g., Rozendaal and Chazdon, 2015), and to a higher degree of equilibrium between generalist and intermediate succession species, to the advanced stages of succession with greater dominance of shadow tolerant species. Therefore, the loss of local diversity could also have a negative impact on the decrease in diversity on a landscape scale when comparing areas of mature forests with areas that have different stages of succession. Differences in β-diversity between plots and sites with the same succession stage are also expected, probably due to the local effect of the spatial heterogeneity by disturbances and environmental predictors (soil parameters), as well as dispersal limitation.

Our analyses indicate that the effects of stand age, as well as soil fertility, are determinants in the changes in richness and β-diversity in our study area. However, it was also possible to observe that these effects were significant for both taxonomic β-diversity and turnover, but not for nestedness according to our models. Our results are in agreement with recent research in Amazonian forests, which shows that the effect of stand age and environmental drivers (i.e., soil parameters) determine species diversity along succession. On the other hand, a previous study observed changes in the soil quality through shifting cultivation intensification (Jakovac et al., 2015). Thus, our study observed changes in the soil structure and chemistry through successional gradient as demonstrated by the different multivariate methods used in our study. This pattern was also reported in Amazonas region, where soils become less clayey and lost basic cations with repeated swidden-fallow cycles (Jakovac et al., 2016). In this sense, our analyses indicated that the effects of soil fertility on β-diversity could also be used as indicators of forest recovery at a local-scale. This specific approach to how shifting cultivation affects soil properties and their relation to species diversity is still quite limited for the Amazon.

Understanding how shifting cultivation affects the long-term recovery of tropical SG is critical to assess the conservation value of biodiversity. While there is a constant pressure for land-use change on Amazonian forests, their future will also depend on the improvement of conservation, management and restoration methods (Villa et al., 2015, 2017). Our results demonstrate the high potential for diversity recovery of those forests after they have undergone agricultural disturbance, as their levels of species richness can approach the ones of OG within two decades. However, it is also necessary to consider the importance of species composition recovery, which is a much slower process yet, may be relevant to the multiple ecosystem functions. In that sense, it should be taken as a premise that a single cycle of shifting cultivation in the northern region of the Amazon still represents an opportune time to take conservation actions. In order to avoid second or further cycles of shifting cultivation in the same previously used areas. Otherwise, such land use pattern based on multiple cycles of shifting cultivation could reduce diversity recovery and consequently expand the proportion of degraded areas in the Amazon forest.

Despite the recent revelation that diversity in tropical forests is made up of different components (e.g., taxonomic, functional, and phylogenetic diversities, Purschke et al., 2013), taxonomic diversity still remains with a particular relevance for the understanding of ecological patterns and processes that take place during succession (Meiners et al., 2015), especially due to its importance for recovery practices. On the other hand, it may be relevant to assess other taxonomic diversity metrics that could also contribute to elucidate emergent patterns during succession.

5. Conclusions

This study reveals a forest recovery pattern after shifting cultivation in the northern Amazon forest, where the species richness recovery rate in a secondary forest two decades after the abandonment of shifting cultivation was on average equal to 70% of the richness in an old-growth forest. However, the recovery of species composition in that same period reached an average 25% of the one in the old-growth forest. During the earliest successional stage, a lower evenness was observed, as a response to a few dominant species in the community. That trend stabilized along the following successional stages, with an increase in richness.

Our results show that the effects of stand age and environmental drivers (i.e., soil properties) determine species diversity along succession. Lastly, we observed that beta diversity was higher in secondary forests than in primary forests, the former of which shows higher species turnover among plots during succession. Therefore, high beta diversity is presumably a determining factor for the rapid recovery of species richness in secondary forests.

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Table 1. Candidate mixed effect models predicting the species richness with Gaussian error distribution (linear mixed effects model - glmer). Result of information-theoretic – based model selection is indicated. Models having ΔAICc < 2 are presented here.

Response variable	Predictor	AICc	ΔAICc	AICcwt
Richness	~ Stand age	316.7	0	0.81
	~ Soil fertility	318.2	1.5	0.19
Beta.SOR	~ Stand age	335.8	0	0.73
	~ Soil fertility	337.6	1.8	0.27
Beta.SIM	~ Stand age	361.1	0	0.92
	~ Soil fertility	362.4	1.3	0.08

Abbreviations: The Akaike information criterion corrected for small samples (AICc), difference between one estimated AICc and the lowest AICc the best model (ΔAICc), and model weights (AICcwt).

Figure captions

Fig. 1. Map and images of study area. Location of study region in the Northern Amazon forest (black square), in South America (A). Map of the Amazon region indicating the Cataniapo basin, in the Northern Amazonas State, Venezuela (B). Map of the Cataniapo basin indicating the location of the study area, between Gavilán and Sardi communities in the Cataniapo basin (C), showing distribution of areas sampled secondary forest (color symbols). Satellite image of the study area showing some secondary forest patch in Gavilán (D). We stratified the sampling of the three sites within one forest landscape from Gavilán (E). Early second growth forest after shifting cultivation (F).

Fig. 2. Individual-based rarefaction (solid lines) and extrapolation curves (dashed lines) of woody species diversity based on the first Hill numbers ($q = 0$) for the sampled forest areas at different successional stages (5, 10, 15, and 20 years old) and in an old-growth forest (OG, 100 years old, figure A). Differences in woody species richness (B). Different letters indicate significant differences (Dunn's test, $P < 0.05$) among the sampled forest areas.

Fig. 3. Principal coordinate analysis (PCoA) based on a Bray-Curtis dissimilarity matrix of the woody species diversity. Relationships between woody species composition and environmental vectors (soil parameters) measured within plots of forest patches at different successional stages (5, 10, 15, and 20 years old) and in an old-growth forest (OG, 100 years old). All soil parameters vectors were shown based on Monte-Carlo test with 999 permutations.

Fig. 4. Canonical correspondence analysis (CCA) showing species and plot scores in function of soil properties sampled within different types of secondary (SG) at different successional stages (5, 10, 15, and 20 years old) and in an old-growth forest (OG, 100 years old).

Fig. 5. Differences in the taxonomic beta diversity components of woody species communities at different successional stages (5, 10, 15, and 20 years old) and in an old-growth forest (OG, 100 years old). Taxonomic beta-diversity (beta.SOR) and its two components, turnover (beta.SIM) and nestedness-resultant (beta.SNE) are indicated. Different letters indicate significant differences ($P < 0.05$) among the sampled.

Fig. 1

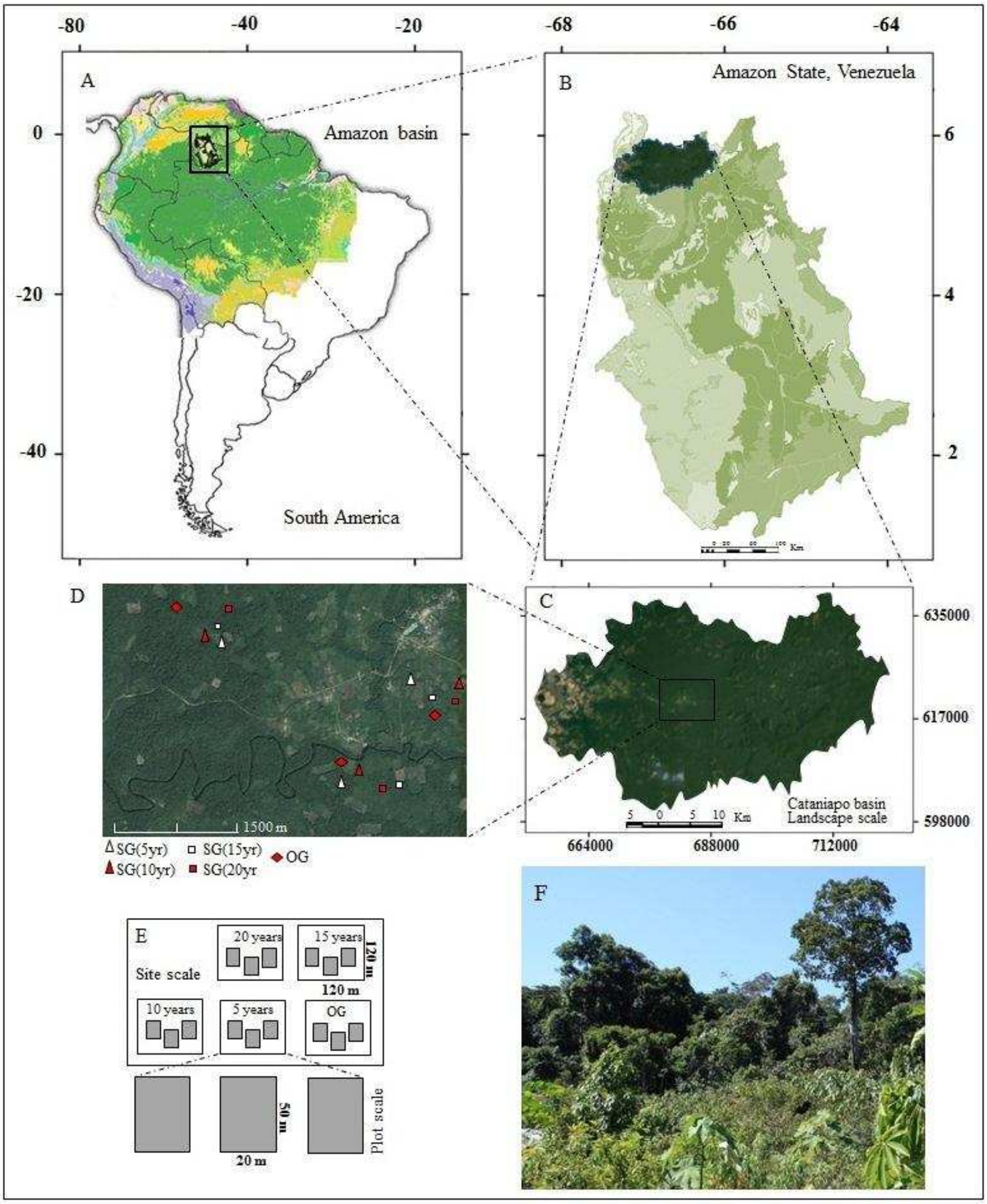

-80
-40
-20
-68
-66
-64
A
Amazon basin
0
-20
-40
South America
B
Amazon State, Venezuela
6
4
2
Km
D
C
635000
617000
598000
Cataniapo basin
Landscape scale
5 0 5 10 Km
664000
688000
712000
1500 m
△ SG(5yr)
▲ SG(10yr)
□ SG(15yr)
■ SG(20yr)
◆ OG
E
Site scale
20 years
15 years
120 m
120 m
10 years
5 years
OG
50 m
20 m
Plot scale
F

Fig. 2

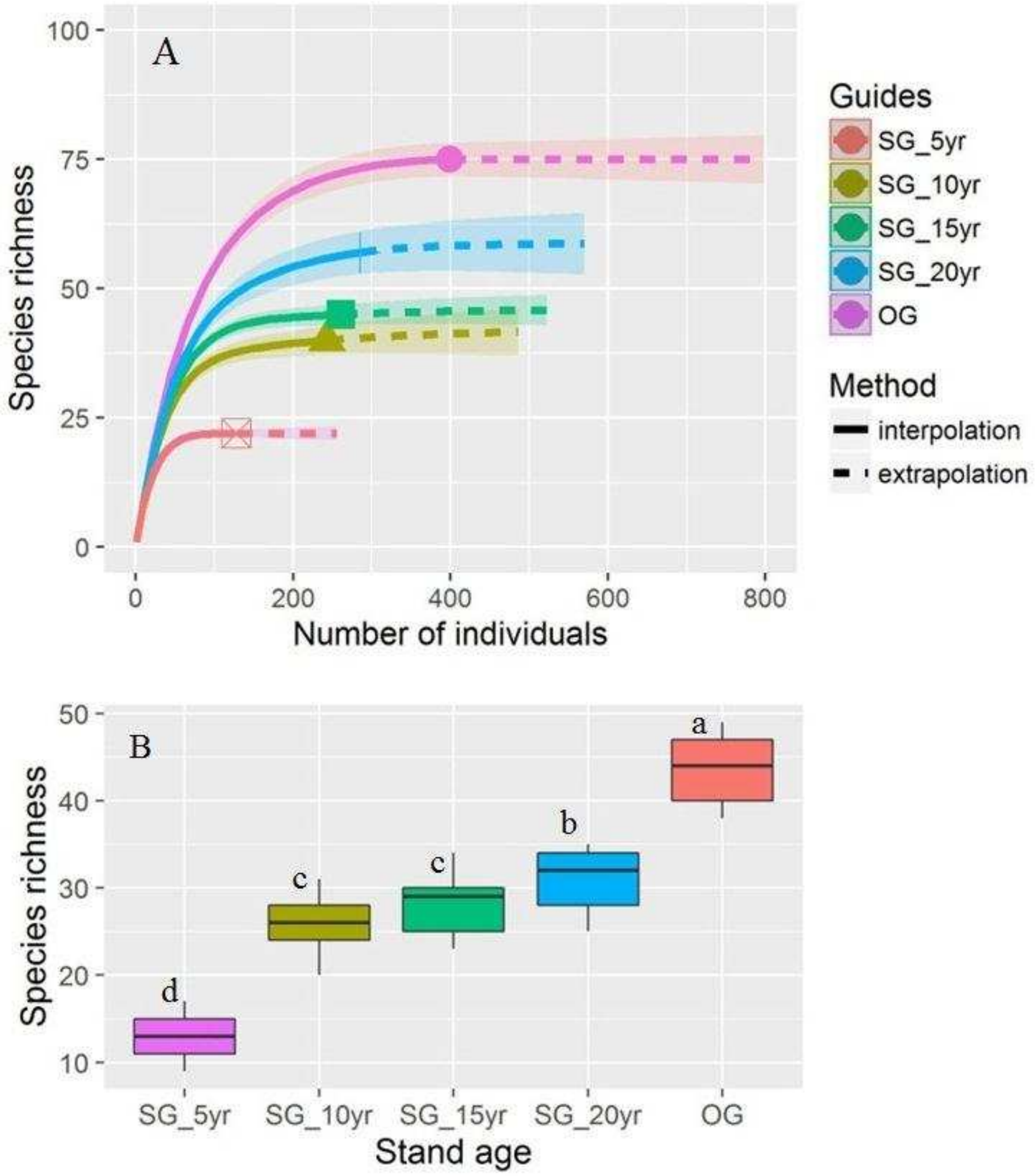

A
Species richness
100
75
50
25
0
0
200
400
600
800
Number of individuals
Guides
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
Method
interpolation
extrapolation
B
Species richness
50
40
30
20
10
a
b
c
c
d
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
Stand age

Fig. 3

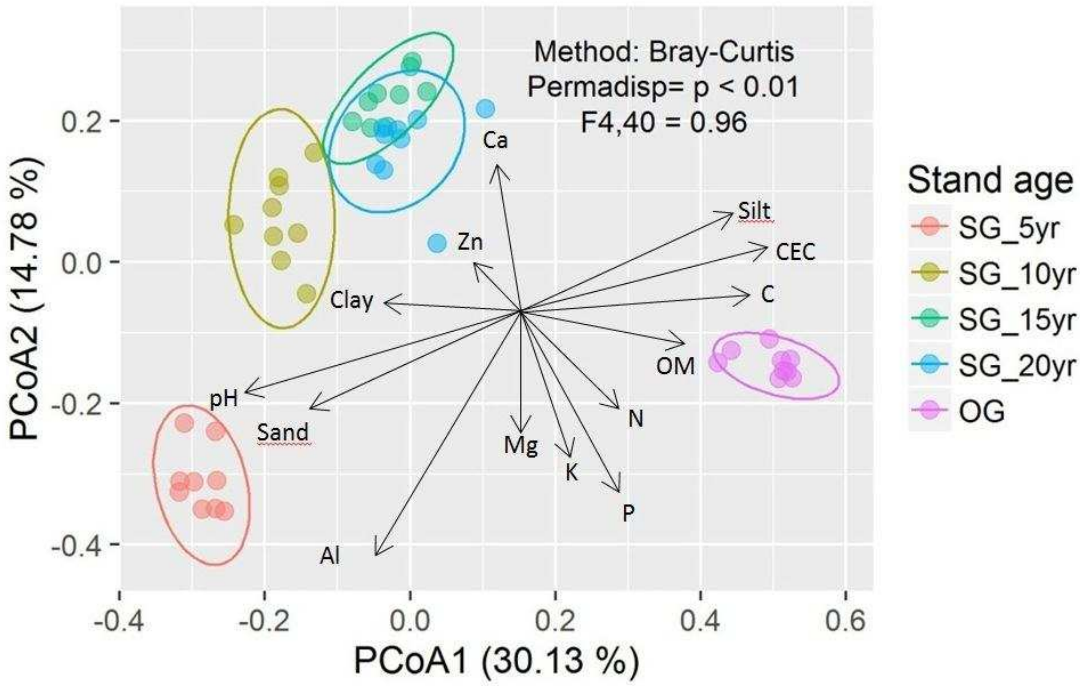

Method: Bray-Curtis
Permadisp= p < 0.01
F4,40 = 0.96
Ca
Zn
Silt
CEC
C
Clay
OM
pH
Sand
N
Mg
K
P
Al
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
0.6
PCoA2 (14.78 %)
PCoA1 (30.13 %)
Stand age
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG

Fig. 4

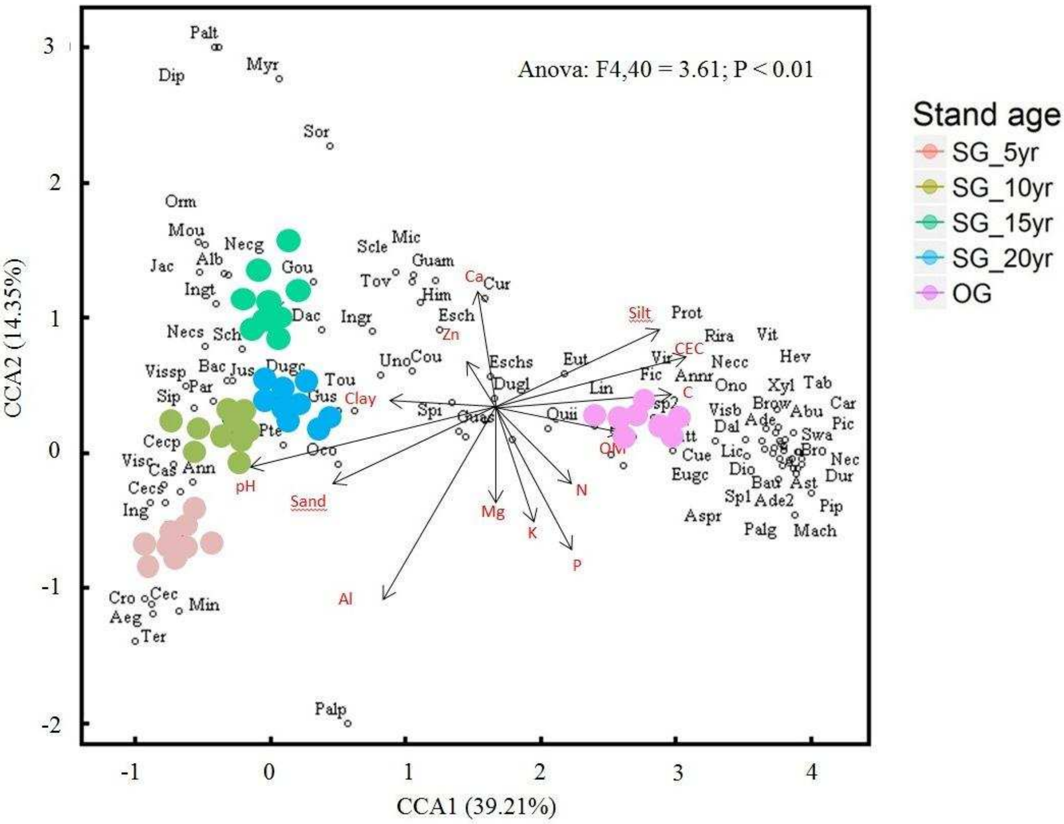
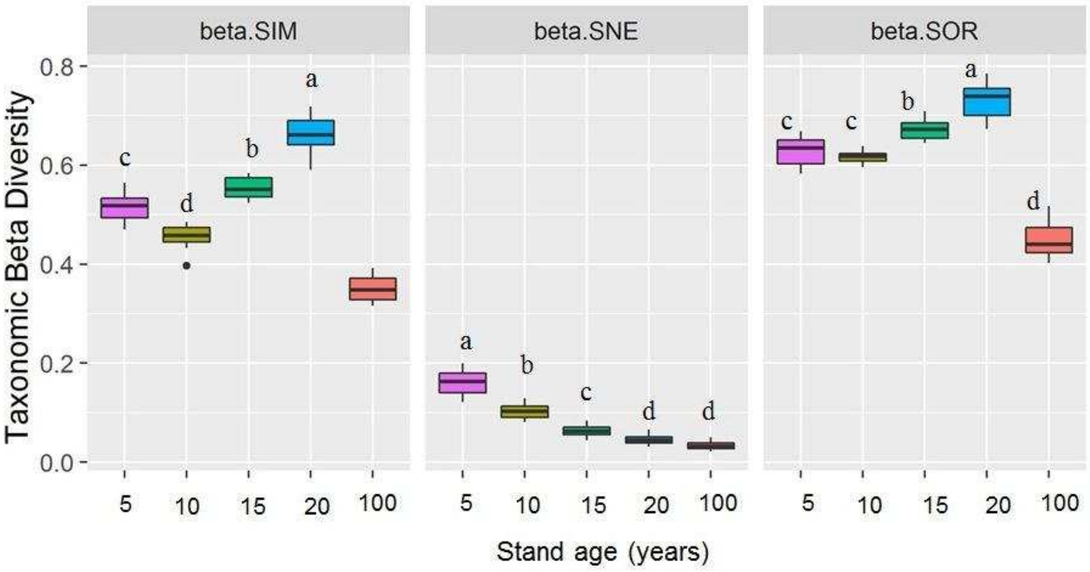

Anova: F4,40 = 3.61; P < 0.01
Stand age
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
CCA1 (39.21%)
CCA2 (14.35%)
-1
0
1
2
3
4
-2
Palt
Dip
Myr
Sor
Orn
Mou
Necg
Jac
Alb
Gou
Ingt
Dac
Ingr
Necs
Sch
Scle
Mic
Guam
Tov
Him
Ca
Cur
Esch
Zn
Vissp
Bac
Jus
Dugc
Tou
Par
Sip
Gus
Clay
Uno
Cou
Eschs
Dugl
Spi
Guas
Pte
Cecp
Oco
Visc
Cas
Ann
pH
Cecs
Sand
Ing
Mg
K
P
N
Al
Cro
Cec
Min
Aeg
Ter
Palp
Silt
Prot
Rira
Vit
CEC
Vir
Eut
Necc
Hev
Fic
Annr
Ono
Xyl
Tab
Lin
C
sp2
Quii
Visb
Brow
Abu
Car
Dal
Ade
Pic
Swa
tt
OM
Cue
Lic
Bro
Nec
Eugc
Dio
Bau
Ast
Dur
Spl
Ade2
Pip
Aspr
Palg
Mach

Fig. 5


beta.SIM
beta.SNE
beta.SOR
Taxonomic Beta Diversity
0.8
0.6
0.4
0.2
0.0
c
d
b
a
a
b
c
d
d
c
c
b
a
d
5
10
15
20
100
Stand age (years)

Appendix A: Supplementary data

Table A.1. Results of the mantel test among the woody sample plots. Observed correlation value and p-value are indicated

Stand age	Observation	P
Plots	0.12	0.72

```
data(dados_amaz)

gen <- quasieuclid(as.dist(dados_amaz $gen))

geo <- quasieuclid(as.dist(dados_amaz $geo))

r1 <- mantel.rtest(geo,gen), main = "Mantel's test"

r1
```

geo is a matrix of geographical distances

gen is a matrix of floristic distances

Table A.2. Seven most dominant woody species in forests at different successional stages (5, 10, 15, and 20 years old) and in an old-growth forest (OG, 100 years old).

	Species	Family	id
5-year secondary forest	***Aegiphila intermedia***	**Lamiaceae**	**Aeg**
	Cecropia ficifolia	**Urticaceae**	**Cec**
	Minquartia guianensis	**Olacaceae**	**Min**
	Inga edulis	**Fabaceae**	**In**
	Cecropia sciadophylla	**Urticaceae**	**Cecs**
	Annona exsucca	**Annonaceae**	**Ann**
	Pterocarpus rohrii	**Fabaceae**	**Pte**
10-year secondary forest	***Pterocarpus rohrii***	**Fabaceae**	**Pte**
	Annona exsucca	**Annonaceae**	**Ann**
	Siparuna guianensis	**Siparunaceae**	**Sip**
	Jacaranda copaia	**Bignoniaceae**	**Jac**
	Mouriri nigra	**Melastomataceae**	**Mou**
	Inga edulis	**Fabaceae**	**Ing**
	Minquartia guianensis	**Olacaceae**	**Min**
15-year secondary forest	***Myrcia lucida***	**Myrtaceae**	**Myr**
	Mouriri nigra	**Melastomataceae**	**Mou**
	Schefflera sp	**Araliaceae**	**Sch**
	Sclerolobium dwyeri	**Fabaceae**	**Scl**
	Unonopsis velutina	**Simaroubaceae**	**Uno**
	Albizia pedicellaris	**Fabaceae**	**Alb**
	Vismia sp1	**Hypericaceae**	**Vis**
20-year secondary forest	***Pterocarpus rohrii***	**Fabaceae**	**Pte**
	Parkia pendula	**Fabaceae**	**Par**
	Schefflera sp	**Araliaceae**	**Sch**
	Aegiphila intermedia	**Lamiaceae**	**Aeg**
	Annona exsucca	**Annonaceae**	**Ann**
	Dacryodes chimantensis	**Burseraceae**	**Dac**
	Inga thibaudiana	**Fabaceae**	**Ingt**
Old-growth forest	***Machaerium acuminatum***	**Fabaceae**	**Mac**
	Vitex compressa	**Lamiaceae**	**Vit**
	Dalbergia monetaria	**Fabaceae**	**Dal**
	Rinorea racemosa	**Violaceae**	**Rin**
	Hevea benthamiana	**Euphorbiaceae**	**Hev**
	Swartia macrophylla	**Fabaceae**	**Swa**
	Aspidosperma cuspa	**Apocynaceae**	**Asp**

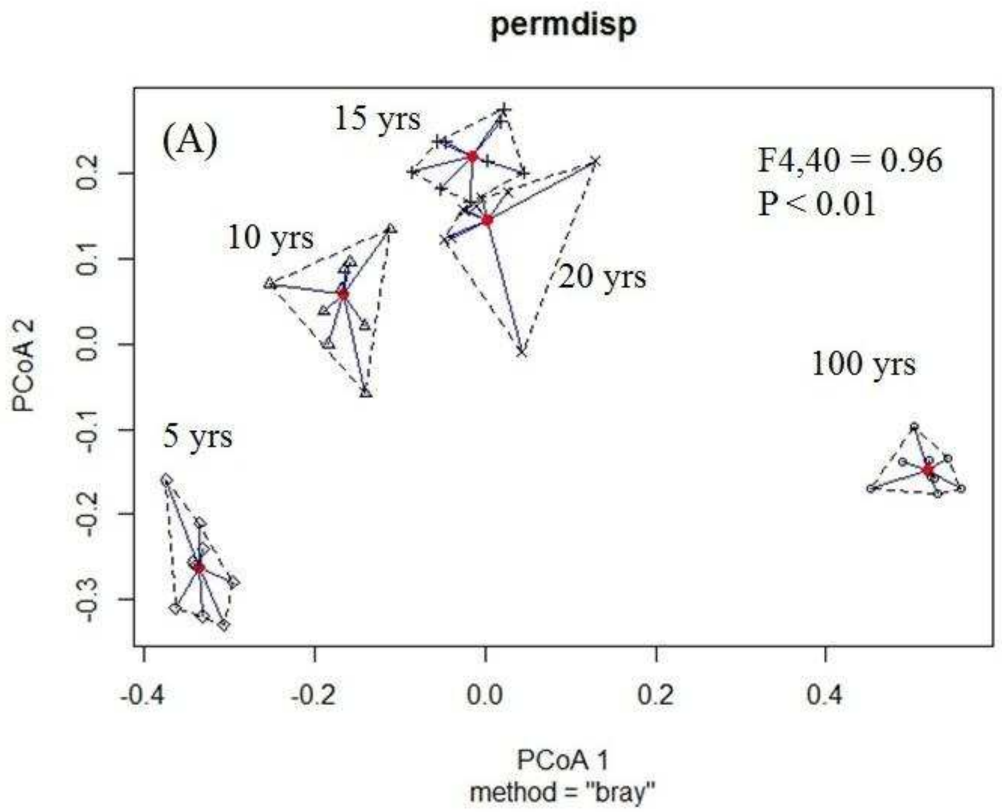


Fig. A.1. Principal coordinate analysis (PCoA) based on a Bray-Curtis dissimilarity matrix of the woody species diversity at different successional stages (5, 10, 15, and 20 years old) and in an old-growth forest (OG, 100 years old).

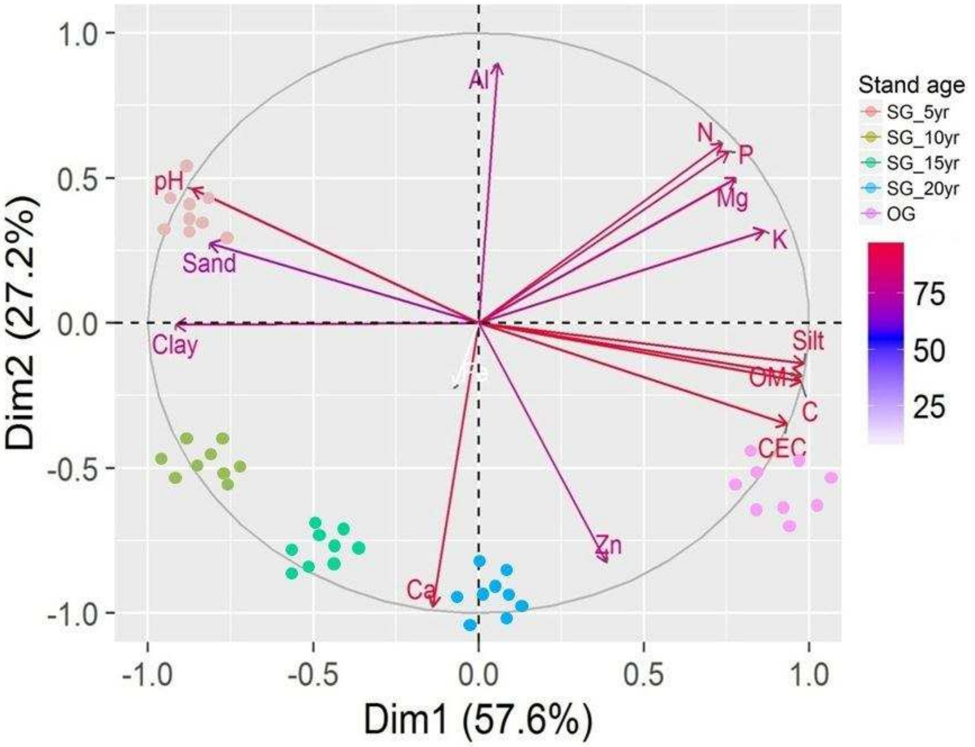


Fig. A.2. Principal Component Analysis (B) of the variables (soil parameters) measured within plots of forest patches at different successional stages (5, 10, 15, and 20 years old) and in an old-growth forest (OG, 100 years old). Color intensity of vectors represents the mean relative contribution of species (cos2).

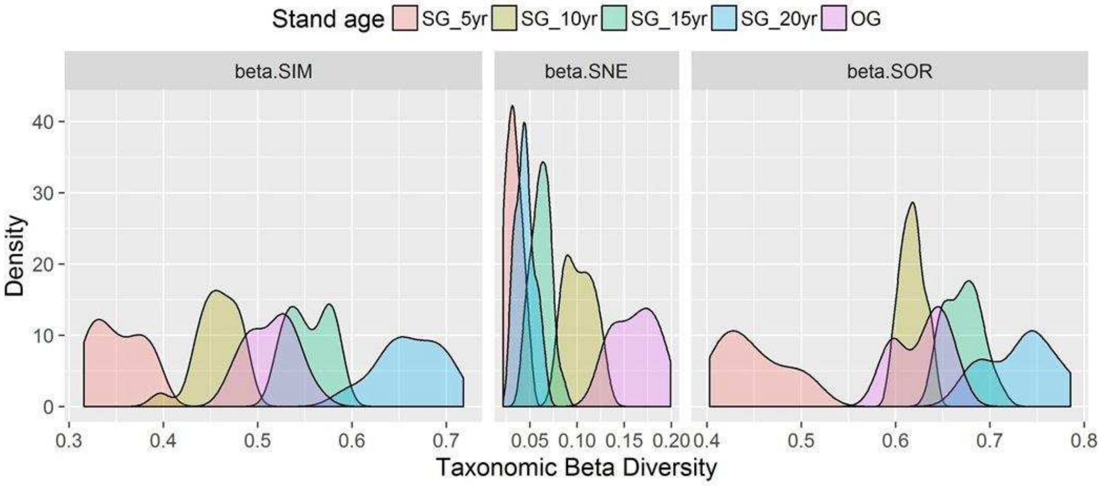


Fig. A.3. Probability density based on a beta-diversity analysis using the kernel smoothing method for the four secondary succession stages (5, 10, 15, and 20 years old) and old growth (OG, 100 years old). The partition of total beta diversity (SOR) into a turnover (SIM) and nestedness (SNE) components are indicated.

CAPITULO III: Ecological patterns and drivers of taxonomic and functional beta diversity during secondary forest succession in the northern Amazon: a temporal and spatial multiscale approach

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Abstract

The Amazon forest is seriously threatened by multiple drivers. However, the importance relative of drivers on the spatial and temporal dissimilarities in tree species composition (*β*-diversity), both taxonomic and functional *β*-diversity, remains poorly understood along succession. Here we examined a large database from 45 plots across four secondary forests and one old-growth forest in the Northern Amazon for to test four alternative hypotheses: 1) the disturbance that follows shifting cultivation can promote the *β*-diversity in secondary forests compared with old-growth forests; 2) the functional *β*-diversity is lower than taxonomic *β*-diversity in old growth forest; 3). Stand age and soil fertility maintain a strong relationship with *β*-diversity; 4) the tree communities having high taxonomic *β*-diversity due to a high taxonomic turnover, and a high functional *β*-diversity can be driven by a high functional turnover if unique species from each community are functionally different during secondary succession. Taxonomic and functional *β*-diversity were examined via novel abundance-based metrics, and considering functional traits related to plant dispersion and growth. Overall, taxonomic and functional β-diversity was consistently greater in initial successional stage among-plots and sites in different successional stages, but old growth forest presented the smallest functional β-diversity. We observed differences in β-diversity components among successional stages and old growth forest. The β-diversity components showed a clear pattern that was higher in the different secondary forest than in the old-growth forest. Soil fertility and stand age explained more variation in taxonomic and functional turnover and β-diversity. The β-diversity explaining more the 70% of the variation in total species richness among sites, probably due to that patches are inserted within a continuous old-growth forest matrix and smaller distance of seed sources for the colonization and establishment of tree species. Thus, functional β-diversity was lower than taxonomic β-diversity, probably due to a lower functional turnover compared with taxonomic turnover.

Keywords: beta diversity; functional traits; functional turnover; secondary forests; taxonomic turnover

1. Introduction

The Amazon basin is one of most extension of continuous tropical forests, harboring about 11% of the global tree species (Cardoso et al., 2017). However, the biodiversity of Amazon old-growth forest is seriously threatened due to land-use changes such as agricultural expansion (Barlow et al., 2016; Lewis et al., 2015). In these emerging forest scenarios under human modification multiple drivers threaten the species richness and composition (Solar et al. 2015; Arroyo-Rodríguez et al. 2013, 2015), and functional diversity of remaining tree communities in tropical forest (Lohbeck et al., 2016; Sfair et al., 2016). These patterns in secondary succession in tropical forests have addressed the analyzing changes in species diversity and composition after shifting cultivation (Chazdon et al., 2014; Guariguata and Ostertag, 2001) based on the chronosequence approach (Chazdon et al., 2007). However, the relative importance of drivers on the spatial and temporal dissimilarities in species composition (β-diversity), both taxonomic and functional β-diversity, remains poorly understood along succession in Amazon forest.

The beta diversity approach has a long history in ecology and can be broadly understood as a measure of the variation in species composition between sites (Tuomisto, 2010; Anderson et al., 2011). The simplest meaning of taxonomic β-diversity, and one of the most frequently used, is the percentage of dissimilarity in species composition between two communities (Koleff *et al*., 2003). Recently, a series of papers brought key conceptual advances for the disentanglement of the patterns underlying pairwise dissimilarity in species composition (Baselga, 2010, 2012; Carvalho *et al*., 2012). Taxonomic β-diversity can indeed be decomposed into taxonomic turnover (i.e. species replacement between communities) and nestedness-resultant components (i.e. those that reflect the difference in the number of species among communities) (Villéger et al. 2013). For instance, a high level of β-diversity can characterize two contrasting situations. It can result from a low proportion of shared species between two communities with a similar number of species, i.e., high replacement rate, but low values for the nestedness-resultant component. In contrast, it can also result from a species richness difference between two communities, when the poorer is a subset of the richer, leading to a low value for turnover but a high value for the nestedness-resultant component (Villéger et al. 2013).

However, it is widely acknowledged that taxonomy is not sufficient to understand the structure of species assemblages (Villéger *et al*., 2008) and their effects on ecosystem functioning (Díaz *et al*., 2007; Mouillot *et al*., 2011) without considering the functional facet of biodiversity (i.e. the diversity of biological strategies, McGill *et al*., 2006). In these sense, by incorporating data on functional traits (measurable aspects of organisms that influence their ecology and performance; McGill et al., 2006), it is possible to gain detailed insight into biodiversity patterns and processes (Fukami et al., 2005; Swenson et al., 2012; Villéger et al., 2012). Thus, many indices of functional diversity have been proposed (Petchey and Gaston, 2006; Mouchet *et al*., 2010), including indices to assess the level of functional dissimilarity among communities (Anderson *et al*., 2006; de Bello *et al*., 2010; Villéger *et al*., 2013). More recently, measures of functional beta diversity and their decomposition into turnover and nestedness components – have been developed (Villéger et al., 2013; Cardoso et al., 2014). Indeed, functional β-diversity is a key facet of biodiversity as it helps disentangle community assembly processes across environmental gradients or spatial scales (Pavoine and Bonsall, 2011; Swenson *et al*., 2011; Münkemüller *et al*., 2012).

In this study, we assessed ecological pattern and drivers of taxonomic and functional beta diversity during secondary succession in the Northern Amazon forest through a temporal and spatial multiscale approach, using forest inventory data from 45 plots across four secondary forests (5, 10, 15, and 20 years old stand after shifting cultivation) and one old-growth forest (> 100 years old). In order to evaluate the ecological patterns of tree beta diversity along forest succession, we asked the following research questions: 1) How do spatial and temporal scales determine changes in partitioning of β-diversity in secondary forests as compared to the old-growth forest? 2) Does taxonomic β-diversity change with functional β-diversity? 3) What is the relative importance of forest stand age and soil fertility on β-diversity, taxonomic and functional? 4) What is the relationship between taxonomic and functional beta diversity along forest succession? Consequently, we hypothesize that: 1) the magnitude of β-diversity decreases with increasing spatial scale and successional stages, both among plots and sites; 2) high environmental heterogeneity during succession promotes a high β-diversity due to a high turnover rate, while it decreases in stable old growth forests; 3) stand age and soil fertility drive taxonomic and functional turnover, and β-diversity along secondary succession; and 4) the relationship between taxonomic and functional β-diversity is determined by changes in species turnover between secondary succession and old growth forest.

Our proposed hypothesis led to the following key predictions: 1) the disturbance that follows shifting cultivation can cause high environmental heterogeneity (which is indirect indicators of niche partitioning), which in turn may promote the β-diversity in secondary forests compared with old-growth forests. This prediction is based on scale dependence of the relative importance of niche partitioning and dispersal limitation at the local scale (i.e. plot and patch scale). Environmental gradients tend to be shorter, thus providing less functional space for the filling of species with different niches. Conversely, moving to a larger spatial scale often results in an increase in environmental heterogeneity and a concomitant increase in among-site compositional dissimilarity (high β-diversity). 2) We predicted that functional β-diversity is lower than taxonomic β-diversity in old growth forest (i.e., the local abiotic environment is relatively constant) due to higher functional redundancy, but the contrary pattern in secondary forests due to high environmental heterogeneity may cause a high taxonomic β-diversity due to a high taxonomic turnover. This difference may be driven by a lower functional turnover compared with a taxonomic turnover while the nestedness-resultant component may be similar for taxonomic and functional β-diversity along forest succession. 3). Stand age and soil fertility may maintain a strong relationship with β-diversity but not with nestedness. 4) We predicted that tree communities having similar species richness but only a few species in common (i.e. high taxonomic β-diversity due to a high taxonomic turnover), a high functional β-diversity can be driven by a high functional turnover if unique species from each community are functionally different during secondary succession, indicating niche differentiation between communities. On the contrary, low functional β-diversity is expected if the species present in the two communities, although different, have the same functional strategies (i.e. functional convergence in old growth forest).

2. Material and methods

2.1. Study area

This study was conducted in a semi-deciduous forest on the Cataniapo river basin belonging to the indigenous communities of Piaroa de Gavilán and Sardi (613020 E, 679290 N, UTM), at the municipality of Atures, Amazon state, Venezuela (Fig. 1B). The study area covers 12 km^2, old-growth forest matrix with embedded secondary forest patches of different ages. The climate in the study area is tropical rainy with a two-month dry season in December and January. Mean annual temperature and mean annual precipitation are/amount 28 °C and 2700 mm, respectively. The predominant soil types are Oxisols (Latosols) and Ultisols (red clay soils), with low cation exchange capacity, low nutrient content and high acidity levels (Villa et al., 2012).

2.2. Forest inventory

With assistance from local farmers and experts, we selected four secondary forest patches at different successional stages: 5, 10, 15, and 20 years of succession and one old-growth forest patch (> 100 years old) in each study site (Fig. 1). All secondary forests were abandoned after a single cycle of traditional shifting cultivation and were left to regenerate naturally. Between January 2009 to December 2012, three plots of 20 x 50 m were established within each patch, totaling 45 plots (Fig. 1C).

In each plot, all trees with diameter at breast height (DBH) ≥ 5 cm were tagged identified to the species level. Collected specimens were identified at the Julian Steyermark herbarium of Puerto Ayacucho (Ministry of the Environment, Amazonas state, Venezuela). The *Angiosperm Phylogeny Group* IV (APG IV, 2016) was used to classify taxa. Overall, 95 tree species belonging to 76 genera and 48 families were sampled across all 45 plots. Most of the species belonged to the Fabaceae (14 species), followed by the Annonaceae (6 species), Lauraceae (5 species), and Lecythidaceae (5 species). The 30 plots from the secondary forests contained 86 species belonging to 45 genera and 38 families; whereas the nine plots from the old-growth forest contained 74 species belonging to 52 genera and 46 families.

2.3. Soil parameter collection

In each plot, we collected composite samples of surface soil (0-20 cm depth) for chemical and physical analysis. Analyses were carried out in the Soil Analysis Laboratory of National Institute of Agricultural Research (Gilbert et al., 2015), following regular protocols (INIA, 2015). The following parameters were assessed: soil organic carbon (C), total N, available P, K, Ca, Mg, Fe, Zn, effective cation exchange capacity (ECEC), exchangeable acidity (H + Al), pH, organic matter (OM), and the soil texture (sand, clay and silt contents).

2.4. Data analysis

2.4.1. Diversity partitioning

We defined alpha-plot diversity as the average number of species per plot in each successional stage and in old growth forest, and alpha-site diversity as the total number of species per site for each successional stage and in old growth forest. To evaluate the relative contribution of the diversity among plots, patches and sites in the regional diversity, we performed an additive diversity partitioning of species richness ($\gamma = \alpha + \beta$), where γ is the total species at landscape scale, α represents the average species within each plot, patch and site, whereas β is the species differentiation among plots, patches and sites (Crist *et al*. 2003). We assessed patterns of taxonomic diversity across successional gradient through partitioned in three spatial scales, i) species average per plot within each site (α-diversity), ii) species turnover average among plots (β_1-diversity), iii) species turnover average among patches (β_2-diversity), iv) average turnover of species among sites (β_3-diversity). We computed diversity values using species richness (Hill number of order 0) which includes the effects on all species irrespective of their frequency (Chao *et al.*, 2014).

For assessing the patterns of tree β-diversity across spatial scales (i.e., among plots, among patches and among sites), we used multiplicative diversity decomposition of effective numbers of species with Hill number of order 0 (Arroyo-Rodríguez et al. 2013; Solar et al. 2015). Then, β-diversity is calculated as ${}^qD\beta = {}^qD\gamma / {}^qD\alpha$, where ${}^qD\gamma$ refers to the observed total (gamma) diversity, and ${}^qD\alpha$ refers to the mean local (alpha) diversity within the study communities. This ${}^qD\beta$ can be interpreted as ‘effective number of completely distinct communities’, as it ranges between 1 (when all communities are identical) and N (i.e. the number of communities; when all communities are completely different from each other) (Jost, 2007). Both alpha and gamma diversities depend on the parameter q (named order q), which determines the sensitivity of the measure to the relative abundances (Jost, 2007; Tuomisto, 2010). To evaluate changes in β-diversity at multiple spatial scales, we considered the following decompositions, from larger to smaller scale: (i) β-diversity among sites: ${}^q\beta_{\text{site}} = {}^q\gamma_{\text{lanscape}} / {}^q\alpha_{\text{site}}$; (ii) β-diversity among patches: ${}^q\beta_{\text{patch}} = {}^q\gamma_{\text{site}} / {}^q\alpha_{\text{patch}}$; and (iii) β-diversity among plots: ${}^q\beta_{\text{plot}} = {}^q\gamma_{\text{patch}} / {}^q\alpha_{\text{plot}}$ (Arroyo-Rodríguez et al. 2013). To assess whether the magnitude of β-diversity differed across spatial scales, we compared the relative compositional dissimilarity between communities using the transformation of beta (${}^qD\beta$) proposed by Jost (2006) for communities with different numbers of samples (e.g., sites: n = 3; patches: n = 5; plots: n = 15): ${}^qDS = 1 - [(1/{}^qD\beta - 1/N)/(1 - 1/N)]$, where N is the number of samples. The value of ${}^qDS$ ranges between 1 (when all the samples are completely distinct) and 0 (when all samples are identical).

2.4.2. Functional beta diversity and multivariate functional space

For most of the tree species, we selected functional traits based on the life history and their relationships with processes and forest structure during succession (Magnago et al., 2014; Meiners et al., 2015; Rozendaal and Chazdon, 2015). We used three categorical traits (fruit dispersal syndrome, fruit type, and regeneration strategy), and two continuous traits (wood density and Dmax). Forest recovery during succession depends on the mechanisms of seed dispersal and colonization (dispersion syndromes, fruit type). For dispersal syndrome, we classified tree species into two categories: non-zoochoric species, which are dispersed abiotically or have mechanisms of self-dispersal, and zoochoric species, whose dispersal is performed by animals (Santo- Silva et al., 2016; Tabarelli and Peres, 2002; Magnago et al. 2014). All fruits were classified into two types: i) Fleshy, when the pericarp is able to accumulate water and organic compounds and ii) dry, when the fruit does not have this capacity (Tabarelli and Peres, 2002; Magnago et al., 2014). For regeneration strategy, we classified species as a pioneer, intermediate, and shade-tolerant species (Rozendaal and Chazdon, 2015; Santo-Silva et al., 2016). Wood density has been used as a functional attribute in previous studies that reflect a trade-off between volumetric growth and survival because of resistance against biophysical hazards (Westoby et al., 2002, Cornelissen et al., 2015; Santo-Silva et al., 2016). We used Neotropical data from the Global Wood Density Database (Chave *et al.*, 2009) to obtain the wood density of each species, using genus or family averages whenever species-level information was not available.

The ‘functional diversity’ of each community was calculated by standardizing trait values and then creating a dissimilarity matrix using Gower’s distance, a metric able to accommodate nominal, ordinal, continuous and missing data (Pavoine *et al*., 2009). For functional composition, the volumes of multivariate trait space shared by two sites and unique to each were used as inputs in the dissimilarity equations (Villéger et al., 2013). We used Principal Coordinates Analysis (PCoA) to generate this multivariate space, where axes are functional traits or synthetic components summarizing functional traits. Species were plotted in this multidimensional functional space according to their respective functional trait values. We calculated a species-by-species' Euclidean distance matrix from scaled and centred trait data. The PCoA was run on this distance matrix and the resulting axes were used as four independent, synthetic traits representing different spectra of tree ecological strategies. The ecological meaning of these axes was interpreted based on the loadings of the raw trait values. Those trait-based principal coordinate scores, along with the species-by-community matrix, were then used to measure the functional diversity of each community, calculated as the ‘minimum convex hull volume’ using the quick hull algorithm (Villéger *et al*., 2008; Villéger et al., 2013).

2.4.3. Decomposition of taxonomic and functional Beta-diversity

The taxonomic beta diversity decomposition proposed by Baselga (2010) and the analogous decomposition functional beta diversity developed by Villéger et al. (2013) was also used. We evaluated the differences of taxonomic and functional compositions among tree communities and sites using three pairwise beta-diversity: i) βsor accounts for the total compositional variation between assemblages (including both turnover and nestedness patterns), ii) βsim captures only compositional changes due to species turnover, and iii) βsne represents the losses from site to site (Baselga et al. 2010; Cardoso et al. 2014). βsne is a resultant dissimilarity and is calculated as the difference between βsor and βsim (Baselga, 2010, 2012). The Sørensen dissimilarity index (β_{sor}), accounts for the total compositional variation between assemblages, including both turnover and nestedness patterns (Eq. 1, 2, 3).

$$\beta sor = \beta \mathrm{sim} + \beta \mathrm{sne} \quad (1)$$

$$\beta sor = \frac{b+c}{2a+b+c} \quad (2)$$

$$\beta sor = \frac{b}{b+a} + (\frac{c-b}{2a+b+c})(\frac{a}{b+a}) \quad (3)$$

where βsor is Sørensen dissimilarity, βsim is Simpson dissimilarity (i.e., turnover component of Sørensen dissimilarity), βsne is the nestedness component of Sørensen dissimilarity, a is the number of species common to both sites; b is the number of species that occur in the first site but not in the second; and c is the number of species that occur in the second site but not in the first (Baselga, 2010, 2012).

2.4.4. Statistical analyses

Prior to statistical analyses, data were tested for normal distribution using Shapiro-Wilk tests and Q-Q plots (Crawley, 2012). We then compared the variation in beta diversity components (βsor, βsim, βsne) among sampled sites with a one-way ANOVA followed by a post hoc Tukey's test (HSD = 0.05) for normally distributed data. For non-normally distributed data, we performed Kruskal-Wallis' test to compare β-diversity of among-plots, patches and sites, followed by Dunn's multiple comparison test (Dinno, 2017). All these statistical analyses were performed using the 'car' and 'dunn.test' packages in R 3.4.2 (Dinno, 2017; Fox et al., 2017). To verify whether space influences simultaneously species composition and successional stages, we performed partial Mantel tests using the 'Mantel test' function on the 'ade4' package (Dray et al., 2017), aiming specifically to assess spatial autocorrelation of the sampling units within each successional stage and the old-growth forest.

Hierarchical diversity partitioning of species richness was partitioned into additive (absolute magnitude of β-diversity) and multiplicative components (pure relational differentiation) (Crist et al. 2003; Jost 2007; Chao et al. 2012), using the *adipart* and *multipart* functions in the 'betapart' package (Baselga, 2017). We generated a null model to evaluate the statistical significance of the observed diversity components in relation to those expected by chance, using 1000 randomization of individuals among samples of all the hierarchical levels (Crist *et al.* 2003). Thus, we calculated the beta diversity index for paired plot among different forest types (secondary and old-growth). β-diversity components were calculated using the function *beta.multi* from the 'betapart' package (Baselga et al., 2017), based on the dataset categorized by successional stage, site, and the relationship between plots.

To quantify functional beta diversity, convex hulls for each tree community in each forest type were used to measure the pairwise functional dissimilarity between communities, likewise using the Jaccard index (Villéger et al., 2008). We tested whether the functional richness of each forest type differs from a random expectation given its taxonomic richness. We thus designed a null model in which the observed number of species in tree assemblage was kept constant, but species identity was randomly chosen among the total pool of species. Then we tested the null hypothesis that the observed values of functional β-diversity (and its two components, βsim and βsne) are not significantly different from a random expectation. Then, we designed a null-model for each pair of tree assemblages which randomly permuted, separately, the identity of the species unique to each assemblage and those of the species shared by the tree assemblages (Villéger et al., 2013). The permutations were repeated 999 times for each pair of assemblages and the simulated values of functional β-diversity (and of its two components) were compared with the corresponding observed values to compute a *p-value* (bilateral test with a confidence level of 5%). To evaluate the relationships between taxonomic and functional beta diversity as well as between their respective components, Mantel permutational tests were used. Partial Mantel tests were also carried out to account for the distance between sites, difference in species richness and the combination of these two variables (Villéger et al., 2013).

We used a generalized linear mixed effects model (GLMMs) to investigate the effect of soil fertility and stand age on β-diversity components assuming Gaussian error distributions. In all models, the identity of the plots in each site was included as a random factor. Soil fertility predictors were determined using an analysis of principal components (PCA) on the correlation matrix, using the ''FactoMineR'' package

(Husson et al., 2017). We included polynomial terms of stand age in order to detect potential humpbacked shape patterns in the relationships between stand age and each of the beta diversity components (Bishop et al. 2015).

To assess the best models, we applied a multi-model inference approach (Burnham and Anderson, 2002) with the ‘dredge’ function from the “MuMIn” package (Barton, 2015), which returns all possible combinations of the explanatory variables included in the global model (Barton, 2015). To determine which of these variables were the most decisive in explaining changes in β-diversity components we used an information theoretical approach based on the Akaike information criterion with a correction for finite sample sizes (AICc) and AIC weights (Burnham and Anderson, 2002). We selected the best model with the lowest AICc, but all models whose difference in AICc with the best model was less than two units are considered equally good (Burnham, Anderson and Huyvaert, 2011). All models were calculated in R using the packages ‘glmer’ (Bates et al. 2014). All ecological and statistical analyses were conducted in R 3.4.2 (R-Core-Team, 2017).

3. Results

3.1. Additive diversity partitioning

Additive diversity partitioning indicated that the total γ-diversity was mainly attributed to β-diversity (Fig. 2). The beta components explained more the 70% of the variation in total species richness among its different sites, distributed in β2 component (between patches, 50.30%) and by β1 component (between plots, 13.6%). Within-plots α-diversity there were significant differences between observed and expected values, representing only 6.6 % of the total richness. However, observed β-diversity between plots and patches of the same site were higher than expected by chance, while observed β-diversity between sites was lower than expected (Fig. 2).

3.2. Taxonomic Beta-diversity among plots, patches and sites

Between plots and sites, β-diversity was greater in initial (5 years) than in further successional stages (10, 15, and 20 years old) or old growth forests (Fig. 3). The latter, presented the smallest β-diversities (Fig. 3). Conversely, we found little difference in site-scale β-diversity among all successional stages and old growth forest (HSD = 10.14, d.f. = 2, P < 0.01, Fig. 3).

3.3. Taxonomic and functional Beta-diversity components along the successional stages

Both components of taxonomic and functional β-diversity were higher in the different secondary forests than in the old-growth forest (Fig. 4). The number of tree species shared among communities was on average half the total number of unique species (Table S.1). Taxonomic β-diversity ranged from 0.60 during early successional stages to 0.40 in old growth forest. Taxonomic and functional turnover as well as β-diversity were higher at 20 years old stands than in further secondary or old growth forest. The taxonomic and functional turnover were higher than nestedness-resultant component (Table S.1).

3.4. Functional Beta diversity and functional space

We observed consistent changes in the functional structure of tree assemblages during succession and in old growth forest (Fig. A.3.). Functional turnover was largely observed through the changes of species with traits indicating dispersal syndromes, wood density and regeneration strategy. Functional nestedness results in extreme trait combinations being lost from the functional space. The first two PCA axes captured c. 80% of the variation present in the functional space of the tree traits (Table 1). Given the loadings of the original traits in the PCA, we interpret axis 1 as a gradient in regeneration strategy (Table 1, Fig. A.3.). The Euclidean distances between species in the three-dimensional functional space obtained using PCoA were strongly correlated with the functional distances computed on species traits using Gower's metric (r = 0.861, $P < 0.001$, Fig. A.2.).

3.5. Effects of stand age and soil fertility on taxonomic and functional Beta-diversity components

In the multi-model comparison applied between sites and forest type, we found that models including single soil fertility and stand age explained more variation in taxonomic and functional turnover and β-diversity (Table 2). According to the best model, stand age was the best predictor for taxonomic β-diversity (GLMM: z = -2.68, p < 0.001), taxonomic turnover (GLMM: z = -1.59, p < 0.001), functional β-diversity (GLMM: z = -4.56, p < 0.001), and functional turnover (GLMM: z = -3.67, p < 0.001) in the study area. Taxonomic and functional turnover and β-diversity declined linearly with increasing soil fertility, whereas that these beta components presented a peak at intermediate stand age before declining for old growth forest, producing a humpbacked shaped relationship (Fig. 5). Functional nestedness marginally declined along stand age.

3.6. Relationships between the taxonomic and functional Beta diversity

Functional β-diversity was significantly correlated with taxonomic β-diversity (r = 0.92, p <0.001; Fig. 6). Functional turnover of taxonomic and functional β-diversity were also strongly correlated (r = 0.89, p < 0.001). In contrast, the functional nestedness-resultant component was almost six times lower than taxonomic nestedness-resultant for secondary forest and tree times for old growth forest (Fig. 6). Taxonomic turnover contributed on average to 80% of taxonomic β-diversity both in secondary and old growth forests (Table S.1.). Also, functional turnover contributed on average to 80% of functional β-diversity only for the secondary forest. However, despite functional turnover in old growth forest was almost six times lower than secondary forest, contributed to only 70 % of functional β-diversity (Table S.1.). When we did a joint analysis between the taxonomic and functional beta diversity components, we observed that functional turnover and functional β-diversity was consistently lower than taxonomic β-diversity in mature forests (Fig. A.4.).

4. Discussion

Our results show ecological patterns and drivers of taxonomic and functional beta diversity during secondary succession in the Northern Amazon forest through a temporal and spatial multiscale approach. Furthermore, analyzing taxonomic and functional β-diversity and their respective components offers a unique opportunity to test the ecological processes during secondary succession. For the first time in a secondary forest mosaic derived from shifting cultivation dynamics in the northern Amazon forest, we reveal the relationship between forest stand age and soil fertility with β-diversity through the analysis of multiple models. Likewise, we demonstrated how community similarity showed marked divergences along the succession (taxonomic and functional β-diversity), indicating that pioneer colonizing species are dominating these secondary forests following a secondary succession, when compared to mature forests with greater richness and dominance of shade-tolerant species with greater basal area. There exists in the literature a large diversity of smaller-scale studies on the taxonomic β-diversity during succession; however, studies conducted in the Amazon analyzing the relationship between taxonomic and functional β-diversity along forest succession in forests through stand age and soil fertility are absent in the literature. Our results represent an important contribution to the establishment of criteria for forest management and conservation in landscapes under human modification of the Amazon.

The total γ-diversity was mainly attributed to β-diversity explaining more the 70% of the variation in total species richness among its different sites. Beta-diversity pattern are determined by two basic processes, the replacement of species and richness difference (Carvalho et al. 2012; Morante-Filho et al., 2016). Species replacement (i.e., turnover) is mainly the consequence of environmental sorting, or spatial and historical constraints (Qian et al. 2006); it is particularly important for species that are strongly associated with their environment such that changes in environmental attributes will result in changes in species composition (Solar et al., 2015; Morante-Filho et al., 2016). These patterns could be reflecting deterministic community-assembly processes. Environmental conditions may selectively filter which species are able to successfully establish and survive at each successional stage. Such filtering would act on the functional trait values of the species. For this case, it would seem that species with extreme trait values are not able to exist at the old-growth forest. For this reason, functional β-diversity is important for disentangle community assembly processes across environmental gradients or spatial scales (Swenson, 2011; Münkemüller *et al*., 2012).

Among-plots and sites β-diversity was consistently greater in initial successional stage than in different successional stages and old growth forest which presented the smallest β-diversity. However, patches β-diversity there are no contrasting differences between successional stages. Thus, we argue that shifting cultivation disturbances generate higher environmental heterogeneity (expressed in resource availability), which in turn promotes species turnover on the landscape. In these sense, because such disturbances are known to have important drivers that threaten plant communities (Laurance et al., 2002; Tabarelli et al. 2008), differences among patches in disturbance regimes can also increase plant β-diversity among patches, particularly in landscapes dominated by edge-affected patches (Arroyo-Rodríguez, et al. 2013). Thus, based on the environmental characteristics of each forest patch, the landscape spatial context surrounding each patch, the life-history traits of the species found in each patch, the land-use history, along with many stochastic events (Chazdon, 2008; Tabarelli et al., 2008), patches located in severely deforested rain forests will most probably exhibit increasing differentiation in ecosystem functioning, as well as in species composition (Arroyo-Rodríguez, et al. 2013). For instance, differences (among patches) in characteristics such as forest dynamics, carbon storage, functional guild composition could gradually accumulate over time, leaving an increasingly pervasive signature of divergence on community composition and functioning (Laurance et al.; 2007).

However, we presume there is a contrasting pattern in our area of study due to the fact that the plots-patches are inserted within a continuous mature-forest matrix, a higher abundance of potential dispersers is likely to occur therein, as is a smaller distance to be covered by seeds for the establishment of tree species and colonization of the landscape (since the mature forest itself, which is the source of seeds, is near the area undergoing succession).

Recent studies have shown that disturbed ecosystems present more related species than undisturbed ones (Verdú and Pausas, 2007; Ding et al., 2011). In this sense, presumably after land use for roving agricultural systems, β-diversity between plots, as well as between spots in the same forest landscape, declines along the succession gradient, from the early stages dominated by generalist species with high (e.g., Rozendaal and Chazdon, 2015), and to a higher degree of equilibrium between generalist and intermediate succession species, to the advanced stages of succession with greater dominance of shadow tolerant species. Therefore, the loss of local diversity could also have a negative impact on the decrease in diversity on a landscape scale when comparing areas of mature forests with areas that have different stages of succession. Differences in β-diversity between plots and sites with the same succession stage are also expected, probably due to the local effect of the spatial heterogeneity of the environment and the disturbances.

Our analyses indicate that the effect of both the stand age as well as soil fertility are determinants in the changes in β-diversity in our study area. However, it was also possible to observe that these effects was significant for both taxonomic and functional β-diversity and turnover, but not for nestedness according to our models. Our results are in agreement with recent research in Amazonian forests, which shows that the effect of stand age on the species composition is shaped by a hierarchy of environmental and anthropogenic drivers (i.e., soil parameters and land-use intensification), where the number of previous swidden-fallow cycles emerged as the main determinant (Jakovac et al., 2016). On the other hand, a previous study observed changes in the soil quality through shifting cultivation intensification (Villa et al. in press). However, our analyses indicated that the independent effects of soil physicochemical parameters on β-diversity could also be used as indicators of reduction of forest recovery or of the levels of forest degradation at a local-scale. This specific approach to how several shifting cultivation affect soil properties and their relation to species diversity and forest structure is still quite limited for the Amazon.

We observed consistent changes in the functional structure of tree assemblages during succession, which functional turnover was largely observed through the changes of species with traits indicating dispersal syndromes, wood density and regeneration strategy. Probably a pattern is maintained where functional β-diversity is random with respect to taxonomic β-diversity, as previously reported (Swenson, 2011; Villéger et al. 2012; Bishop et al 2015). This implies that the traits we investigate have no role in driving the successional patterns of taxonomic β-diversity; thus we suggest that two factors combine to produce this result. First, there are low species turnover during succession than in old-growth forest. Second, the structure of trait space and the species occurrence data (observed species β-diversity) are kept constant during each iteration of the analysis. The combination of these factors produces a sampling effect whereby greater functional volumes are achieved with more species, giving rise to our patterns of functional turnover and nestedness.

Our study demonstrates that functional β-diversity was significantly correlated with taxonomic β-diversity, and functional turnover and functional *β*-diversity was consistently lower than taxonomic β-diversity in old-growth forest. This pattern is consistent with the reports of similar studies carried out in other studies (Villéger et al., 2012, 2013; Pool et al. 2016), but not yet reported for secondary succession of tropical forests. For instance, two communities with few species in common (high taxonomic β-diversity) would show a low functional β-diversity if their respective species are functionally similar. Nevertheless, comparing only taxonomic and functional β-diversity does not unveil the underlying patterns, i.e. replacement of species (or functional strategies) and difference in species (or functional) richness (Villéger et al., 2013). Indeed, as for taxonomic β-diversity, a high level of functional β-diversity can actually result from a high level of functional turnover (i.e. the communities host different functional strategies) or a low level of functional nestedness (i.e. one community hosts a small subset of the diversified functional strategies present in the old growth forest). Therefore, despite the high taxonomic β-diversity, the large overlap between tree assemblages in the functional space explains the low level of functional β-diversity and turnover in old growth forest. Therefore, the frequent species replacements occurring between tree species are probably between species that are functionally redundant, including species with the most extreme trait combinations.

5. Conclusions

This study shows that β-diversity explaining more the 70% of the variation in total species richness among sites, probably due to that patches are inserted within a continuous old-growth forest matrix, a higher abundance of potential dispersers with smaller distance of seed sources for the colonization and establishment of tree species. This ecological context also justifies the high taxonomic turnover observed during the succession. However, community similarity showed marked divergences through the succession (taxonomic and functional β-diversity), indicating that pioneer species are dominating these secondary forests, when compared to old-growth forest with greater richness and dominance of shade-tolerant species. Thus, functional β-diversity was lower than taxonomic β-diversity, probably due to a lower functional turnover compared with taxonomic turnover. However, the nestedness-resultant component was similar for taxonomic and functional β-diversity, probably due to a relatively short distance between the patches and sites. Finally, the original decomposition of functional β-diversity presented above allows the quantification of the respective contributions of functional turnover (i.e. functional space not shared by communities) and functional nestedness-resultant component (i.e. influenced by the difference in the functional space filled by communities) to the functional dissimilarity between communities. However, if there is a functional convergence among old-growth forest or shade tolerant species, the functional divergence among patches during early successional species will be probably lower than the compositional differentiation.

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Table 1. Results of the Principal Components Analysis on functional traits. Percentages of variance explained by each axis, and cumulative percentage of variance (CPV) by groups of successional stages (SG) and old growth forest (OG).

% of variance by stand age	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
SG -5 years	36.92	21.70	18.51	11.41
CPV	36.92	58.62	77.13	88.54
SG-10 years	33.78	22.52	15.15	10.10
CPV	33.78	56.30	71.45	81.55
SG-15 years	32.35	27.23	18.32	12.62
CPV	32.35	59.58	77.90	90.52
SG-20 years	36.59	23.35	16.34	10.21
CPV	36.59	59.94	76.28	86.49
OG-100 years	38.86	24.55	18.58	12.46
CPV	38.86	63.41	81.99	94.45

Table 2. Candidate mixed effect models predicting the species richness with Gaussian error distribution (linear mixed effects model - glmer). Result of information-theoretic – based model selection is indicated. Models having ΔAICc < 2 are presented here.

Response variable	Predictor	AICc	ΔAICc	AICcwt
Beta.SOR	~ Stand age	369.8	0	0.94
	~ Soil fertility	376.2	1.67	0.70
Beta.SIM	~ Stand age	353.12	0	0.94
	~ Soil fertility	363.21	0.81	0.63
Betafunc.SOR	~ Stand age	316.7	0	0.80
	~ Soil fertility	322.2	1.13	0.45
Betafunc.SIM	~ Stand age	325.8	0	0.73
	~ Soil fertility	339.6	1.52	0.34

Abbreviation: The Akaike information criterion corrected for small samples (AICc), difference between one estimated AICc and the lowest AICc the best model (ΔAICc), and model weights (AICcwt).

Figure captions

Fig. 1. Map and design of the study area. Location of study region in the northern Amazon basin (black square), in South America (A). Map of the Amazon region indicating the Cataniapo basin, in northern Amazonas State, Venezuela (B). Map of the Cataniapo basin indicating the location of the study area, between Gavilán and Sardi villages in the Cataniapo basin (C), showing the distribution of secondary forest sites that were sampled (red points). Satellite image of the study area showing some secondary forest patches in Gavilán (D). We stratified the sampling of the five areas patches within each site (E).

Fig. 2. Additive diversity partitioning based on species richness (q =0) into their α and β components along secondary forest succession and in an old-growth forest. The α component represents the mean percent of the number of species per plot, β1 represents species turnover among plots; β2 reflects the species turnover among patches; and β3 species turnover among sites. Observed values were compared statistically with expected values (*P < 0.001). Symbols > or <, represent greater or lower values than expected.

Fig. 3. β-diversity among plots, patches and sites accounting for proxies of species abundance (Hill numbers of order 0). β-diversity was calculated as the multiplicative Whittaker's β. Data are presented as average β-diversity per plots (a) and per patch (b) among sites (a) and among sites within the landscape (c). We used P<0.05 to determine significance and errors bars are standard errors.

Fig. 4. Differences in the taxonomic and functional components of the beta diversity of trees communities along succession and in an old-growth forest. Taxonomic and functional beta-diversity (beta.SOR) and its two components, turnover (beta.SIM) and nestedness-resultant (beta.SNE) are indicated. Different letters indicate significant differences (P < 0.05) among the sampled.

Fig. 5. Relationships between tree beta diversity and stand age, and soil fertility. Solid lines represent fit (predicted) values of the models, and the shaded polygons the 95 % associated with the modeled predictions.

Fig. 6. Relationships between the taxonomic and functional beta diversity of tree communities along succession. Taxonomic and functional beta-diversity (beta.SOR) and its two components, turnover (beta.SIM) and nestedness-resultant (beta.SNE) are indicated. Multiple regressions on distance matrices (MRM) for the statistical

significance were represented. Solid lines represent fit (predicted) values of the models, and the shaded polygons the 95 % associated with the modeled predictions.

Fig. 1

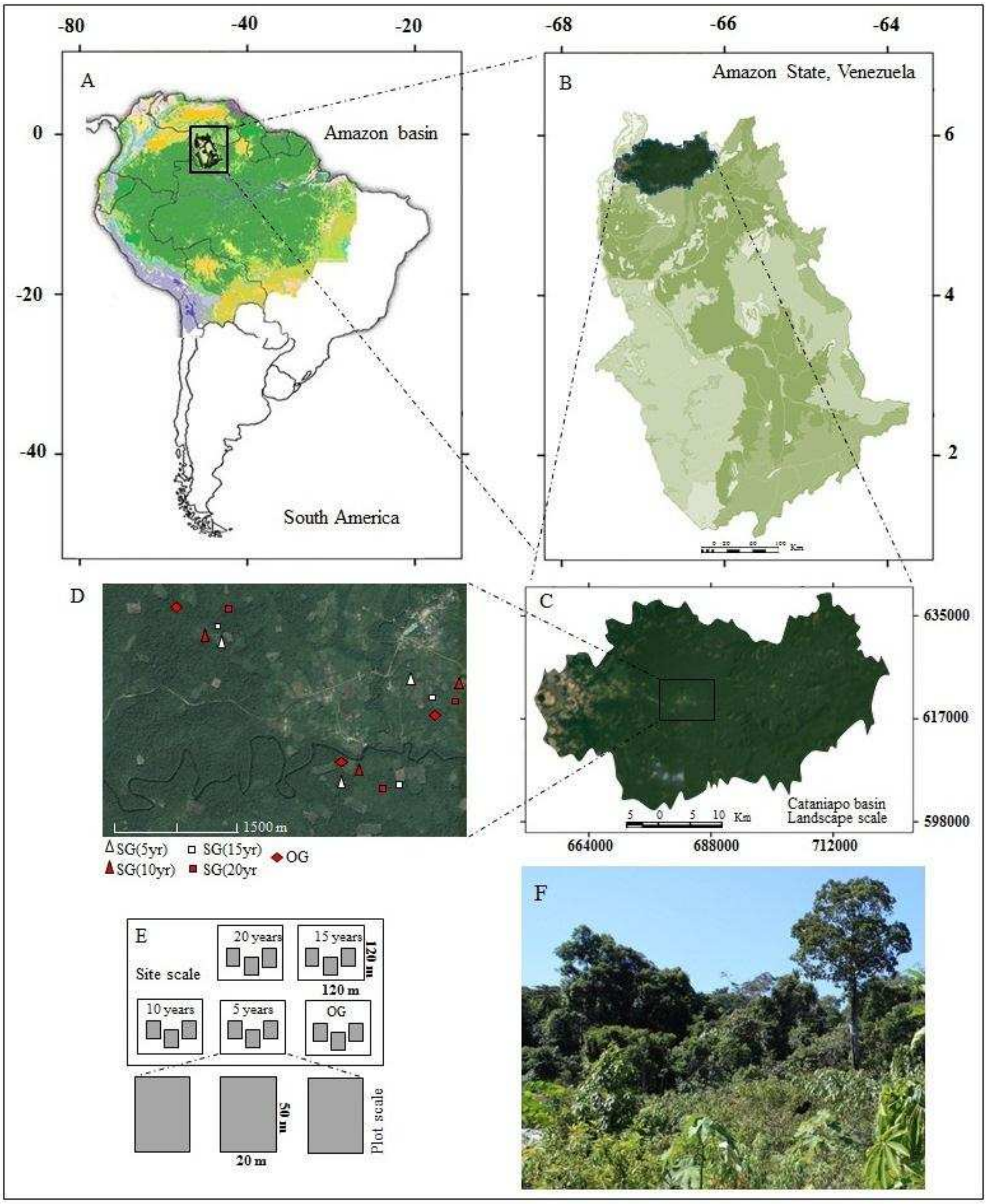
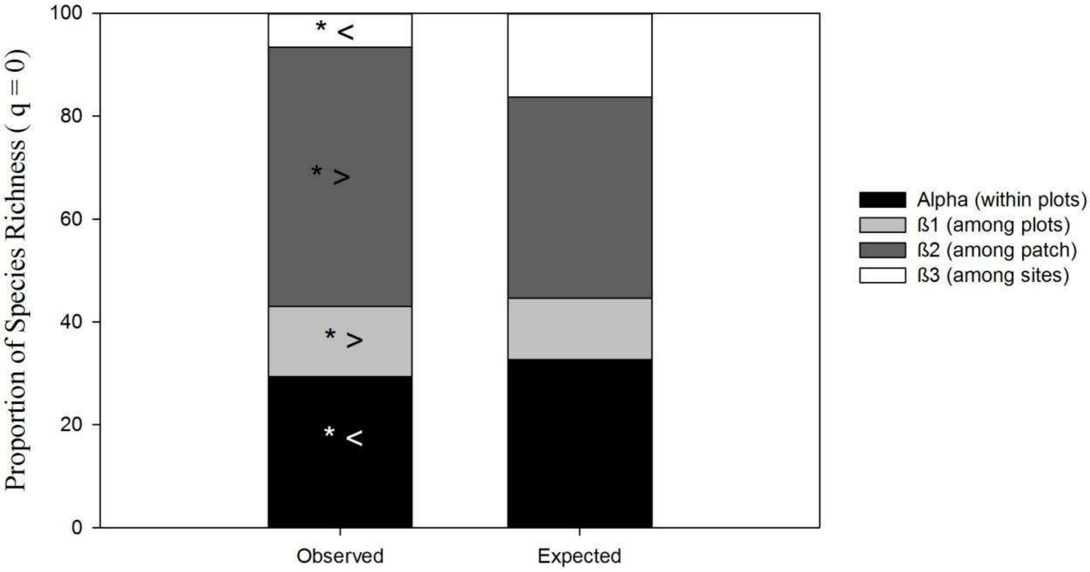
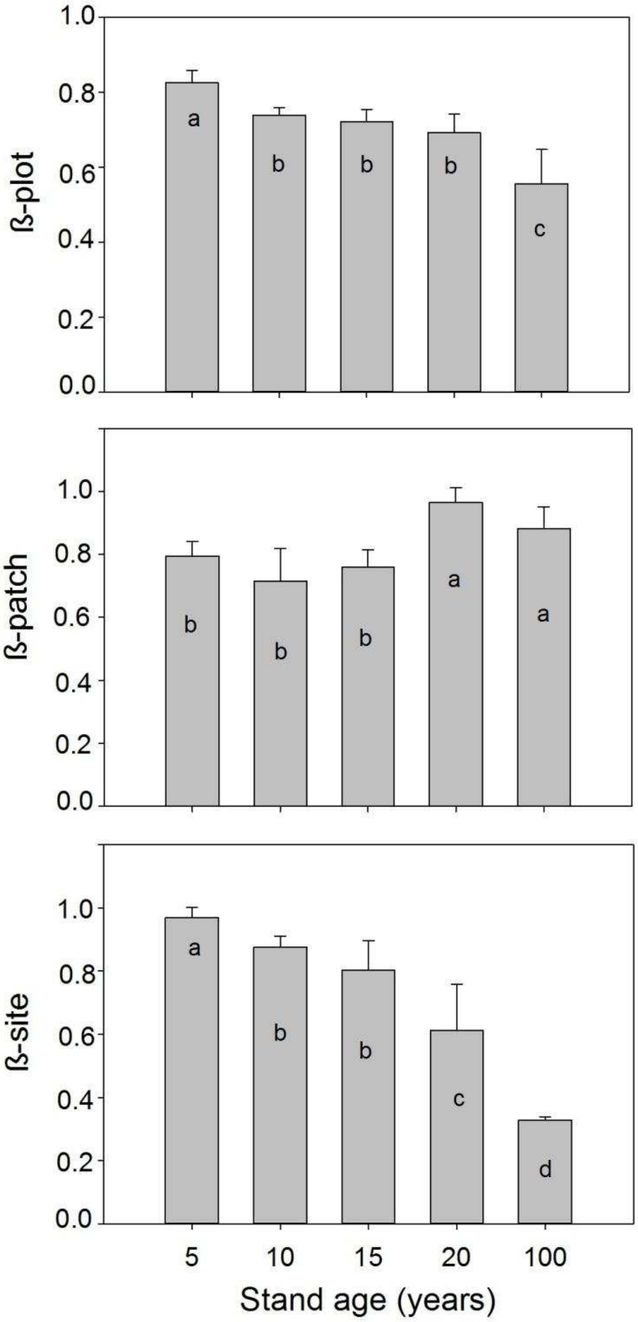

-80
-40
-20
-68
-66
-64
A
Amazon basin
South America
0
-20
-40
B
Amazon State, Venezuela
6
4
2
0 20 60 100 Km
D
1500 m
SG(5yr)
SG(15yr)
OG
SG(10yr)
SG(20yr)
C
Cataniapo basin
Landscape scale
5 0 5 10 Km
635000
617000
598000
664000
688000
712000
E
Site scale
20 years
15 years
120 m
120 m
10 years
5 years
OG
50 m
20 m
Plot scale
F

Fig. 2



Proportion of Species Richness (q = 0)
100
80
60
40
20
0
Observed
Expected
* <
* >
* >
* <
Alpha (within plots)
ß1 (among plots)
ß2 (among patch)
ß3 (among sites)

Fig. 3



ß-plot
1.0
0.8
0.6
0.4
0.2
0.0
a
b
b
b
c
ß-patch
1.0
0.8
0.6
0.4
0.2
0.0
b
b
b
a
a
ß-site
1.0
0.8
0.6
0.4
0.2
0.0
a
b
b
c
d
5
10
15
20
100
Stand age (years)

Fig. 4

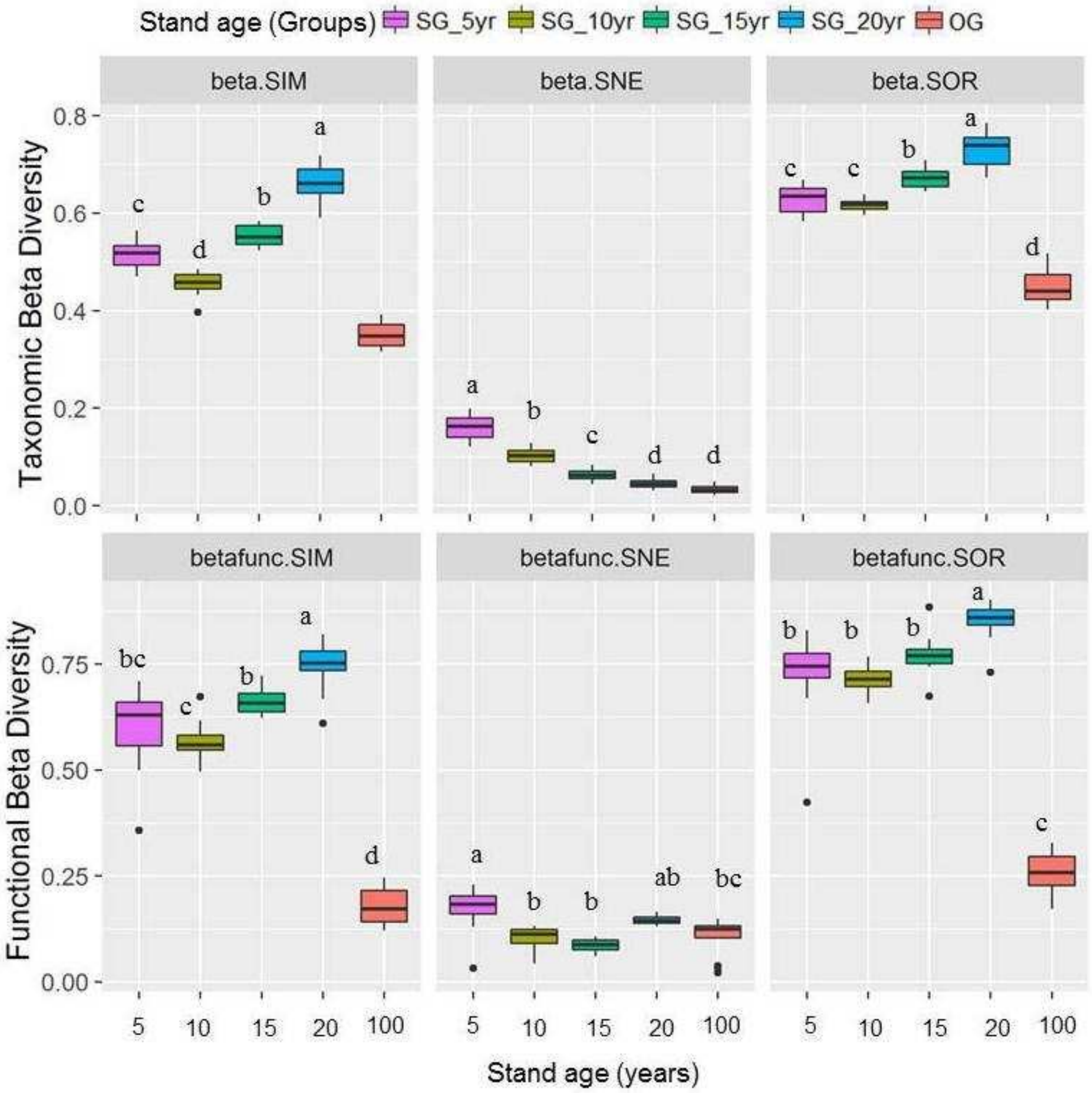

Stand age (Groups)
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
beta.SIM
beta.SNE
beta.SOR
betafunc.SIM
betafunc.SNE
betafunc.SOR
Taxonomic Beta Diversity
Functional Beta Diversity
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
c
d
b
a
a
b
c
d
d
c
c
b
a
d
bc
c
b
a
d
a
b
b
ab
bc
b
b
b
a
c
5
10
15
20
100
Stand age (years)

Fig. 5

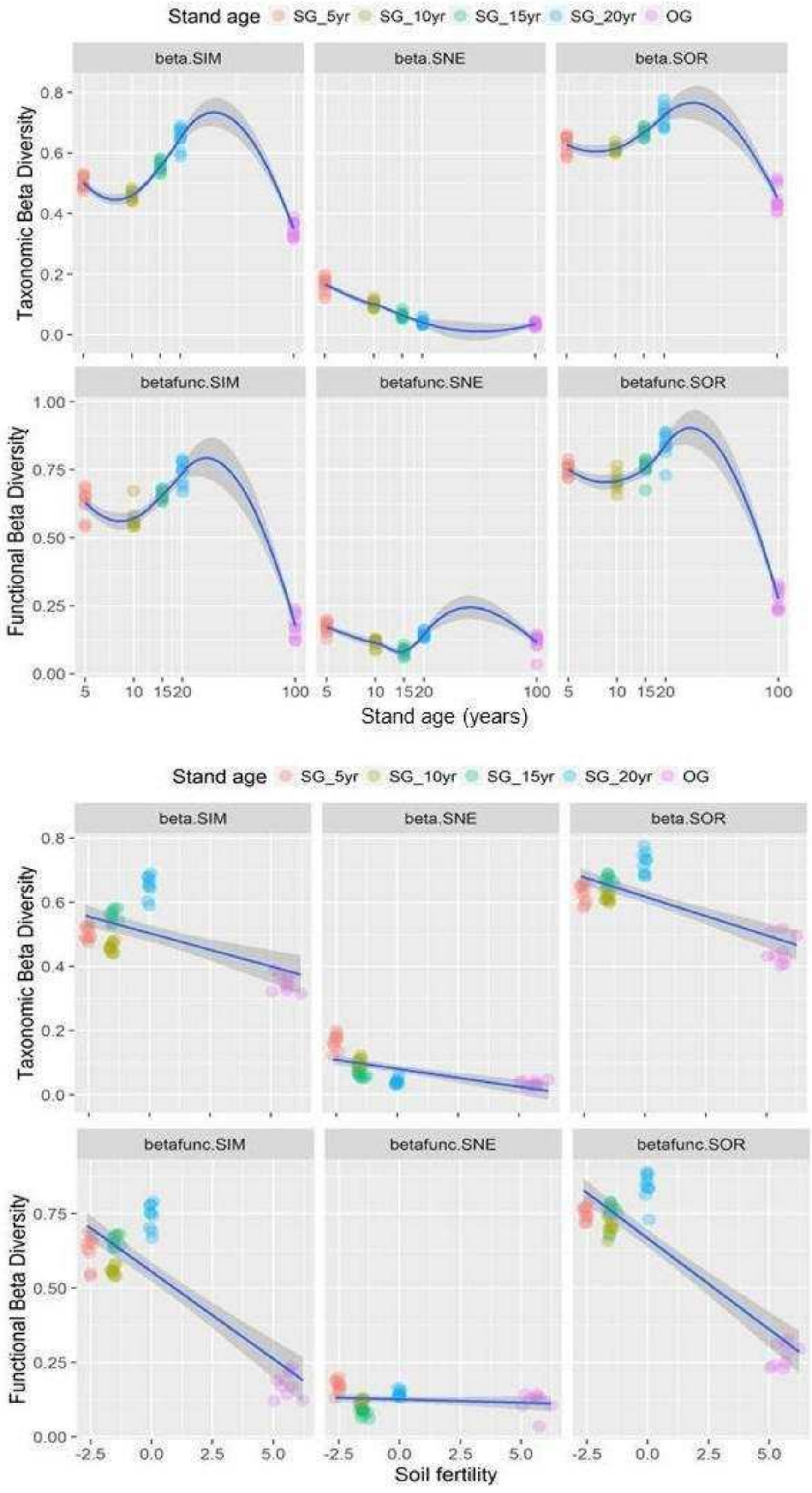
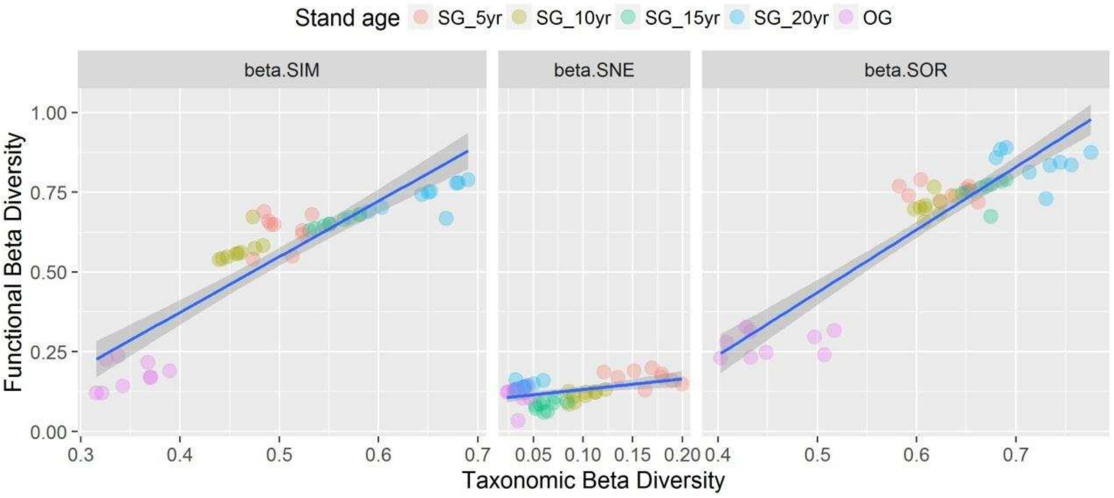

Stand age
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
beta.SIM
beta.SNE
beta.SOR
betafunc.SIM
betafunc.SNE
betafunc.SOR
Taxonomic Beta Diversity
Functional Beta Diversity
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
1.00
5
10
15
20
100
Stand age (years)
Stand age
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
beta.SIM
beta.SNE
beta.SOR
betafunc.SIM
betafunc.SNE
betafunc.SOR
Taxonomic Beta Diversity
Functional Beta Diversity
-2.5
0.0
2.5
5.0
Soil fertility

Fig. 6


Stand age
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
beta.SIM
beta.SNE
beta.SOR
Functional Beta Diversity
1.00
0.75
0.50
0.25
0.00
0.3
0.4
0.5
0.6
0.7
0.05
0.10
0.15
0.20
0.4
0.5
0.6
0.7
Taxonomic Beta Diversity

Appendix A: Supplementary data

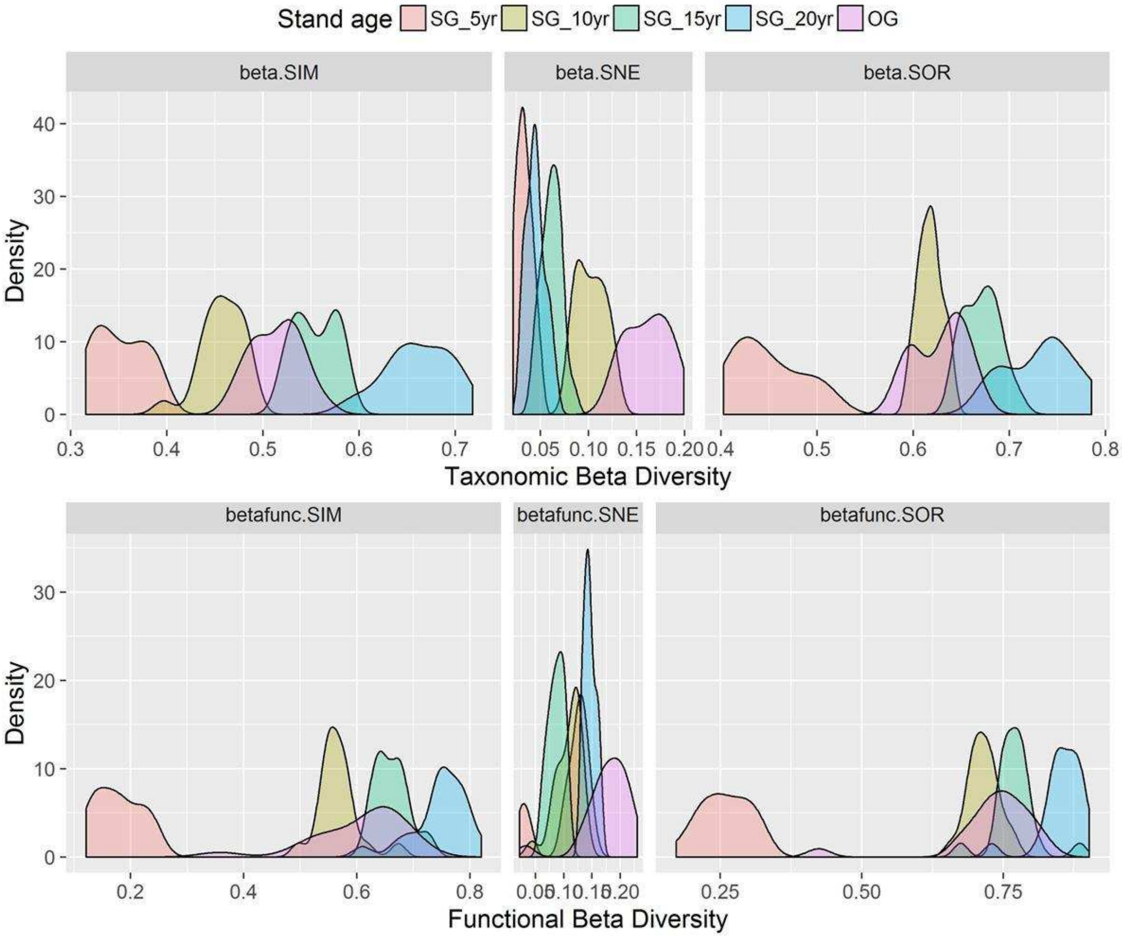


Fig. A.1. Probability density based on a beta-diversity analysis using the kernel smoothing method for the four secondary succession stages (5, 10, 15, and 20 years old) and old growth (OG, 100 years old). The partition of total beta diversity (SOR) into a turnover (SIM) and nestedness (SNE) components are indicated.

Table S.1. Taxonomic and functional beta-diversity (beta.SOR) and its two components, turnover (beta.SIM) and nestedness-resultant (beta.SNE); mean ± standard deviation or the four secondary succession stages (5, 10, 15, and 20 years old) and old growth (OG, 100 years old).

Stand age	**Taxonomic**			**Functional**		
	beta.SOR	beta.SIM	beta.SNE	beta.SOR	beta.SIM	beta.SNE
SG_5yr	0.62 ± 0.04	0.51 ± 0.03	0.11 ± 0.03	0.73 ± 0.08	0.60 ± 0.08	0.13 ± 0.02
SG_10yr	0.61 ± 0.03	0.45 ± 0.02	0.16 ± 0.05	0.71 ± 0.02	0.57 ± 0.04	0.14 ± 0.02
SG_15yr	0.67 ± 0.07	0.55 ± 0.02	0.12 ± 0.02	0.77 ± 0.03	0.66 ± 0.04	0.11 ± 0.03
SG_20yr	0.73 ± 0.03	0.66 ± 0.03	0.07 ± 0.02	0.85 ± 0.03	0.74 ± 0.03	0.11 ± 0.02
OG	0.41 ± 0.05	0.35 ± 0.04	0.06 ± 0.01	0.25 ± 0.05	0.17 ± 0.04	0.08 ± 0.02

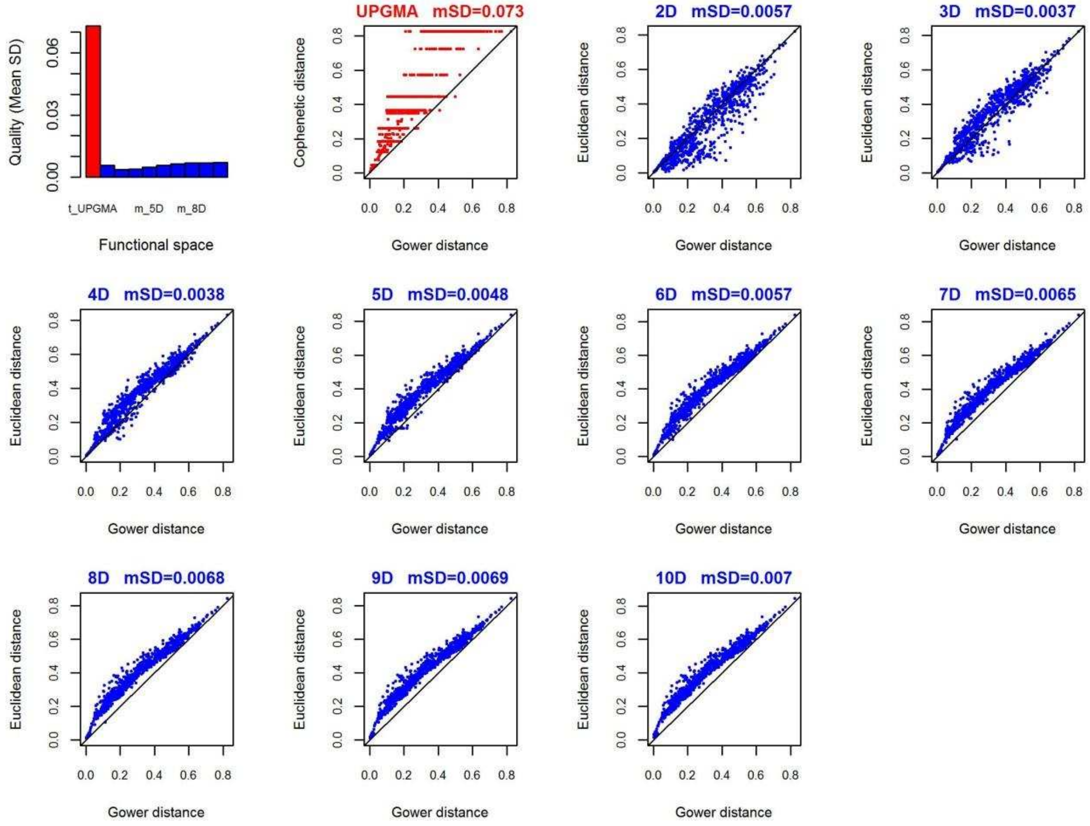


Fig. A.2. Relationships between Euclidean and Gower's distance computing all functional spaces based on PCoA (up to 10 axes). Mean Squared-Deviation of 0.0029 means that average deviation between Euclidean distance and Gower's distance is of (0.0029)^0.5=0.054, so it can be seen as an average error of 5%.

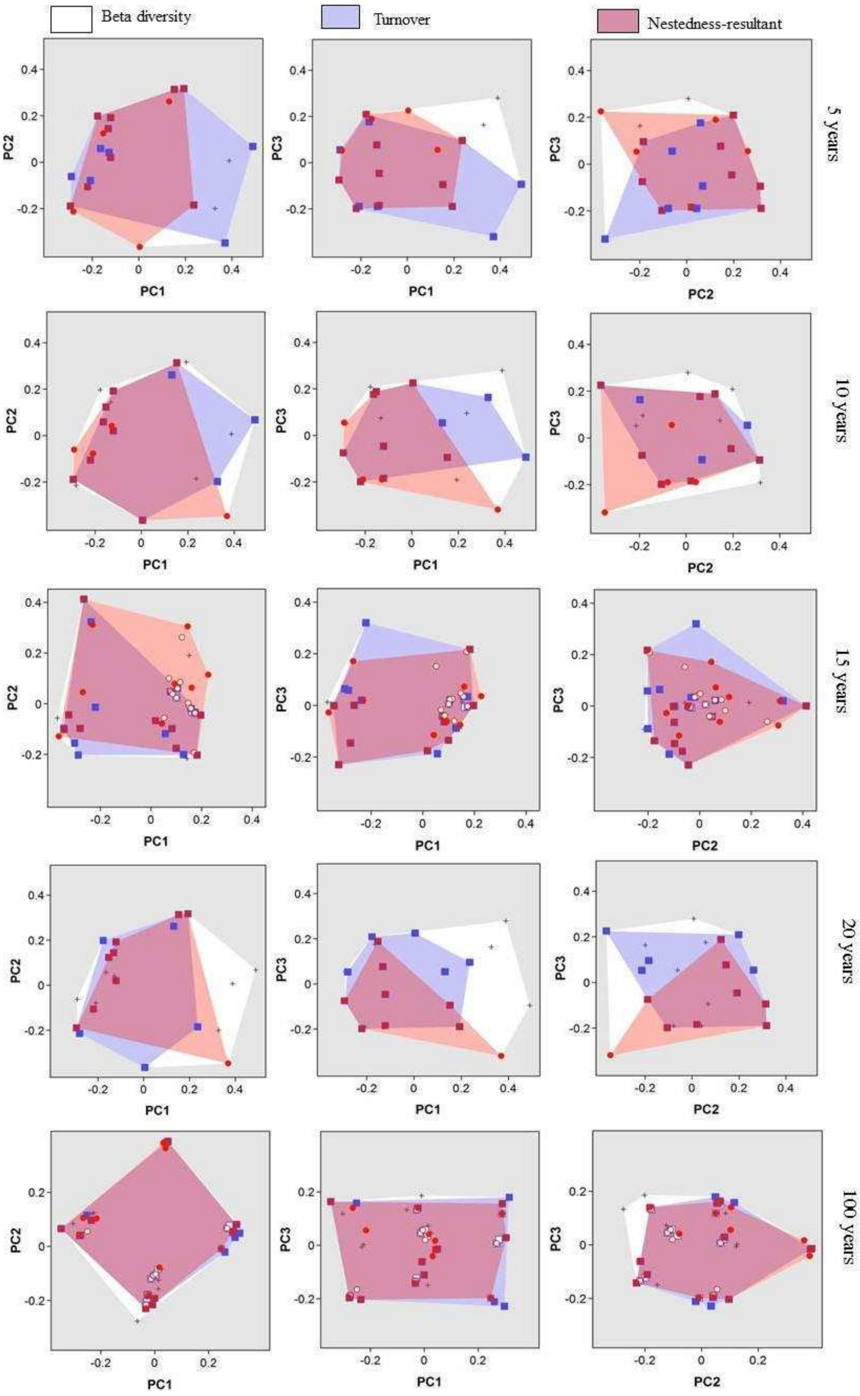


Fig. A.3. Multidimensional functional beta diversity indices represented in Components Analysis (PC) on functional traits and occurrences from species weights. The indices computation for all pairs of assemblages and plot only on 3 first axes by groups of successional stages (5, 10, 15, 20 years old) and old growth forest (100 years old). Functional beta diversity is illustrated by the white polygon. The coloured polygons within it show the Beta functional diversity components (turnover and nestedness) of the most abundant tree species.

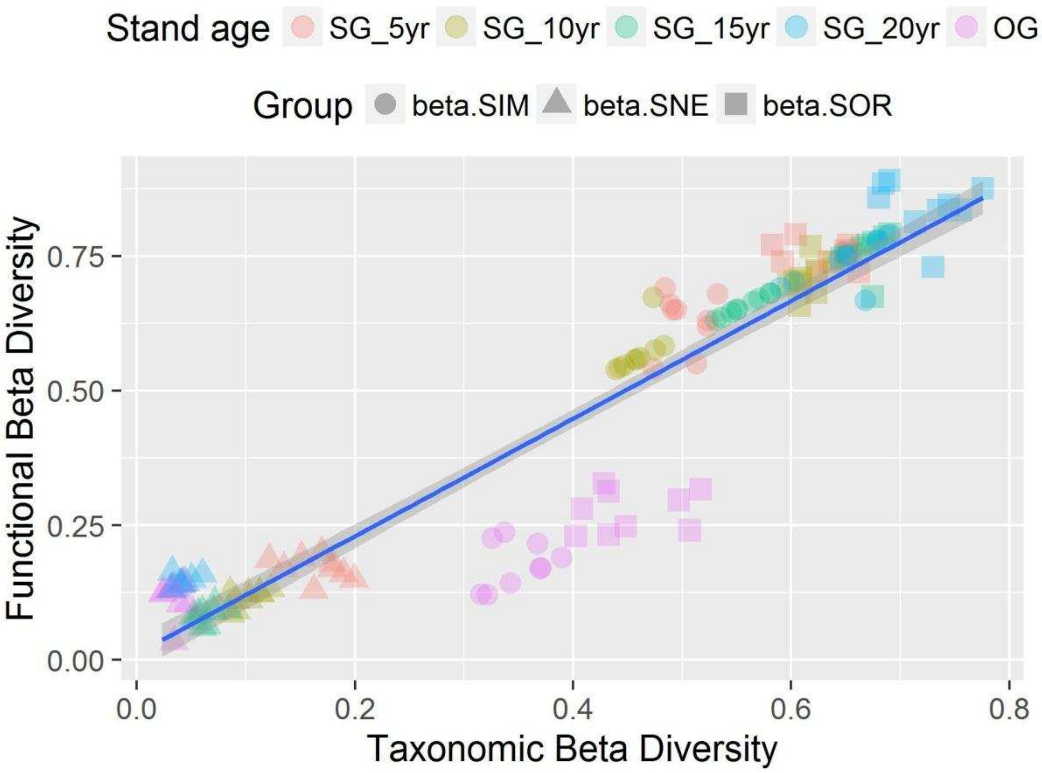


Fig. A.4. Relationships between the taxonomic and functional beta diversity of trees communities along succession (5-20 years) and old-growth forest (OG). Taxonomic and functional beta-diversity (beta.SOR) and its two components, turnover (beta.SIM) and nestedness-resultant (beta.SNE) are indicated. Solid lines represent fit (predicted) values of the models and the shaded polygons the 95 % associated with the modeled predictions.

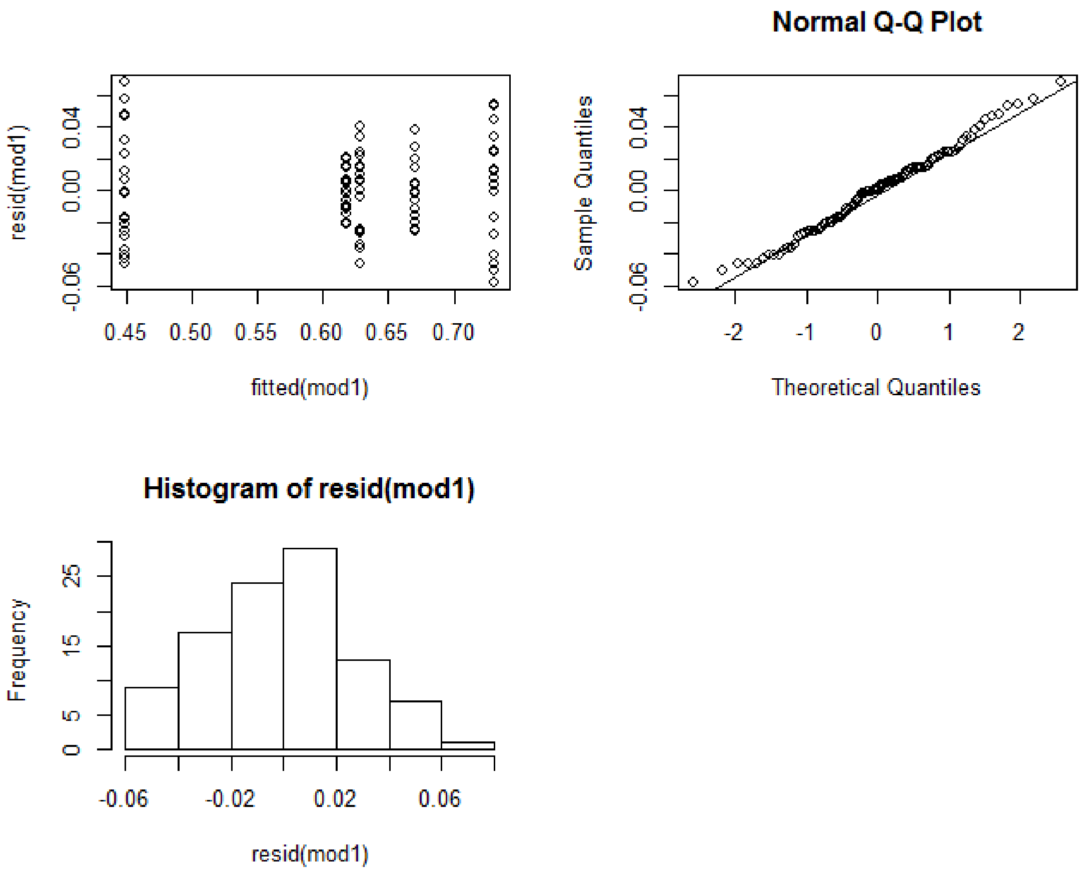


Fig. A.5. Analysis of residuals with Q-Q plots as a premise to select generalized mixed linear models (GLMM).

CAPITULO IV: Tempo de sucessão e solos determina estoque de biomassa acima do solo através da diversidade e dominância funcional em uma floresta Amazônica

Proposto para Ecological Applications

Resumo

Florestas tropicais estão fortemente afetadas pelos disturbios antropogênicos com impactos negativos sobre a relação biodiversidade e funcionamento ecossistêmico (i.e. estocagem de biomassa). Por este motivo, é necessario elucidar processos subjacentes modelados pela diversidade e composiçao funcional sobre a biomassa acima do solo para mehorar criterios de manejo e conservação. Nós hipotetizamos que o incremento da biomassa acima do solo é promovido pelos efeitos simultâneos do tempo de sucessão e qualidade do solo por meio da diversidade funcional (FD), relacionada com a hipótese de complementariedade de nicho (NCH), e média ponderada da comunidade dos valores dos traços funcionais (CWM), relacionada com a hipótese de razão de massa (MRH) nas comunidades de floresta secundaria tropical. Avaliamos diferentes modelos de equação estrutural para determinar efeitos direitos e indiretos do tempo de sucessão, solos e de efeito residuais de FD e CWM sobre biomassa acima do solo através de inventário florestal de 45 parcelas em quatro florestas secundárias com diferentes estagios de sucessão e uma floresta madura no norte da região Amazonas. O modelo MRH representou 84, 16, e 10% da variação na biomassa aérea, CWM do diâmetro do caule e CWM da densidade da madeira, respectivamente. Por outro lado, o modelo NCH explicou 80, 73, 72 e 59% de variação na biomassa aérea, riqueza funcional, equabilidade funcional e divergência funcional, respectivamente. Nossos resultados demonstram as relações significativas de modeladores ambientais, diversidade e dominância funcional, sobre a estocagem de biomassa. Os modelos testados sobre dominância funcional (CWM) e diversidade funcional (FD), permitiram explicar variações na biomassa acima do solo de forma individual. No modelo integral (RMH + NCH) o CWM da densidade da madeira e diâmetro do caule são bons preditores da biomassa acima do solo, corroborando as hipóteses de razão de biomassa como principal modelador deste funcionamento ecossistêmico de uma floresta semidecidual.

Palavras chave: biodiversidade-função ecossistêmica, diversidade de traços funcionais, complementariedade de nicho, média ponderada da comunidade, razão de massa.

1. Introdução

Suficientes evidências demostram que existe uma relação positiva entre a biodiversidade e o funcionamento do ecossistema (BEF) nas florestas tropicais (Poorter et al., 2017). A relação BEF é muito importante para entender como a diversidade de espécies afeta a dinâmica de produção e armazenamento de biomassa acima do solo (e.g., Chisholm et al., 2013; Poorter et al., 2015) e, mais recentemente, foi utilizada no estudo de áreas durante a sucessão secundaria em paisagens florestais sob modificação humana (Lohbeck et al, 2015; de Ávila et al., 2018). Assim, deve-se notar que a maioria dos estudos BEF em floresta tropicais tem sido desenvolvidos para analisar a produtividade e estocagem de biomassa acima do solo (Lasky et al., 2014), pois, fazem parte dos componentes mais importantes para o armazenamento de carbono e equilíbrio global com a atmosfera (e.g., Brienem et al., 2015). Além disso, novas pesquisas têm demostrado que os traços funcionais das plantas também permitem explicar BEF, analisando seus efeitos diretos ou indireitos sobre a estruturação das comunidades e funcionamento ecossistemico de floresta tropicais (e.g., Lohbeck et al, 2015; van der Sande et al., 2017; de Avila et al., 2018). No entanto, ainda existem limitações para entender como a composição e diversidade de traços funcionais associados a modeladores ambientais, como fertilidade do solo, influenciam simultaneamente a biomassa acima do solo durante a sucessão secundaria de florestas tropicais.

Existem duas importantes hipóteses que permitem explicar parcialmente como os traços funcinais das especies dentro das comunidades vegetais podem modelar diferentes processos ecossistêmicos simultaneamente, as hipóteses razão de massa (Grime, 1998) e complementaridade de nicho (Tilman *et al*. 1997). A hipotese de razão de massa (MRH, *Mass ratio hypothesis*) postula que os processos ecosistemicos são conduzidos pelos traços funcionais das especies mais abundantes das comunidades (Grime, 1998). Assim, existem importantes evidencias que suportam esta hipótese onde traços conservativos (i.e. traços do caule) das espécies mais dominantes representam fortes modeladores da estocagem de biomassa e carbono (Finegan et al., 2015; Prado-Junior et al., 2016), enquanto traços Traços ligados à aquisição de recursos (i.e., traços foliares) são importantes para o incremento de biomassa e sequestro de carbono (Poorter and Bongers, 2006; Finegan et al., 2015). A hipótese de complementaridade de nicho (NCH, *Niche complementarity hypothesis*) propõe que a amplitude de traços funcionais de uma comunidade afeta positivamente o funcionamento do ecossistema mediante a utilização complementar de recursos (Tilman et al., 1997; Tilman et al., 2014). A diversidade funcional pode ser quantificada através da amplitude de valores dos traços funcionais ponderado pela abundancia relativa das espécies dentro do espaço multidimensional do nicho (Petchey and Gaston, 2006; Villéger et al., 2008). NCH explica que diferentes traços funcionais podem ter a mesma importância relativa através de efeitos simultâneos sobre uma função ecossistêmica (Laughlin et al., 2014). Portanto, a teoria postula que o incremento da biomassa (estocagem e produtividade) esta positivamente correlacionada com o incremento da diversidade devido ao uso diferencial de recursos ou complementariedade do nicho (Loreau et al., 2002; Cardinale et al., 2011). Essas hipóteses tem sido utilizadas de forma complementar para explicar o funcionamento ecossistêmico de floresta tropicais (e.g., Finegan et al. 2015; Prado-Junior et al. 2016) e durante a sucessão secundaria (e.g., Lohbeck et al, 2015, 2016).

A importancia do estudo da sucessão secundaria de florestas tropicais com esta abordagem baseada na relação de traços funcionais e condições ambientais é que tem permitido elucidar padrões emergentes dos processos ecossistêmicos, principalmente da produção e estocagem de biomassa (e.g., Poorter et al., 2017). Assim, a divegência funcional (FD, relacionada com a complementariedade de nicho) e média ponderada da comunidade (CWM, relacionado com a razão de massa) são duas metricas independentes de diversidade mais ussadas para testar efeitos sobre a biomassa acima do solo (Díazl et al., 2007; Lohbeck et al, 2016; Ali et al., 2017). Neste sentido, tem incrementado as evidencias de que a dominancia funcional (e.i., CWM), muito além da diversidade de traços funcionais (e.i., FD) afeita fortemente à produção de biomassa em florestas tropicais (Becknell and Powers, 2014; Finegan et al. 2015; Lohbeck et al, 2016). Além disso, a relação de biomassa, e CWM e FD dos traços funcionais das plantas estão ao mesmo tempo influenciados por o tempo de sucessão (Becknell and Powers, 2014; Zhang and Chen, 2015), e fertilidade do solo (e.g., van der Sande et al., 2017). O efeito simultaneo desses dois modeladores, tempo de sucessão e fertilidade do solo, e sua relação com a diversidade e dominância funcional durante a sucessão ainda é pouco conhecido.

Por outro lado, a sucessão das florestas tropicais não só dependem dos traços funcionais (i.e., WCM ou FD) diretamente ligados com a produtividade e estocagem de biomassa (i.e., densidade da madeira, diâmetro das árvores), mas também depende de diferentes traços funcionais associados com os mecanismos de dispersão de sementes, colonização e estratégias de crescimento das árvores, que podem ter efeitos indiretos sobre a produção de biomassa (Westoby et al. 2002; Wright et al., 2004; Chave et al., 2009; Kooyman et al., 2012; Magnago et al., 2014). Por outro lado, padrões opostos na relação entre biomassa e CWM ou FD dos traços funcionais em comunidades florestais pode estar associado com a fraca relação entre traços individuias e amplas estrategias funcionais das plantas, principalmente os *trade-offs* entre o ‘rapido crescimento e baixo estaocagem de biomassa’ e “lento crescimento e maior estocagem de biomassa’ como tem sido reportado pelas varições do espectro económico dos traços funcionais ao longo de gradientes ambientais, como por exemplo, a densidade da madeira das árvores (Wright et al., 2004; Chave et al., 2009). Por este motivo, a relação de traços funcionais e biomassa acima do solo depende diretamente do que tipo de traço funcional que está sendo mensurado, pois, porque estratégias funcionais das árvores podem mudar de aquisitivos a conservativos ao longo da sucessão (Lasky et al., 2014; Lohbeck et al., 2015).

Por este motivo, neste estudo avaliamos os efeitos do tempo de sucessão e qualidade do solo (fertilidade e textura) sobre a estocagem de biomassa acima do solo através da diversidade funcional (NCH) e dominância funcional (MRH) numa floresta Amazônica. Neste estudo avaliamos os efeitos individuais e conjuntos da diversidade e dominância dos traços funcionais sobre a biomassa acima do solo, depois de considerar simultaneamente os efeitos do tempo de sucessão e qualidade do solo. Assim, foi possível avaliar os efeitos simultâneos das hipóteses de razão de massa e complementariedade do nicho como mecanismos complementares na estrutura funcional das comunidades de árvores e seu impacto sobre a relação biodiversidade-função ecossistêmica. Apresentamos dados de inventário florestal de 45 parcelas em quatro florestas secundárias (5, 10, 15 e 20 anos após de um sistema agricola itenerante) e uma floresta de crescimento antigo (> 100 anos). Selecionamos traços funcionais baseados na história da vida das espécies e suas relações com processos associados com a sucessão secundartia e estocagem de biomassa (Magnago et al., 2014; Meiners et al., 2015; Rozendaal and Chazdon, 2015).

Nesse estudo propomos responder três perguntas principais: 1) O tempo de sucessão e parâmetros do solo determinam variações na biomassa acima do solo através de variações da diversidade e dominância funcional? 2) Qual é a contribuição relativa da diversidade e dominância dos traços funcionais para explicar a variação da biomassa acima do solo? 3) Qual é o efeito relativo dos diferentes preditores sobre a biomassa acima do solo, depois de analisar o efeito direito do tempo de sucessão e parâmetros do solo sobre cada preditor? Assim, propomos como hipóteses que a biomassa cima do solo incrementa com o tempo de sucessão e qualidade do solo, e que a variação da biomassa pode ser explicada de forma individual (Fig.1A e 1B), ou conjunta (Fig. 1C), pelos traços funcionais das espécies através da diversidade funcional (FD) e dominância funcional (CWM) nas comunidades de floresta secundária. Finalmente, estabelecemos como principal predição que AGB terá uma forte relação com dominância funcional pela importância relativa dos traços conservativos de caule (densidade da madeira, diâmetro do caule), e comparação à divergência funcional.

2. Métodos

2.1. Área de estudo

Este estudo foi realizado em uma floresta semi-decídua da bacia do rio Cataniapo, nas proximidades das comunidades indígenas de Piaroa de Gavilán e Sardi (5 ° 32'28 S, 67 ° 24'13 E), no município de Atures, estado do Amazonas, Venezuela. Ambas as comunidades pertencem ao grupo étnico Piaroa estabelecido há 60 anos na área e mantendo sistemas agrícolas intinerantes de corte e queima (coivaras) baseados principalmente no cultivo da mandioca (*Manihot esculenta* Crantz) (Villa et al., 2012). O clima da área de estudo corresponde a um sistema tropical chuvoso, com média de temperatura próxima de 28°C e de precipitação de 2.700 mm, com uma estação seca de dois meses entre dezembro e janeiro.. Os tipos predominantes de solo são caracterizados por Latossolos e Argissolos com baixa capacidade de troca de catiônica e baixo conteúdo de nutrientes e altos níveis de acidez (Villa et al., 2012).

2.2. Desenho experimental e amostragem da vegetação

Selecionamos três locais dentro de uma área de 12 km^2 entre Piaroa de Gavilán e Sardi, onde manchas de floresta secundária com diferentes estágios de sucessão natural após um ciclo de coivara estão inseridos em uma matriz de floresta madura. Os locais de amostragem foram sistematicamente selecionados de acordo com seus estágios de sucessão, sendo identificados com a assistência de agricultores locais. Um total de 45 parcelas (20 x 50 m = 1000 m^2, cada) foram estabelecidas de janeiro de 2009 até dezembro de 2012. Em cada local, selecionamos quatro florestas secundárias com diferentes estágios sucessionais: 5, 10, 15 e 20 anos; e uma floresta de crescimento antigo (> 100 anos) (Fig. 1D). Em cada local, foram estabelecidas três subparcelas dentro de cada floresta secundária, bem como dentro da floresta de crescimento antigo.

Em cada parcela, todas as árvores com diâmetro na altura do peito (DBH) ≥ 5 cm foram identificadas ao nível da espécie. Foram identificados espécimes no herbário Julian Steyermark de Puerto Ayacucho (Ministério do Meio Ambiente, estado do Amazonas, Venezuela). As espécies foram classificadas de afor com o *Angiosperm Phylogeny Group* IV (APG IV, 2016). No geral, 95 espécies arbóreas pertencentes a 76 gêneros e 48 famílias foram amostradas em todas as 45 parcelas. A maioria das espécies pertencia às Fabaceae (14 espécies), seguido das Annonaceae (6 espécies), Lauraceae (5 espécies) e Lecythidaceae (5 espécies). As 30 parcelas das florestas secundárias continham 86 espécies pertencentes a 45 gêneros e 38 famílias, enquanto as nove parcelas da floresta de crescimento antigo continham 74 espécies pertencentes a 52 gêneros e 46 famílias.

2.3. Estimação de biomassa acima do solo (AGB)

O AGB foi calculado usando a equação alométrica geral proposta por Chave et al. (2014), com base no DBH (cm) e densidade da madeira (ρ, g cm^{-3}). Utilizamos dados neotropicais do *Global Wood Density Database* (Chave et al., 2009) para obter a densidade da madeira de cada espécie, usando médias de gênero ou família sempre que a informação no nível de espécie não estava disponível. O AGB foi calculado da seguinte formula:

$$AGB = 0.0673\,(\rho\ \times DBH^2 \times\ H)^{0.976}$$

O AGB total por parcela foi a soma dos AGB de todas as árvores com DBH ≥ 5 cm, que foi então convertido em megagramas por hectare (Mg ha^{-1}) (Ali et al., 2016). A biomassa no nível de espécie foi calculada como a soma da biomassa de todos os caules de uma espécie.

2.3. Amostragem de parâmetros físico químicos do solo

Para medir as propriedades físico-químicas do solo para cada parcela, foram coletadas amostras compostas da superfície do solo (0-10 cm de profundidade). As análises foram realizadas no Laboratório de Análise do Solo do Instituto Nacional de Pesquisas Agrícolas (Gilabert et al., 2015), seguindo protocolos regulares. Foram avaliados os seguintes parâmetros: carbono orgânico do solo (C), N total, P, K, Ca, Mg, Fe, Zn, capacidade de troca catiônica efetiva (CEC), acidez intercambiável (H + Al), pH, matéria orgânica (OM), e a textura do solo (areia, argila e silte).

2.4. Traços funcionais das árvores

Selecionamos diferentes tipos de traços funcionais baseados na história da vida das espécies de árvores relacionados com processos de regeneração durante a sucessão florestal (Magnago et al., 2014; Meiners et al., 2015; Rozendaal and Chazdon, 2015). Dentro desses tipos de traços funcionais ligados à sucessão secundária, utilizamos três traços categóricos (síndrome de dispersão de frutos, tipo de fruta e estratégia de regeneração das árvores) e dois traços contínuos (densidade de madeira e diâmetro das árvores como *proxy* da altura). A recuperação florestal durante a sucessão depende dos mecanismos de dispersão e colonização da semente (síndromes de dispersão, tipo de fruta). Para a síndrome de dispersão, classificamos as árvores em espécies não zoocóricas, que são dispersas abioticamente ou possuem mecanismos de auto-dispersão e espécies zoocóricas, cuja dispersão é realizada por animais. Esses critérios foram previamente adotados em outros estudos (Santo-Silva et al., 2016, Tabarelli and Peres, 2002; Magnago et al., 2014). Todas as frutas foram classificadas em dois tipos: i) Carnoso, quando o pericarpo é capaz de acumular água e compostos orgânicos e ii) seco, quando a fruta não possui essas características (Tabarelli and Peres, 2002; Magnago et al., 2014). Para a estratégia de regeneração, classificamos espécies como espécies pioneiras, intermediárias e tolerantes à sombra (Rozendaal and Chazdon, 2015; Santo-Silva et al., 2016). A densidade da madeira tem sido usada como um atributo funcional em estudos anteriores que mostram um *trade-off* entre crescimento volumétrico e sobrevivência devido à resistência contra os riscos biofísicos (Westoby et al., 2002; Cornelissen et al., 2003; Santo-Silva et al., 2016).

2.6. Quantificação das métricas de diversidade funcional

A média ponderada da comunidade (CWM) dos traços funcionais e índices de diversidade funcional (FD) foram calculados para cada parcela das florestas com diferentes estágios de sucessão. Esta abordagem discrimina duas principais propriedades genéricas da diversidade numa comunidade, a dominância de traços funcionais (espécies mais abundantes) e a diversidade dos traços funcionais (e.g., Conti and Díaz, 2013). Usamos a abundancia relativa das espécies em vez de área basal para evitar redundância circular derivada do uso de DBH para calcular diversidade funcional de traços e biomassa acima do solo (Ali et al., 2017). O valor de CWM de cada traço funcional (eq. 2) foi calculado como o valor médio do traço na comunidade, ponderando pela abundancia das espécies (Garnier et al. 2004).

$$\mathrm{CWM}\chi = \sum_{i=1}^{S} (\mathrm{pi} * \mathrm{ti})$$

Onde CWMχ é a média ponderada da comunidade para o traço χ, S é o número de espécies na comunidade, p_i é a abundancia relativa da espécie i na comunidade, e t_i é o valor do traço para a espécie i.

Para a diversidade funcional, usamos três índices complementares (Mason et al. 2005; Villéger et al., 2008): riqueza funcional (FRic), que representa o volume do espaço funcional multidimensional ocupado pela comunidade; equabilidade funcional (FEve) que indica como é a distribuição da abundância das espécies deste espaço funcional multidimensional; e divergência funcional (FDvi), que representa o grau de divergência na distribuição dos traços das espécies dentro do volume ocupado por cada traço funcional (Villéger et al., 2008; Magnago et al., 2014). Os índices serão calculados para cada parcela a partir da matriz de abundância de espécies e da matriz de espécie por traços funcionais (estratégia de vida, síndrome de dispersão e traços estruturais das árvores). Estes índices de diversidade funcional são ortogonais, uma vez que não existe auto dependência entre eles (Manson et al., 2005). Os índices WCM e FD foram calculados usando o pacote *FD* no R versão 2.15.1 (Laliberté and Shipley 2011; Villéger et al., 2013).

2.7. Análises estatísticas

Usamos o método de Escalonamento Multidimensional Não Métrico (NMDS) para examinar diferenças entre as áreas de floresta amostradas em termos de composição de espécies usando o índice de dissimilaridade de Jaccard (Clarke, 1993). Realizamos o NMDS usando a função ‘metaMDS’ do pacote *vegan* (Oksanen et al., 2015). Utilizamos a análise de variância permutacional multivariado (PERMANOVA, 9999 permutações) para determinar as diferenças na composição das espécies utilizando a função ‘adonis’ disponível no pacote *vegan* (Oksanen et al., 2015) em R (R Core Team 2017) e para diferenciar o gradiente de distribuição de biomassa cima do solo (Solar et al., 2016). Os preditores de qualidade do solo, textura (PCA1) e fertilidade (PCA2) foram determinados pela análise dos componentes principais biplot (PCA) na matriz de correlação, utilizando o pacote *FactoMineR* (Husson et al., 2017).

Usamos o teste de ajuste de Shapiro-Wilk e gráfico Q-Q para avaliar a normalidade de todas as variáveis (Crawley, 2012). Conforme recomendado (Grace et al., 2016) todas as variáveis numéricas, incluindo a biomassa aérea, a diversidade de espécies, a variação de DBH, área basal, densidade da madeira, tempo de sucessão foram transformados usando logaritmos naturais e padronizados para atender às premissas de normalidade e linearidade, permitindo assim comparações entre múltiplos preditores e modelos (Zuur et al., 2009). Em seguida, comparamos a variação da biomassa acima do solo entre os tipos de floresta com o ANOVA unidirecional seguido de um teste *post hoc* Tukey (HSD = 0,05) para dados normalmente distribuídos. Todas essas análises estatísticas foram realizadas usando os pacotes *car* e *dunn.test* no software R (Dinno, 2017; Fox et al., 2017).

Nós construímos uma série de modelos de equação estrutural (SEM) para encontrar os modelos mais parcimoniosos que permitam explicar o efeito das variáveis preditores sobre a riqueza, área basal, biomassa acima do solo, diversidade e dominância funcional através de um gradiente de fertilidade e textura do solo, e do tempo de sucessão. Variáveis preditoras foram textura do solo, definida como o primeiro componente principal do PCA; e fertilidade do solo como o segundo componente principal do PCA. Conforme recomendado (Grace et al., 2016), construímos os SEM com base nas relações hipotéticas conhecidas entre riqueza, área basal, FD, CWM e a biomassa acima do solo, depois de avaliar o efeito do tempo de sucessão, textura e fertilidade do solo. As variáveis explicativas foram agrupadas em três categorias, "fertilidade do solo", "textura do solo" e "tempo de sucessão", e foram incluídos como variáveis estritamente exógenas (independentes) nos modelos SEM. Para cada SF e OGF, calculamos a área basal total de cada parcela (m^2 ha^{-1}). A fertilidade do solo resumiu as variáveis explicativas através de uma análise de componente principal em que incluímos os 15 parâmetros analisados, enquanto que para a textura do solo, apenas foram avaliadas três propriedades (areia, limo, argila). Avaliamos a colinearidade entre variáveis preditivas usando a análise de correlação de kendall e, quando duas variáveis foram fortemente correlacionadas ($r \geq 0,6$), selecionamos o preditor mais convincente.

Para a interpretação dos resultados dos modelos SEM, analisamos as relações bivariadas entre cada um dos caminhos causais hipotetizados, usando análises de regressão simples (Grace et al., 2016; Ali et al., 2017). Especificamente, nos ajustamos a cada par de variáveis usando uma análise de regressão linear simples para testar as relações bivariadas de biomassa acima do solo com o tempo de sucessão, textura e fertilidade do solo, CWM e FD de valores de traços. Também testamos as relações bivariadas entre o tempo de sucessão, textura e fertilidade do solo com CWM e FD de valores de traços (Ali et al., 2017).

Vários testes foram usados para avaliar o ajuste dos modelos SEM: o teste do qui-quadrado (χ^2), índice de bondade de ajuste (GFI), índice de ajuste comparativo (CFI), média de padrão padronizado resíduo quadrado (SRMR), e critério de informação de Akaike (AIC) (e.g., Ali et al., 2016; Ali et al., 2017). O efeito indireto de um preditor foi calculado multiplicando os efeitos padronizados de todos os caminhos, de um preditor para o mediador, e depois para a biomassa acima do solo, enquanto o efeito total foi calculado pela adição de efeitos diretos e indiretos padronizados (Grace et al., 2016). Os modelos SEM foram desenvolvidos usando o pacote *lavaan* (Rosseel, 2012) em R 3.2.2 (R Development Core Team, 2017).

3. Resultados

O NMDS mostrou que a composição das espécies de árvores variou consideravelmente de acordo com o tempo de sucessão (Fig. 2a), separando cinco grupos com diferenças significativas (PERMANOVA, $F_{4,40} = 7.42$; $P < 0.001$). O NMDS mostrou um marcado padrão de distribuição da biomassa acima do solo através do tempo de sucessão, com diferenças significativas entre estágios de sucessão e floresta madura (Fig. 2b).

As relações bivariadas mostraram que a biomassa acima do solo, riqueza e área basal aumentou significativamente com o tempo de sucessão (Fig. 3A, C, D) e está fortemente influenciada pela textura do solo (Fig. 3B). Encontramos uma forte relação positiva significativa entre média ponderada da comunidade da densidade da madeira e diâmetro das arvores com relação à textura do solo; por enquanto se apresenta uma relação negativa significativa com fertilidade do solo (Fig. 3E-H). A métrica de diversidade funcional (FDiv) e as de dominância funcional (CWM WD, CWM DBH) respondem positivamente ao tempo de sucessão, enquanto a métrica funcional FEve responde negativamente (Fig. 3I-L). Finalmente, observamos que a biomassa aumenta significativamente como o aumento da CWM WD, CWM DBH (Fig. 3M-N); no entanto existe houve uma fraca relação entre biomassa e as métricas de diversidade funcional (Fig. 3). Não houve associação significativa entre a biomassa e variação de riqueza de espécies.

O modelo básico de equação estrutural representou 89, 41, e 28% da variação na biomassa aérea, riqueza de espécies e área basal, respectivamente (Fig. 4A). Textura do solo e tempo de sucessão tiveram um efeito positivo sobre biomassa acima do solo. Neste modelo a riqueza de espécies e fertilidade do solo não tiveram efeito significativos sobre biomassa acima do solo (Tabela 1). O modelo MRH (CWM da hipótese da relação de massa) representou 84, 16, e 10% da variação na biomassa aérea, CWM do diâmetro do caule e CWM da densidade da madeira, respectivamente (Fig. 4B). O tempo de sucessão (*Stand age*) teve o efeito direto positivo mais forte sobre a biomassa acima do solo ($\beta = 0{,}91$, $P < 0{,}001$), seguido do efeito positivo da CWM de DBH ($\beta = 0{,}67$, $P = 0{,}001$) e do efeito positivo de CWM de WD ($\beta = 0{,}14$, $P = 0{,}01$, Tabela 1). Houve um efeito negativo significativo da fertilidade do solo sobre CWM de

DBH (β = -0,46, P = 0,001), e CWM WD (β = -0,35, P = 0,01); mas um efeito negativo não significativo sobre biomassa acima do solo (Fig. 3B).

Com relação ao modelo NCH (FD, hipótese de complementaridade de nicho), observamos que explicou 80, 73, 72 e 59% de variação na biomassa aérea, riqueza funcional, equabilidade funcional e divergência funcional, respectivamente (Fig. 4C). O tempo de sucessão teve o efeito direto positivo mais forte na biomassa aérea (β = 0,50, P < 0,001), seguido dos efeitos positivos de textura do solo (β = 0,38, P = 0,01), FDiv (β = 0.17, P = 0,01) e fertilidade do solo (β = 0,23, P = 0,001, Tabela 1.A. material suplementar). Enquanto, FEve tive um efeito significativo negativo sobre a biomassa aérea (β = -0,19, P = 0,02, Tabela 1; Fig. 4C).

O modelo integral MRH + NCH sobre o efeito conjunto da relação de massa e dos mecanismos de complementaridade de nicho, observamos que só a média ponderada da comunidade dos traços analisados tiveram efeitos significativos sobre a biomassa acima do solo (DBH, β = 0,30, P < 0,001; WD, β = 0,13, P = 0,02), além do efeito direto positivo moderado da textura do solo (β = 0,17, P = 0,01). Houve um efeito direto negativo significativo do tempo de sucessão sobre FEve (β = --0,84, P = 0,001) e um efeito direto positivo sobre FDiv (β = 0,85, P < 0,001, Fig. 4D). No entanto, as métricas de diversidade funcional não apresentaram efeitos importantes sobre a biomassa aérea (Fig. 4).

5. Discussões

Nossos resultados demonstram as relações significativas dos modeladores ambientais diversidade e dominância funcional sobre o funcionamento ecossistêmico (estocagem de biomassa). Este estudo representa uma primeira contribuição onde se avalia o efeito de diferentes modeladores ambientais (*stand age, soil texture and fertility*) através do analises da média ponderada da comunidade (CWM) e diversidade funcional (FD) baseados em traços funcionais relacionados à regeneração de uma floresta Amazônica. Assim, com esta abordagem foi possível testar as hipóteses de complementariedade de nicho e razão de biomassa de forma individual e conjunta para elucidar padrões emergentes que explicam o funcionamento ecossistêmico durante a sucessão secundaria. Estudos recentes em florestas tropicais descobriram que as árvores tardias (com maior densidade da madeira e lento crescimento) são substituídas por espécies pioneiras (com baixa densidade da madeira e rápido crescimento) devido a uma maior intensificação dos distúrbios (e.g., ciclos repetidos de corte e queima), que dominam as paisagens florestais fragmentadas (Pütz et al., 2011; de Ávila et al., 2018).

Esta substituição pode induzir uma homogeneização biótica e afetar negativamente a capacidade de produção de biomassa e armazenamento de carbono (Paula et al., 2011; Pütz et al., 2014). No entanto, a relação entre estes modeladores ambientais e traços funcionais das espécies e seus efeitos sobre funções ecossistêmicas durante a sucessão em florestas da Amazônia ainda não haviam sido avaliados.

Nosso estudo destaca o papel fundamental dos valores de CWM e FD de traços para predizer a biomassa acima do solo em florestas tropicais secundárias. De acordo com nossa hipótese, este estudo mostrou que a biomassa acima do solo aumenta com o tempo de sucessão e textura do solo e a variação residual na biomassa acima do solo é explicada satisfatoriamente por CWM e FD individualmente (Fig. 3B e C), enquanto no modelo integral foi bem explicada somente por CWM de traços de caule (Fig. 3D). A principal novidade deste estudo foi que a maior estocagem de biomassa acima do solo nas florestas secundárias estudadas está associada com a razão de massa (em termos de diâmetro e densidade da madeira das árvores). Nossos resultados coincidem com estudos que mostram que o armazenamento de biomassa pode ser melhor explicado pela hipótese da razão de biomassa que pela hipótese de complementaridade de nicho (Conti and Díaz, 2013, Finegan et al., 2015, Lohbeck et al., 2015). Contudo, existem estudos onde, as duas hipóteses são igualmente relevantes para explicar o funcionamento ecossistêmico (Mensah et al. 2016; Ali et al. 2017).

Neste estudo, a associação positiva significativa de divergência funcional e negativa de equabilidade funcional com a biomassa acima do solo ao longo da sucessão (Fig. 3C) poderia estar indicando o papel positivo de uma estratégia aquisitiva diversificada, juntamente com a diversidade do diâmetro das árvores (Zhang e Chen, 2015; Ali et al., 2016). Este padrão tem sido reportado em outro estudo em floresta seca tropical (Prado-Junior et al., 2016), onde a alta divergência funcional indica que a área basal está concentrada nos extremos do espaço com características multivariadas, enquanto que a baixa equabilidade funcional indica que a área basal é concentrada em uma parte restrita desse mesmo espaço multidimensional (Villéger et al. 2008). Por outro lado, a relação positiva entre CWM do diâmetro das árvores e biomassa acima do solo (Fig. 3B), indica que a elevada biomassa acima do solo pode estar associada a espécies de árvores de maior porte ou de rápido crescimento em média (mecanismo associado com traços aquisitivos). Pelo contrário, a relação CWM da densidade da madeira das árvores e biomassa pode explicar a importância de espécies tolerantes à sombra como maior capacidade de estocar biomassa durante estágios avançados de sucessão e floresta madura. Assim, fazendo uma analise integral entre dominância e diversidade funcional, nós presumimos que a baixa diversidade de traços (alta divergência funcional e baixa equabilidade funcional) e alta CWM para densidade de madeira e Diâmetro sugerem que, em altos níveis de biomassa, a área basal é concentrada em espécies com maior Diâmetro e WD.

Com nossos resultados, deixamos em evidencia que a relação da diversidade de traços funcionais e a biomassa acima do solo devem ser correlacionadas de forma interativa com o tempo de sucessão e parâmetros do solo como filtros ambientais. Neste estudo, também encontramos um importante efeito direto significativo do tempo de sucessão sobre a CWM, FDiv, e FEve (nos três modelos analisados, Fig. 3B,C,D) assim como sobre a biomassa acima do solo. A forte mudança direcional na CWM dos traços de caule com relação ao tempo de sucessão é consistente com a hipótese de filtragem de produtividade (Grime, 2006). No entanto, observamos uma fraca relação direta negativa da fertilidade do solo sobre a biomassa acima do solo em todos os modelos, quando se compara com o efeito direto positivo significativo da textura do solo. Esta foi uma tendência não esperada neste estudo, porém, também coincide com prévios estudos onde os processos da dinâmica de biomassa foram principalmente impulsionados pela hipótese razão de massa, enquanto encontraram-se efeitos negativos ou mesmo sem efeitos da fertilidade do solo e complementação de nicho (Prado-Junior, et al. 2016).

As diferenças existentes entre florestas tropicais poderiam estar respondendo aos efeitos de outros modeladores ambientais (climáticos ou antropogénicos) que determinam grandes variações nos valores dos traços funcionais. Por exemplo, florestas secas e florestas úmidas apresentam diferentes relações traços de produtividade (e.g., Lohbeck et al., 2013). Em florestas secas, a dominância das espécies conservativas, em detrimento das espécies aquisitivas, está associada ao alto crescimento e armazenamento de biomassa (Prado-Junior, et al. 2016). Traços conservativos promovem uma menor produtividade da biomassa em florestas úmidas (Malhi et al., 2004; Finegan et al., 2015) e podem aumentar o desempenho e a produtividade das espécies em florestas secas (Prado-Junior, et al. 2016). Por esta razão, segundo nosso modelo integral e por tratar-se de uma floresta semidecidual, dominância funcional de traços (WD) pode ser o principal modelador da biomassa acima do solo no contexto climático do norte da Amazônia.

Embora traços de folhas têm sido reportados como os preditores mais importantes de incrementos de biomassa (Finegan et al., 2015), foi possível testar nossas hipóteses ecológicas utilizando somente traços funcionais associados diretamente com a estocagem de carbono (WD e DBH). Portanto, as florestas dominadas por espécies com grande porte potencial quando adultos (diâmetro máximo elevado do caule) e valores de traços conservativos (maior densidade de madeira) apresentaram maior biomassa acima do solo. As espécies grandes têm um grande volume de caule e as espécies com madeira densa têm maior volume de biomassa por unidade de peso (Chave et al. 2009), levando a uma maior estocagem de biomassa (Slik et al., 2010). Estudos comparativos mostram consistentemente que WD é o melhor preditor de incremento individual do diâmetro para espécies arbóreas tropicais (Poorter et al., 2008; Wright et al., 2010). No entanto, para a produtividade de biomassa os traços de folhas são preditores mais importantes de incrementos de biomassa do que CWM WD ou Hmax (Finegan et al., 2015).

Nosso primeiro modelo básico indica como o tempo de sucessão, área basal, e textura de solo foram bons preditores da biomssa acima do solo, mas sem efeitos sigificativos da riqueza de especies. Estes resultados corroboram resultados de estudos previos, onde a diversidade estrutural da floresta pode ter uma forte relação positiva com a biomassa acima do solo (Ali et al. 2016; Ali et al. 2017), porém sem efeitos da riqueza (Loreau 2002; Paquette and Messier 2011; Zhang et al. 2012;), tornandose um fraco preditor do funcionamento ecossitemico (Yuan et, al. 2016). Neste sentido, uma abordagem baseada só na diversidade taxonômica não pode analisar as diferenças ecológicas entre as espécies. Por isso, os trabalhos feitos usando traços individuais não permitem fazer correlações multivariadas entre traços à escala da comunidade, e abordagens baseadas em grupos funcionais não consideram o fato de que as espécies dentro dos grupos funcionais podem ser funcionalmente diferentes (Wrigth et al., 2004; Marquard et al., 2009, Reich, 2014). Por este motivo, tem surgido a abordagem baseada en traços funcionais (*trait-based approach*) para vincular as mudanças da composição de traços funcionais e funcionamento ecossitemico, que vai muito além da identidade taxonômica (Petchey and Gaston 2002; Laughlin et al., 2014).

Estudos prévios sobre comunidades de espécies vegetais durante a sucessão avaliaram principalmente as mudanças temporais da composição taxonômica, ou sobre as mudanças de traços individuais ou grupos funcionais (Chazdon et al., 2007; Meiners et al., 2015), assim como também da produção e acumulação de biomassa (Norden et al., 2009; Lohbeck et al., 2014). No entanto, é evidente que os filtros abióticos e bióticos podem mudar durante a sucessão secundária induzindo mudanças da composição de traços funcionais (Lohbeck et al., 2013; Meiners et al., 2015). Portanto, a filtragem ambiental causada pelos disturbios inicias pode promover uma maior amplitude de traços baseados em dispersão de sementes anemocoricas (frutos secos) que deverão dominar durante estágios iniciais de sucessão. Pelo contrário a filtragem biótica é cada vez mais importante nas fases posteriores de sucessão (Lasky et al., 2014; Meiners et al., 2015), com maior abundancia de especies zoocoricas tolerantes à sombra (Chazdon, 2014). Por exemplo, a intensidade e frequência dos distúrbios na borda de fragmentos florestais induzem a uma redução da equabilidade funcional em comparação ao interior, o que pode estar ligado com a perda de importantes grupos funcionais, como espécies com dispersão zoocorica, frutos carnosos, secundarias tardias durante sucessão (Magnago et al., 2014).

Por outro lado, quando o filtro abiótico seleciona indivíduos com base a sua tolerância à disponibilidade de recursos, isto leva a uma restrição na gama de valores dos traços com diferentes funções, e também uma distribuição convergente com pouca dispersão em torno da média dos traços (Kunstler et al., 2012; Kraft and Ackerly, 2014). Portanto, quando esse filtro é ligado à perturbação pode levar a um excesso de dispersão ou divergência de valores de traços, especialmente aqueles relacionados à regeneração (Verdú and Pausas, 2007; Ding et al., 2011). Pelo contrario, os filtros bióticos dependentes da densidade podem ter efeitos contrastantes com relação às distribuições dos traços, como por exemplo, quando muda a importância relativa da similaridade limitante e exclusão competitiva durante a sucessão (Webb et al., 2002; Schwilk and Ackerly, 2005; Violle et al., 2011). Finalmente, é importante indicar que a estrutura funcional de uma comunidade também depende da variabilidade intra e interespecífica dos traços funcionais (Ackerly et al., 2007; Kunstler et al., 2012), que repercute no funcionamento dos ecossistemas (Tilman, 1997; Grime, 1998; Hooper et al., 2012). Por este motivo, propomos para futuras pesquisas explorar esta relação intra e interespecífica dos traços funcionais para testar ambas as hipóteses (RMH-NCH) durante a sucessão secundaria da floresta.

5. Conclusões

Nossos resultados proporcionam o entendimento da relação BEF durante a sucessão secundaria de uma floresta tropical. Primeiro, os modelos SEM testados sobre dominância funcional (CWM) e diversidade funcional (FD), permitiram explicar variações na biomassa acima do solo de forma individual. Pelo contrário, no modelo integral (RMH + NCH) para explicar o efeito conjunto, só CWM dos traços funcionais analisados tiveram efeitos diretos significativos sobre a biomassa cima do solo. Isto indica que CWM da densidade da madeira e diâmetro do caule são bons preditores, corroborando a hipóteses de razão de biomassa como principal modelador do funcionamento ecossistêmico na floresta semidecidual estudada. Além disso, no modelo SEM básico a área basal também demostrou ser um preditor importante da biomassa acima do solo, mas a riqueza de espécies não apresentou efeito significativos. No entanto, esse modelo está limitado por não considerar a amplitude de valores de traços funcionais. Segundo, o tempo de sucessão foi o melhor preditor para explicar variações da biomassa acima do solo em todos os modelos SEM explorados, seguidamente da textura solo que teve afeitos significativos positivos sobre a biomassa acima do solo, em comparação à fertilidade do solo que apresentou efeitos negativos e não significativos. Terceiro, o tempo de sucessão, textura e fertilidade do solo também apresentam efeitos diretos significativos sobre a dominância funcional e diversidade funcional, assim como também induz mudanças da composição de traços funcionais associados com a regeneração (e.g. tipos de frutos, sindromes de diespersõa e estrategis de regeneração). Nosso estudo contribui no entendimento da relação BEF ao longo da sucessão secundaria, e pode ajudar a predecir como as florestas tropicais respondarão aos cenarios futuros de mudanças climaticas.

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Tabela 1. Resultados do modelo de equação estrutural usado para avaliar como a biomassa acima do solo (AGB) pode ser afetada pela dominância funcional, e diversidade funcional, e pelo efeito direto e indireto do tempo de sucessão, textura e fertilidade do solo.

Modelo MRH + NCH	**Est.std**	**SE**	**z**	***p*-value**
Analises de caminho				
CWM WD ~ PCA1	0.22	0.08	2.20	0.01
CWM DBH~ PCA1	0.45	0.02	3.59	0.001
FRic ~ PCA1	0.08	0.03	0.31	0.75
FDiv~ PCA1	-0.30	0.03	-1.27	0.20
FEve~ PCA1	0.68	0.02	2.57	0.01
AGB ~ PCA1	0.17	0.03	3.05	0.001
CWM WD ~PCA2	-0.36	0.04	-5.54	0.001
CWM DBH ~ PCA2	-0.46	0.03	-5.73	0.001
FRic ~PCA2	-0.42	0.02	-2.48	0.01
FDiv ~ PCA2	-0.04	0.02	-1.23	0.79
FEve~ PCA2	0.01	0.01	1.18	0.92
AGB ~ PCA2	-0.30	0.02	-1.23	0.90
CWM WD ~ Stand age	0.68	0.05	4.36	0.001
CWM DBH ~ Stand age	0.29	0.02	2.44	0.01
FRic ~ Stand age	0.20	0.03	0.83	0.40
FDiv ~ Stand age	0.85	0.03	3.78	0.001
FEve~ Stand age	-0.84	0.03	-3.40	0.01
AGB ~ Stand age	0.63	0.04	4.34	0.001
AGB ~ CWM DBH	0.69	0.29	3.67	0.001
AGB ~ CWM WD	0.13	0.53	1.92	0.01
AGB ~ FRic	0.09	0.15	0.34	0.73
AGB ~ FDiv	0.12	0.01	0.19	0.76
AGB ~ FEve	-0.06	0.02	-0.82	0.41

Modelo MRH (hipóteses de razão de massa) + NCH (hipóteses de complementariedade nicho), Est.std (coeficiente estandarizado do analise de caminho), SE (erro padrão), CWM (média ponderada da comunidade, WD (densidade da madeira), DBH (diâmetro máximo das arvores), PCA1 (textura do solo), PCA2 (fertilidade do solo), tempo de sucessão (stand age), FRic (riqueza funcional), FDiv (divergência funcional), FEve (equabilidade funcional).

Lista de figuras

Fig. 1. Modelos hipotéticos para a predição da biomassa acima do solo (AGB) durante sucessão secundaria numa floresta no norte da Amazônia. Nos modelos hipotéticos se explica como o tempo de sucessão e solos (textura e fertilidade) influi na diversidade funcional (FD) e dominância funcional (CWM) de traços funcionais relacionados com a regeneração de florestas secundarias, e como esses modeladores afeitam a biomassa acima do solo (AGB) simultaneamente. São propostos três modelos baseados em efeitos individuais e conjuntos de FD e CWM sobre AGB, depois de considerar os efeitos dos modeladores tempo de sucessão e solos: A) Modelo de razão de massa (MRH); B) modelo de complementariedade de nicho (NCH); e C) Modelo integrado de MRH e NCH.

Fig. 2. Analises de ordenação. (A) Escalamento multidimensional não métrico baseado na composição de espécies ao longo de um gradiente de distribuição de biomassa acima do solo (AGB) de florestas secundaria com diferentes estágios de sucessão (*Stand age*, 5, 10, 15, 20 anos de sucessão) e floresta madura (OG, > 100 anos); (B) boxplot da AGB entre tipos de floresta, secundaria (SG) e madura (OG).

Fig. 3. Relação bivariada entre variáveis resposta e explicativas para todas as hipóteses estabelecidas nos analises de caminhos baseados em modelos de equações estruturais (A-B) biomassa acima do solo (AGB), área basal (BA), riqueza de espécies (Richness) em função do tempo de sucessão (*Stand age*, SA) e textura do solo (PCA1); (E-H) representam media ponderada da comunidade (CWM) do diâmetro máximo (DBH), densidade da madeira (WD) em função PCA1 e fertilidade do solo (PCA2); (I-L) índices de divergência funcional (FDiv), equabilidade funcional (FEev), CWM-DBH e CWM-WD em função do SA; e (M-P) a relação de AGB versus CWM-DBH, CWM-WD e FEeve, e finalmente FEve versus PCA1. Somente relações significativas são apresentadas (R^2, $P < 0.05$).

Fig. 4. Modelos de equação estruturais (analises de caminhos) representando como a biomassa acima do solo (Aboveground biomass) pode ser afetada pelo efeito direto do tempo de sucessão (stand age), textura e fertilidade do solo, assim como, pela estrutura (A), dominância funcional (B), diversidade funcional (C) e pelo efeito integral de diversidade e dominância funcional (D). Indicam-se a área basal (BA), media ponderado da densidade da madeira da comunidade (CWM WD) (CW), media ponderada do diâmetro máximo das árvores (CWM BDH), riqueza funcional (FRic),

divergência funcional (FDiv) e equabilidade funcional (FEve). Linhas pretas significam que existe uma relação positiva no caminho, e vermelha uma relação negativa. Linha continua significa que relação é significativa ($P < 0.05$), enquanto linhas tracejadas indicam relações não significativas ($P > 0.05$). Para cada caminho é apresentado o coeficiente de regressão estandarizado. Entre parênteses é apresentado o valor total da variação explicada pela combinação das variáveis independentes (R^2). A caixa na base da figura contém os valores de ajuste dos testes estatísticos.

Fig. 1.

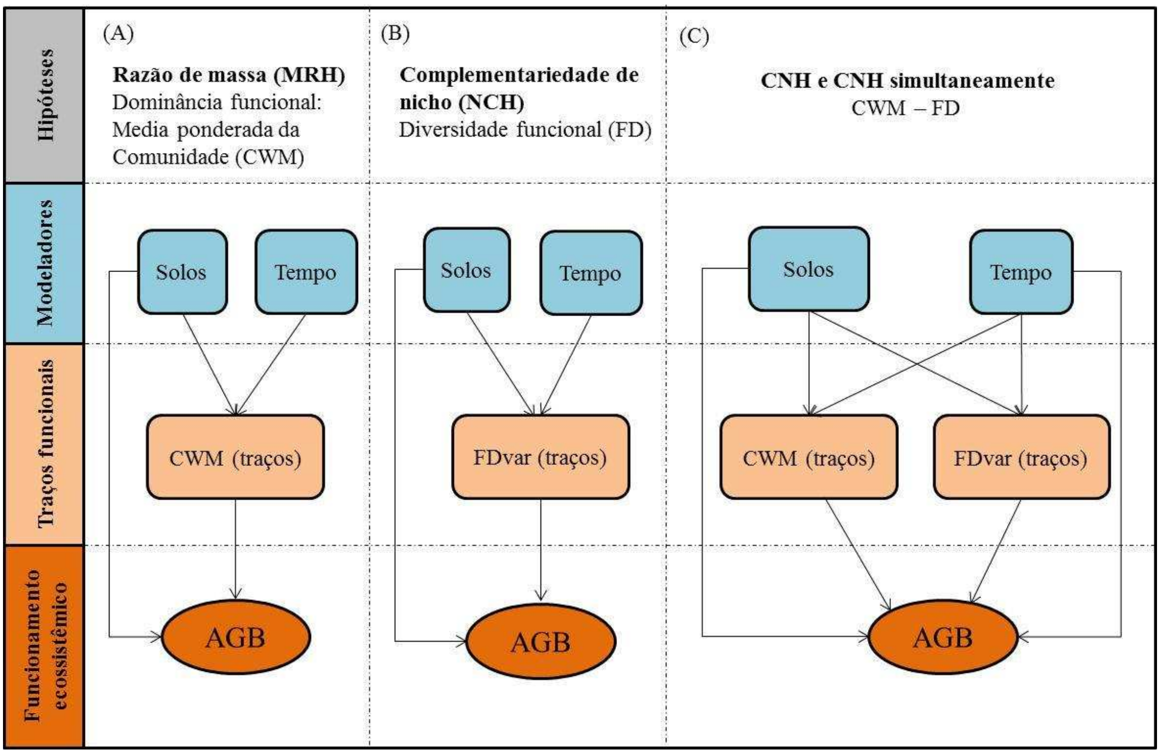

Hipóteses
Modeladores
Traços funcionais
Funcionamento ecossistêmico
(A)
Razão de massa (MRH)
Dominância funcional:
Media ponderada da
Comunidade (CWM)
(B)
Complementariedade de nicho (NCH)
Diversidade funcional (FD)
(C)
CNH e CNH simultaneamente
CWM – FD
Solos
Tempo
CWM (traços)
FDvar (traços)
AGB

Fig. 2.

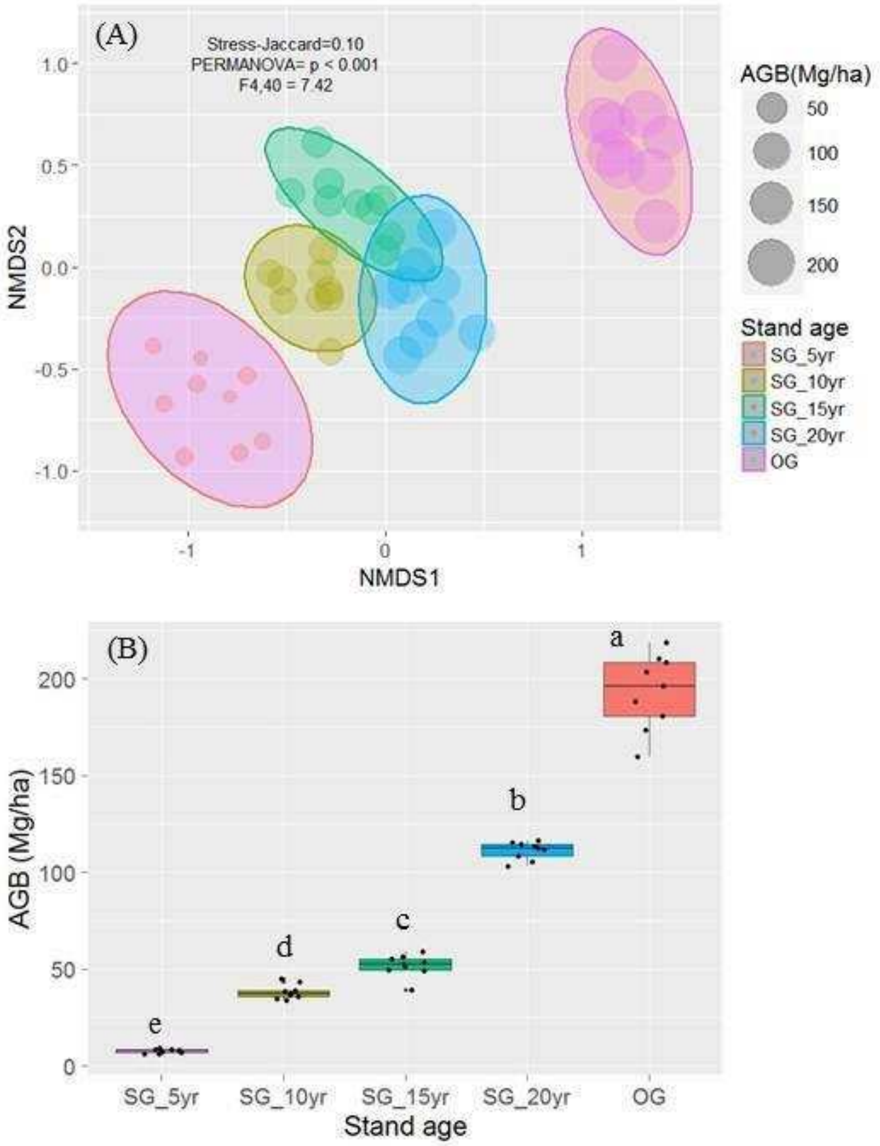
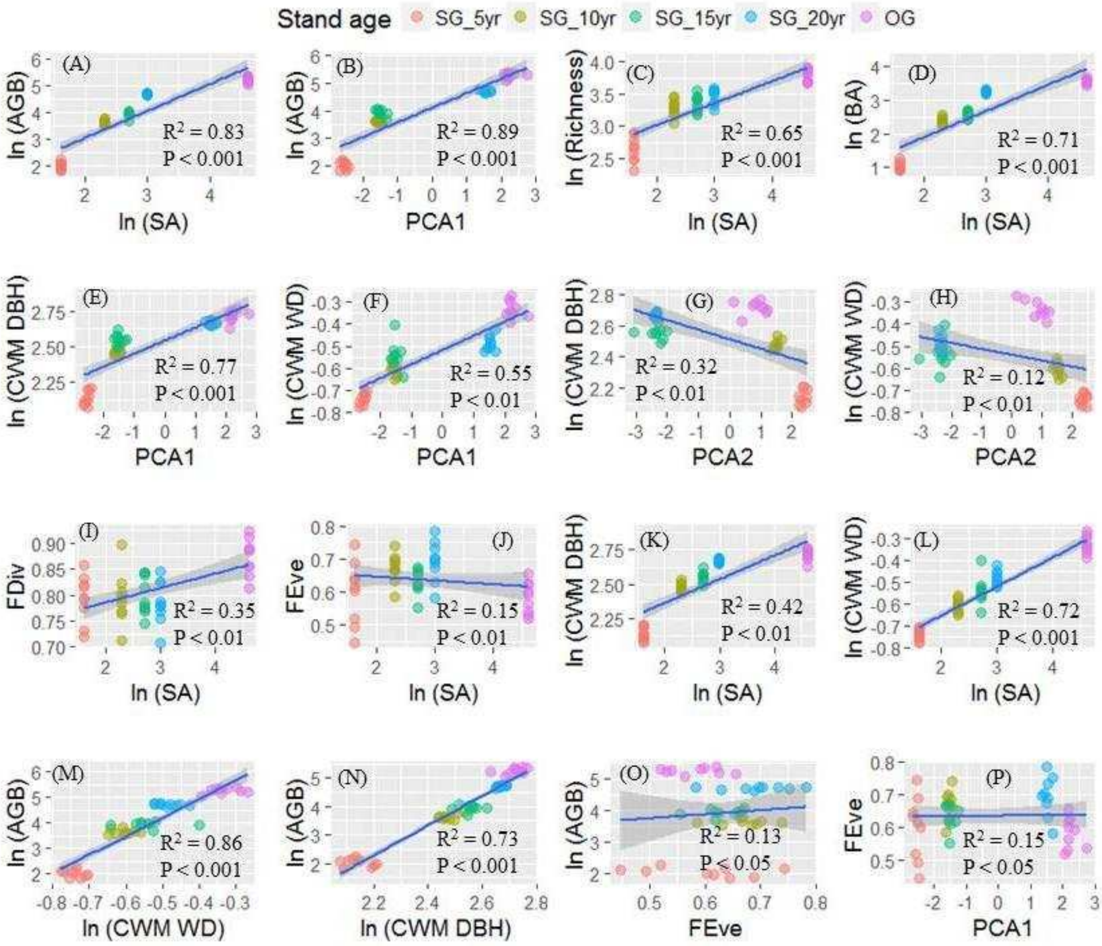
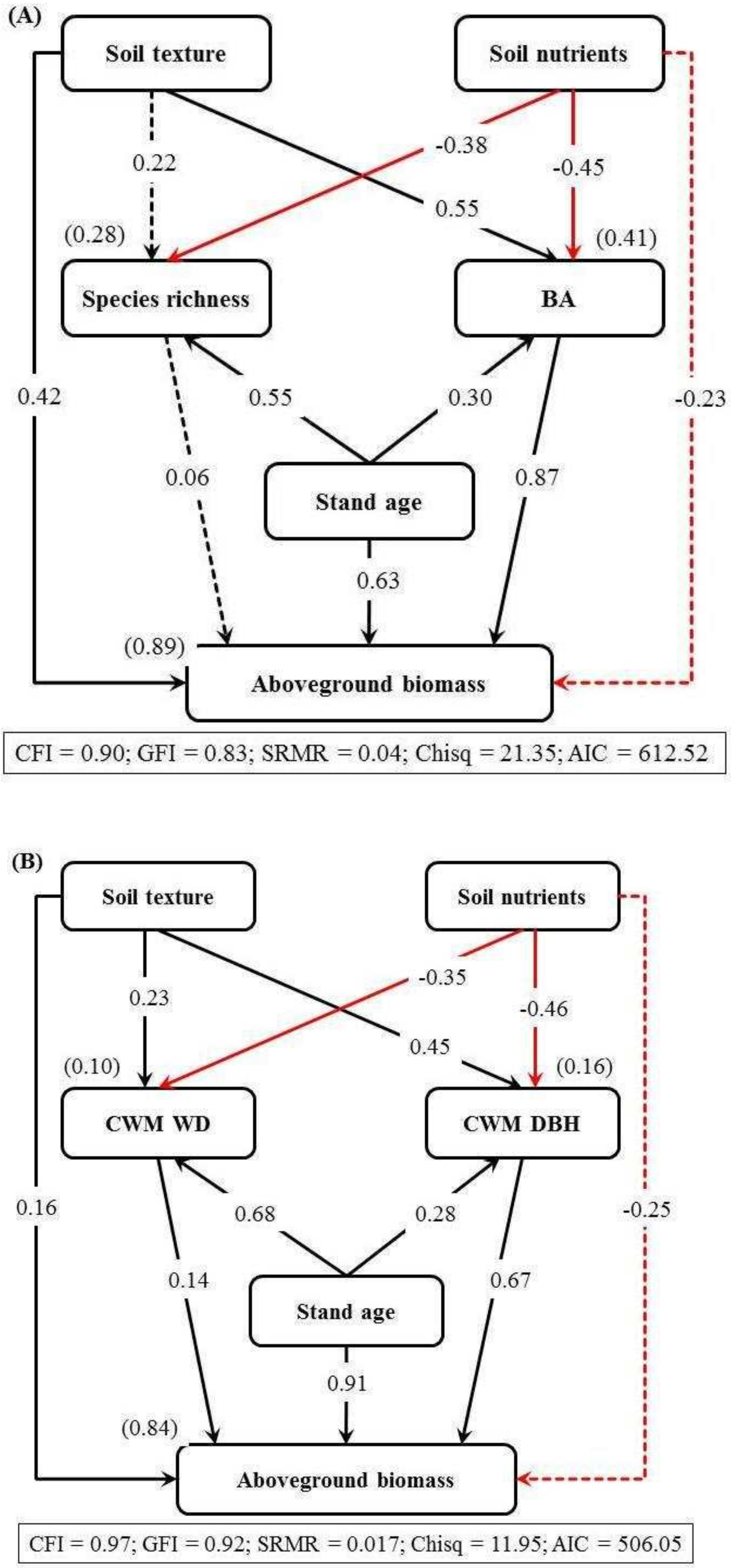

(A)
Stress-Jaccard=0.10
PERMANOVA= p < 0.001
F4,40 = 7.42
NMDS2
NMDS1
1.0
0.5
0.0
-0.5
-1.0
-1
0
1
AGB(Mg/ha)
50
100
150
200
Stand age
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
(B)
AGB (Mg/ha)
200
150
100
50
0
a
b
c
d
e
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
Stand age

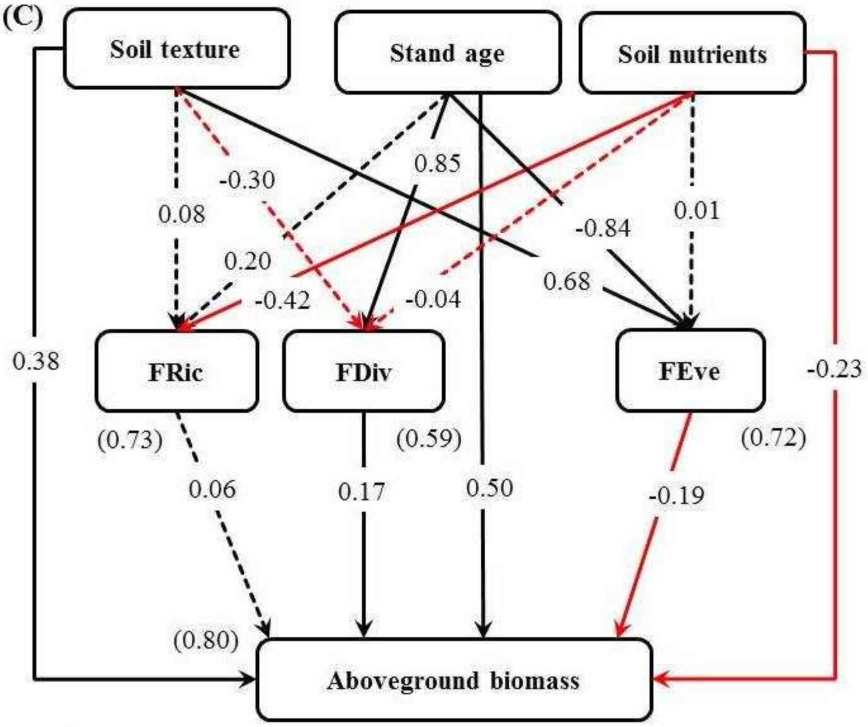
Fig. 3.



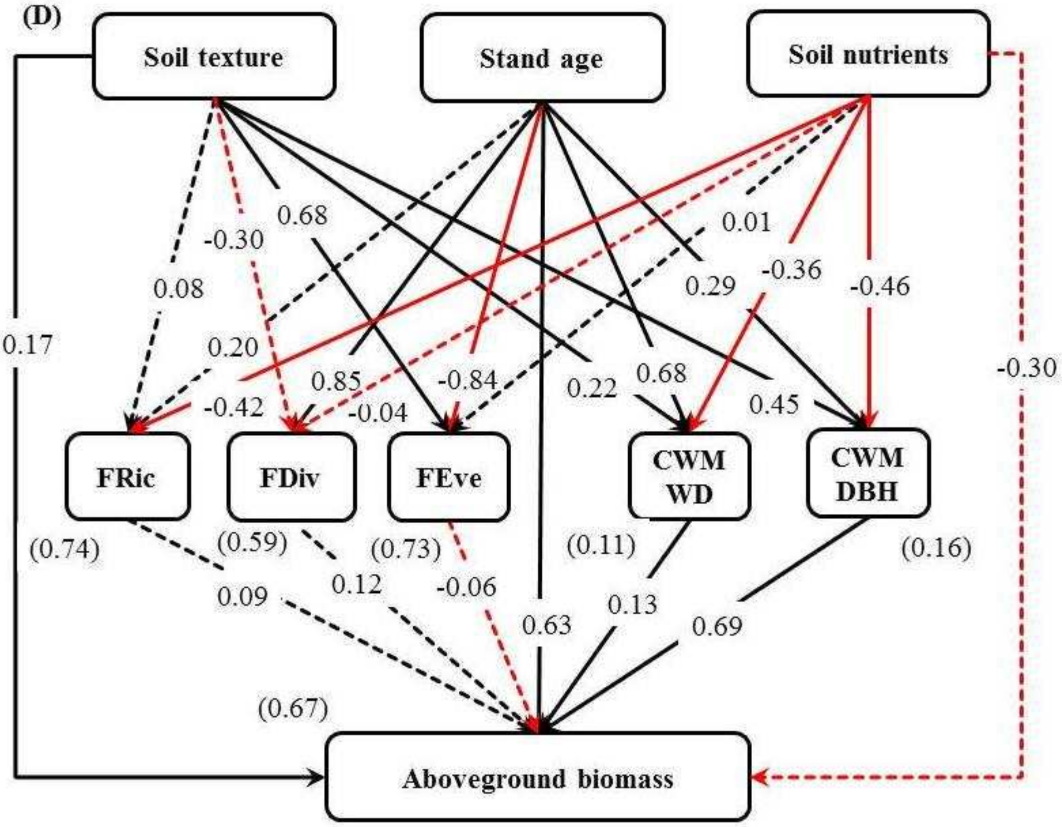
Stand age
SG_5yr
SG_10yr
SG_15yr
SG_20yr
OG
(A)
ln (AGB)
ln (SA)
R² = 0.83
P < 0.001
(B)
ln (AGB)
PCA1
R² = 0.89
P < 0.001
(C)
ln (Richness)
ln (SA)
R² = 0.65
P < 0.001
(D)
ln (BA)
ln (SA)
R² = 0.71
P < 0.001
(E)
ln (CWM DBH)
PCA1
R² = 0.77
P < 0.001
(F)
ln (CWM WD)
PCA1
R² = 0.55
P < 0.01
(G)
ln (CWM DBH)
PCA2
R² = 0.32
P < 0.01
(H)
ln (CWM WD)
PCA2
R² = 0.12
P < 0.01
(I)
FDiv
ln (SA)
R² = 0.35
P < 0.01
(J)
FEve
ln (SA)
R² = 0.15
P < 0.01
(K)
ln (CWM DBH)
ln (SA)
R² = 0.42
P < 0.01
(L)
ln (CWM WD)
ln (SA)
R² = 0.72
P < 0.001
(M)
ln (AGB)
ln (CWM WD)
R² = 0.86
P < 0.001
(N)
ln (AGB)
ln (CWM DBH)
R² = 0.73
P < 0.001
(O)
ln (AGB)
FEve
R² = 0.13
P < 0.05
(P)
FEve
PCA1
R² = 0.15
P < 0.05

Fig. 4.


(A)
Soil texture
Soil nutrients
0.22
-0.38
-0.45
0.55
(0.28)
(0.41)
Species richness
BA
0.42
0.55
0.30
-0.23
0.06
Stand age
0.87
0.63
(0.89)
Aboveground biomass
CFI = 0.90; GFI = 0.83; SRMR = 0.04; Chisq = 21.35; AIC = 612.52
(B)
Soil texture
Soil nutrients
-0.35
0.23
-0.46
0.45
(0.10)
(0.16)
CWM WD
CWM DBH
0.16
0.68
0.28
-0.25
0.14
0.67
Stand age
0.91
(0.84)
Aboveground biomass
CFI = 0.97; GFI = 0.92; SRMR = 0.017; Chisq = 11.95; AIC = 506.05



CFI = 0.95; GFI = 0.94; SRMR = 0.059; Chisq = 10.54; AIC = 401.41



CFI = 0.92; GFI = 0.85; SRMR = 0.056; Chisq = 40.74; AIC = 209.13

Material suplementar

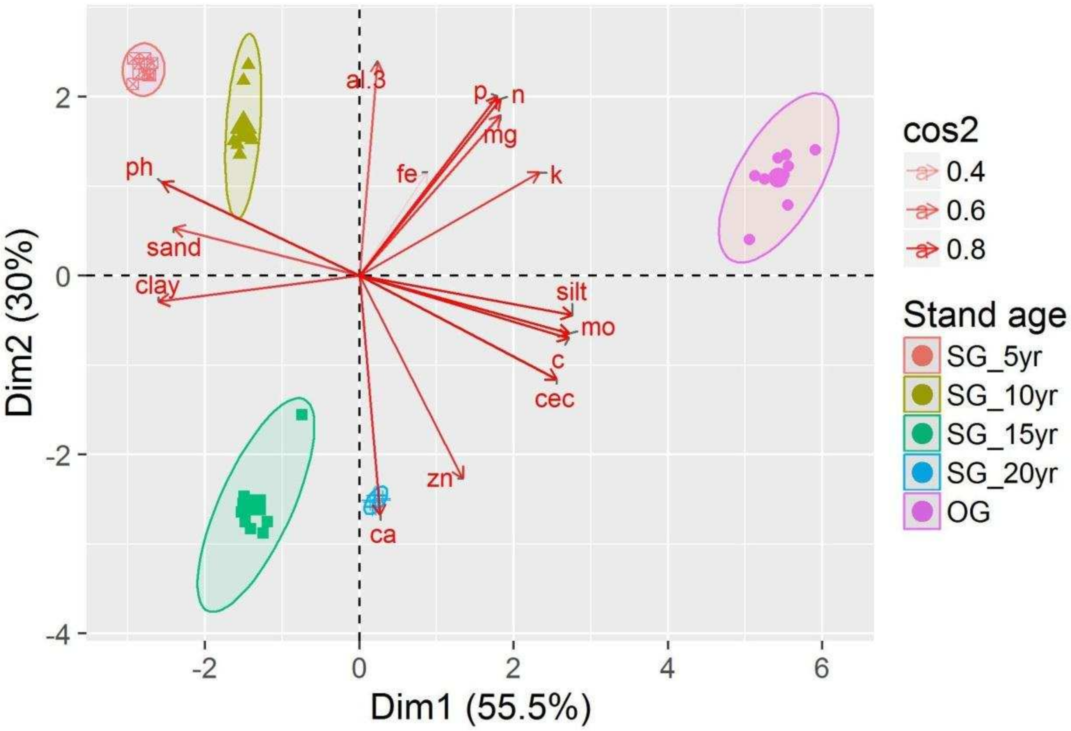


Fig. A.1. Análise de Componentes Principais das variáveis (parâmetros edáficos) medidas em parcelas em diferentes florestas secundarias com diferentes estágios de sucessão (*Stand age*, 5, 10, 15, 20 anos de sucessão) e em uma floresta de crescimento antigo (OG, > 100 anos). A intensidade de cor dos vetores representa a contribuição relativa média dos parâmetros (cos2).

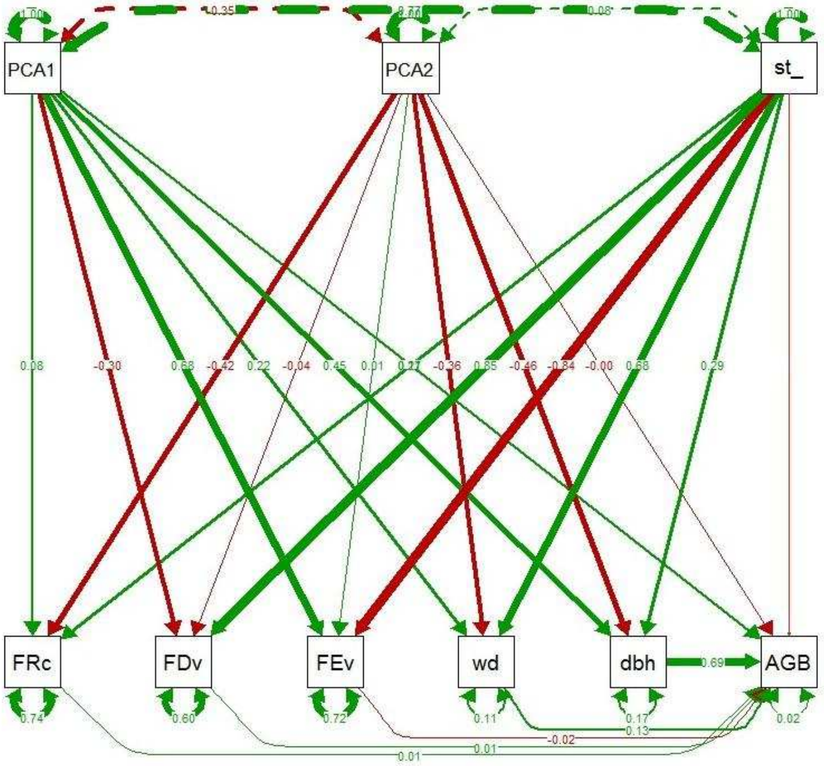


Fig. A.2. Exemplo de modelo de equação estrutural integrado RMH + NCH gerado com a função ‘semPaths’ do pacote *semPlot*, depois de estimar os diferente caminhos como o pacote *lavaan*. Modelo de equação estruturais (analises de caminhos) representando como a biomassa acima do solo (AGB) pode ser afetada pelo efeito direto do tempo de sucessão (st), textura (PCA1) e fertilidade do solo (PCA2). Indicam-se a media ponderada da densidade da madeira da comunidade (CWM WD), media ponderada do diâmetro máximo das árvores (CWM BDH), riqueza funcional (FRic), divergência funcional (FDiv) e equabilidade funcional (FEve).

Tabela A.1. Resultados de modelos de equação estrutural usado para avaliar como a biomassa acima do solo (AGB) pode ser afetada pela dominância funcional, e diversidade funcional, e pelo efeito direto e indireto do tempo de sucessão, textura e fertilidade do solo.

Modelos/caminhos	Est.std	SE	z	p-value
Modelo 1				
BA ~ PCA1	0.55	0.052	5.04	0.001
Richness ~ PCA1	0.22	0.035	1.35	0.17
AGB ~ PCA1	0.42	0.024	0.26	0.01
BA ~PCA2	-0.45	0.031	-5.16	0.001
Richness ~ PCA2	-0.38	0.021	-3.72	0.001
AGB ~ PCA2	-0.23	0.016	-1.69	0.10
BA ~ Stand age	0.30	0.01	2.60	0.01
Richness ~ Stand age	0.55	0.02	3.56	0.001
AGB ~ Stand age	0.63	0.04	2.90	0.01
AGB ~ Richness	0.06	0.08	1.65	0.15
AGB ~ BA	0.87	0.05	3.23	0.01
Modelo 2: MRH				
CWM WD ~ PCA1	0.23	0.08	2.20	0.01
CWM DBH~ PCA1	0.45	0.02	0.10	0.001
AGB ~ PCA1	0.16	0.03	2.97	0.01
CWM WD ~PCA2	-0.35	0.04	-5.54	0.001
CWM DBH ~ PCA2	-0.46	0.03	-5.73	0.001
AGB ~ PCA2	-0.25	0.02	-1.23	0.83
CWM WD ~ Stand age	0.68	0.05	4.36	0.001
CWM DBH ~ Stand age	0.28	0.02	2.44	0.01
AGB ~ Stand age	0.91	0.03	1.87	0.001
AGB ~ CWM DBH	0.67	0.29	3.67	0.001
AGB ~ CWM WD	0.14	0.53	2.15	0.01
Modelo 3: NCH				
FRic ~ PCA1	0.08	0.03	0.30	0.75
FDiv~ PCA1	-0.30	0.01	-1.27	0.20
FEve~ PCA1	0.68	0.02	2.57	0.01
AGB ~ PCA1	0.38	0.06	3.66	0.01
FRic ~PCA2	-0.42	0.02	-2.48	0.01
FDiv ~ PCA2	-0.04	0.02	-1.23	0.79
FEve~ PCA2	0.01	0.01	1.18	0.20
AGB ~ PCA2	-0.23	0.02	-5.27	0.001
FRic ~ Stand age	0.20	0.02	0.82	0.40
FDiv ~ Stand age	0.85	0.03	3.78	0.001
FEve~ Stand age	-0.84	0.03	-3.40	0.01
AGB ~ Stand age	0.50	0.04	4.34	0.001
AGB ~ FRic	0.06	0.33	1.16	0.24
AGB ~ FDiv	0.17	0.09	1.32	0.01
AGB ~ FEve	-0.19	0.07	2.27	0.01

Modelo1 indica que esta baseado unicamente em riqueza de espécies e área basal (BA). Modelo MRH (hipóteses de razão de massa) + NCH (hipóteses de complementariedade nicho), Est.std (coeficiente estandarizado do analise de caminho), SE (erro padrão), CWM (media ponderada da comunidade, WD (densidade da madeira), DBH (diâmetro máximo das arvores), PCA1 (textura do solo), PCA2 (fertilidade do solo), tempo de sucessão (stand age), FRic (riqueza funcional), FDiv (divergência funcional), FEve (equabilidade funcional).

CAPITULO V: Predictores antropogénicos y biofísicos de deforestación en la Amazonía: hacia la integración de actividades REDD+

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Resumen

La Amazonía es uno de los bosques tropicales más importantes del mundo, que proporcionan importante bienes y servicios a la humanidad; sin embargo, se encuentra amenazado por los continuos cambios en el uso de la tierra. La deforestación y degradación forestal son las dos razones que contribuyen significativamente con las emisiones de carbono a la atmósfera y pérdida de la biodiversidad. Aunque existen alternativas para reducir las emisiones de carbono por deforestación y degradación forestal evitadas (REDD), aún son pocas las investigaciones sobre métodos de evaluación y monitoreo de la relación de estos procesos con la biodiversidad, así como de los impactos generados por el sistema socioecológico en la estabilidad y recuperación de servicios ecosistémicos. El objetivo de esta revisión consiste en i) describir la relación biodiversidad-función ecosistémica, para ii) analizar los posibles impactos sinérgicos de predictores biofísicos y antropogénicos de la deforestación y degradación, con la finalidad de iii) proponer la implementación integral de estrategias REDD+ en la cuenca Amazónica. Para incrementar la eficiencia REDD+ en la Amazonía, es fundamental evaluar simultáneamente los predictores antropogénicos y biofísicos que repercuten directamente sobre la demanda actual de los bienes y servicios ecosistémicos. Por este motivo, es importante describir la magnitud de los efectos multifactoriales que tienen los predictores de deforestación para la integración de actividades REDD+, a través de la rehabilitación de áreas degradadas con sistemas agroforestales sucesionales y permanentes, así como con la aplicación de diferentes métodos de restauración.

Palabras clave: agroforestería**,** almacenamiento de carbono, cambio en el uso de la tierra, biomasa, restauración forestal.

Introducción

La cuenca Amazónica es la mayor extensión de bosque tropical continuo con cerca del 25 % de las especies vegetales descritas del mundo, y almacena aproximadamente 50 % del carbono presente en bosques tropicales (Strassburg *et al.* 2010, Mitchard *et al.* 2014). La Amazonía es importante por los servicios ecosistémicos que provee, como el mantenimiento de la biodiversidad, regulación bioclimática, y procesos biogeoquímicos (Peres *et al.* 2010, Strassburg *et al.* 2010, Aragão *et al.* 2014). Por esta razón, el estudio de procesos ecosistémicos en Amazonas tienen alta importancia frente a los alarmantes cambios climáticos globales y cambios en el uso de la tierra a escala regional, presentando las mayores tasas de deforestación histórica y acumulada entre los bosques tropicales (Lapola *et al.* 2013, Aragão *et al.* 2014). Se destaca que del total de las emisiones de carbono a la atmósfera durante los últimos 10 años, la deforestación es responsable de hasta 47 % (Aguiar *et al.* 2016). Por esta razón, existe la preocupante y reciente evidencia de que estos bosques no garantizarían completamente un balance estable de carbono entre la atmósfera y biósfera a largo plazo (Brienen *et al.* 2015). Estos escenarios negativos deben revertirse a través de acciones integrales, rápidas y factibles para reducir las emisiones por deforestación y degradación forestal, además de actividades integrales para la conservación, manejo sostenible e incremento de las reservas de carbono (REDD+) en el marco de los acuerdos de la Convención Marco de las Naciones Unidas sobre Cambio Climático (Jagger *et al.* 2013).

Así mismo, es bien conocido que la Amazonía es una de las regiones biogeográficas que presenta una alta diversidad biológica en comparación a otros bosques tropicales en diferentes latitudes del mundo (Strassburg *et al.* 2010), y que a pesar de las tasas de deforestación, así como el incremento reciente de las tasas de mortalidad de árboles (Bennett *et al.* 2015, Brienen *et al.* 2015), continúa presentando un alto potencial para el almacenamiento de carbono como uno de los servicios ecosistémicos de mayor impacto global, con aproximadamente 93 Pg de carbono entre la biomasa aérea y subterránea (Malhi *et al.* 2006). Estos procesos tienen importante implicaciones en el contexto REDD+ que tiene como objetivo principal fomentar trayectorias de desarrollo de baja emisión, aumentando el valor de los bosques en relación a diferentes tipos de uso de la tierra (Angelsen y McNeill 2013). Por este motivo, el acuerdo de Cancún de 2010 estableció un conjunto de salvaguardias sociales y ambientales para la implementación de las actividades de REDD +, que promuevan la conservación de los bosques naturales y sus servicios ecosistémicos, además de proporcionar otros beneficios socioambientales (Jagger *et al.* 2013). En este sentido, se destaca que para mantener los objetivos de REDD+ se requiere la transformación de las actividades económicas dentro y fuera de los bosques, que son reconocidos como las causas directas e indirectas de la deforestación y la degradación forestal (Angelsen y McNeill 2013, Jagger *et al.* 2013).

El Amazonas es reconocida como la cuenca de mayor ocupación indígena en el trópico (Roosevelt 2013), con más de 350 pueblos indígenas que han venido dependiendo de estos bosques desde hace más de 13.000 años como fuente de bienes y servicios, y que según evidencias arqueológicas, han sido obtenidos principalmente a través de la agricultura de tala y quema a pequeña escala, la recolección de alimentos y la cacería (Arroyo-Kalin 2012, Bush *et al*. 2015, Piperno *et al*. 2015). Esta relación del hombre con la naturaleza es ampliamente reconocida como un sistema socioecológico donde los ecosistemas son afectados para el aprovechamiento de recursos que favorecen el bienestar humano (Cumming y Allen 2017). En gran parte del Amazonas no existian asentamientos humanos permanentes con sistemas agrícolas estables, lo que habría permitido la regeneración natural del bosque a largo plazo (Bush *et al*. 2015). La alta biodiversidad de estos ecosistemas ha sido fundamental para la supervivencia de estas comunidades indígenas hasta la actualidad (Arroyo-Kalin 2012), manteniendo el mismo patrón ancestral de agricultura de subsistencia (Piperno *et al*. 2015). Por este motivo, actualmente existe una mayor preocupación por el incremento acelerado de poblaciones sedentarias con una fuerte influencia de la cultura occidental dentro de la Amazonía y de la inmigración de población mestiza que provoca la intensificación en el uso de la tierra a través de sistemas agrícolas itinerantes, asi como el aprovechamiento de recursos forestales con fines económicos. Sin embargo, no existen publicaciones sobre la relación de estos tipos de uso de la tierra con estimaciones de emisión de carbono para toda la cuenca, sólo se reconoce que contribuyen significativamente con la deforestación y degradación forestal (Lapola *et al.* 2013, Aragão *et al*. 2014).

Más recientemente las reformas agrarias en algunos países de la cuenca, basadas en medidas de desarrollo económico a partir del año 1960, incentivaron procesos de colonización con la expansión de la frontera agrícola de forma heterogénea, intensificándose el proceso de deforestación a partir del año 1970, principalmente entre el sur y sureste de la cuenca con el establecimiento de plantaciones de soja, ganadería y tala selectiva (Nepstad *et al*. 2014, Rodrigues-Filho *et al*. 2015, Aguiar *et al*. 2016). En este contexto, una primera aproximación para alcanzar los objetivos REDD+, es comprender los patrones y procesos asociados con los cambios en el uso de la tierra, a través del análisis de diferentes causas antropogénicas y biofísicas de la deforestación y degradación forestal (Figura 1). Estas causas también son reconocidas como predictores durante el uso de modelos matemáticos, especialmente cuando se analiza su relación con varibles respuestas (cobertura vegetal, biomasa, riqueza) asociadas con la deforestación y degradación (Laurance *et al.* 2002, D'Oliveira *et al*. 2011, Wandelli y Fearnside 2015). Los predictores antropogénicos permiten estimar los impactos causados por el hombre durante la explotación del bosque para la provisión de bienes y servicios ecosistémicos (Perz y Skole 2003, Lapola *et al.* 2013). Por otro lado, los predictores biofísicos proporcionan información sobre el efecto de la variabilidad ambiental (clima, geoformas, suelos) en la dinámica de los ecosistemas forestales (Laurance *et al.* 2002). En todo caso, estos predictores están actuando sinérgicamente (Laurance *et al*. 2002, Aragão *et al*. 2014, Rodrigues-Filho *et al*. 2015). Si bien, existen algunas investigaciones que explican cómo diferentes predictores antropogénicos y biofísicos influyen directamente en la dinámica de deforestación de la Amazonía (Laurance *et al.* 2002, Verburg *et al*. 2014, Pérez *et al*. 2015 Rodrigues-Filho *et al*. 2015, Aguiar *et al*. 2016), todavía es necesario entender como los procesos sociales y económicos también pueden ser importantes causas de deforestación que deben considerarse para el futuro de la conservación de los bosques en la región.

Por otra parte, todavía es necesario seguir evulando los impactos causados por los cambios en el uso de las tierras forestales sobre la biodiversidad y carbono bajo un mismo escenario, sobre todo evaluando la relevancia de actividades REDD+ (Thompson *et al*. 2012, Kapos *et al*. 2012, Villa *et al*. 2015). De esta forma, ha sido propuesta la implementación integral de actividades REDD+, como alternativas para la conservación, recuperación e incremento de carbono y biodiversidad en la región, a través de sistemas agrícolas sustentables, restauración simultanea de áreas forestales degradadas y rehabilitación de áreas a través de la agroforestería (Kapos *et al*. 2012, Villa *et al*. 2015). No obstante, dentro de las políticas de desarrollo rural y resultados de investigaciones científicas, existen pocas propuestas sistemáticas sobre los cambios en uso de la tierra dentro del sistema socioecológico, que además contemple diferentes estrategias REDD+ bajo una perspectiva de biodiversidad y carbono simultáneamente (Figura 1).

Con el propósito de contribuir con la eficiencia en el manejo y conservación de bosques en la Amazonía que se encuentran bajo modificación humana, en este artículo se desarrolla una revisión descriptiva y analítica para contextualizar las características de predictores biofísicos y antropogénicos de deforestación y degradación, que deberían considerarse como premisas para la integración de actividades REDD+. Por lo tanto, se proponen como objetivos, 1) describir la relación biodiversidad-función ecosistémica haciendo énfasis en la importancia del almacenamiento de carbono como servicio ecosistémico; 2) analizar los posibles impactos sinérgicos de predictores antropogénicos y biofísicos de la deforestación. Finalmente, 3) discutir actividades REDD+ ajustadas a la dinámica del sistema socioecológico, con énfasis en la conservación, recuperación, e incremento del carbono y biodiversidad de la Amazonía. Las actividades REDD+ consideradas para el desarrollo de esta revisión han sido seleccionadas de protocolos actuales de la Unión Internacional de Organizaciones de Investigación Forestal (*International Union of Forest Research Organizations*, IUFRO), para el entendimiento de la relación entre “biodiversidad, carbono, bosques y personas” como componentes clave para el desarrollo de propuestas REDD+ (Kapos *et al.* 2012).

Relación biodiversidad-función ecosistémica

El análisis de la relación biodiversidad y función ecosistémica (BEF, por sus siglas en inglés) ha sido muy importante para entender como la riqueza de especies afecta diferentes procesos ecológicos de los ecosistemas (Oliver *et al*. 2015), así como por la necesidad práctica de conservar y manejar servicios ecosistémicos que tienen transcendentales impactos sobre la humanidad (Cardinale *et al*. 2012). Sin embargo, aunque es evidente la disminución de la biodiversidad a nivel mundial (Strassburg *et al*. 2010), no se conoce cuál es el impacto sobre la pérdida de funciones ecosistémicas (Oliver *et al*. 2015), y menos sobre las tendencias futuras de demanda de bienes y servicios a escala regional. La mayoría de los estudios sobre mecanismos BEF se han enfocado principalmente en la productividad de biomasa vegetal, debido a que el carbono acumulado en la vegetación es determinante en el balance global con la atmósfera (Lasky *et al*. 2014, Brienen *et al*. 2015). Por este motivo, comprender el papel de la biodiversidad en el mantenimiento de las funciones ecosistémicas bajo diferentes niveles de degradación generados por un complejo sistema socioecológico en Amazonas (Figura 1), es fundamental para establecer medidas de conservación y estrategias efectivas REDD+. De igual modo, es necesario identificar la importancia relativa de los predictores de deforestación y de gradación, estimando los impactos sobre las reservas de carbono en la biomasa (Figura 2A) através de gradientes climáticos de la Amazonía (Figura 2B), así como en diferentes tipos de bosques con diferentes etapas de regeneración natural (Figura 2C).

Se ha demostrado como los rasgos funcionales de especies arbóreas pueden ser buenos predictores de la producción de biomasa durante diferentes etapas de sucesión secundaria (Lasky *et al*. 2014), sobre la dinámica de la relación biodiversidad-carbono que es dependiente de la escala espacial (Pooter *et al*. 2015), incluso en sistemas agroforestales (Arshad y Mattsson 2017). Sin embargo, es poco lo que se conoce sobre el efecto que tienen las especies más dominantes en estos procesos ecosistémicos. Por ejemplo, a escala de toda la Amazonía, se ha estimado que apenas 1 % del total de especies de árboles son responsables del 50% de la productividad y almacenamiento de carbono en toda la cuenca, distribuidos en aproximadamente 182 especies hiperdominantes de biomasa, y 184 especies hiperdominantes de productividad (Fauset *et al*. 2015). Esta premisa es fundamental para la selección de especies durante la restauración de servicios ecosistémicos con actividades REDD+, conectando la importancia relativa de los rasgos funcionales a escala de individuos hasta escala de ecosistemas, con la finalidad de categorizar áreas potenciales de restauración en función de filtros ambientales y demanda del sistema socioecológico (Figura 2D). Al mismo tiempo, la información sobre procesos biofísicos podría ser utilizada para generar indicadores de las funciones ecosistémicas, bien para saber el nivel de vulnerabilidad de los ecosistemas y gestión de riesgo frente a presiones de cambios climáticos y antropogénicos, o para evaluar y predecir la capacidad de regeneración de los ecosistemas a través de acciones REDD+.

Cabe destacar que la composición de especies de las comunidades vegetales está cambiando rápidamente a causa de los cambios en el uso de la tierra y el cambio climático, con consecuencias potencialmente graves para la capacidad de recuperación de funciones de los ecosistemas (Cardinale *et al*. 2012, Oliver *et al*. 2015). Una de las principales consecuencias es que la tasa de mortalidad de árboles a nivel mundial está incrementando a causa de intensos y prolongados periodos de sequía, incluyendo el Amazonas, donde árboles grandes están presentando las mayores tasas en comparación con árboles pequeños (Bennett *et al*. 2015). Estos resultados podrían cuestionar la importancia relativa de las especies hiperdominantes en el secuestro y almacenamiento de carbono en Amazonas, porque también podría incrementer la tasa de mortalidad de las especies funcionalmente mas importantes. Finalmente, se resalta la relevancia del fuego en la dinámica de la biomasa y carbono en bosques de la Amazonía, que representan una constante amenaza de degradación (Aragão *et al*. 2014), principalmente en bosques estacionales semideciduales, sabanas estacionales y bosques mixtos con dominancia de bambú, durante periodos de prolongadas sequías interanuales (Brando *et al*. 2014, Nogueira *et al*. 2015, Aguiar *et al*. 2016).

Predictores biofísicos

Ha sido bien demostrado que los suelos de la Amazonía son altamente lixiviados, predominantemente ácidos y de baja fertilidad, mientras que la alta asignación de biomasa está influenciada principalmente por un ciclo cerrado de nutrientes que depende de la alta producción de hojarasca, altas tasas de descomposición, y alta eficiencia en el uso de nutrientes (Quesada *et al*. 2012). Sin embargo, todavía es poco conocida la relación existente de estos procesos ecosistemicos con la biodiversidad y sobre todo, su repercusión en el funcionamiento de los ecosistemas de acuerdo a los predictores biofísicos de cada localidad.

Poorter *et al*. (2016) demostraron que los bosques secundarios neotropicales, incluyendo los de la Amazonía, difieren drásticamente en su capacidad de recuperación de biomasa (promedio de 66 años para recuperar 90% de la biomasa aérea), principalmente impulsado por la variación en la disponibilidad de agua, debido a que las altas precipitaciones y el bajo déficit hídrico, permiten extender la temporada de crecimiento e incrementar la producción de biomasa. Así mismo, explican que la fertilidad de suelos tiene un efecto positivo significativo en la recuperación relativa de biomasa, pero ningún efecto sobre la recuperación absoluta debido a que las grandes diferencias con el macroclima pueden anular efectos más sutiles de la fertilidad del suelo. Por esto mismo, analizando los patrones y procesos determinantes en la estabilidad de la estructura y funcionamiento de los bosques amazónicos (maduros y secundarios) a través de gradientes climáticos, principalmente por el efecto de la precipitación y suelos como predictores biofísicos, es posible estimar la contribución relativa de los efectos que pueden generar los cambios en el uso de la tierra (Figura 1). Es decir, que las futuras investigaciones sobre BEF y acciones REDD+ en la Amazonía, también deberían enfocarse en el análisis simultáneos de predictores antropógenicos y biofísicos sobre variables respuestas como la recuperación de biomasa (Figura 2D).

Una primera aproximación sobre algunos predictores biofísicos que influyen en la deforestación de algunas regiones de la Amazonía, ha sido analizando el efecto que tienen los menores valores de precipitación, mayor déficit hídrico (> 5 meses secos, figura 2B), y suelos con baja fertilidad, sobre la vulnerabilidad y capacidad de regeneración de los bosques lluviosos estacionales semideciduales y sabanas estacionales en el sureste de la cuenca (Brando *et al*. 2014, Nogueira *el at*. 2015), siendo una región conocida como el “arco de deforestación” (Laurance *et al*. 2001). La mayor concentración de población rural, y la continua incidencia de fuegos antropogénicos en esta subregión, son predictores importantes de la degradación forestal. Además, actualmente continúan siendo las zonas con mayor deforestación y fragmentación de toda la cuenca (Brando *et al*. 2014, Lapola *et al*. 2014, Rodrigues-Filho *et al*. 2015, Aguiar *et al*. 2016). Se presume que la tendencia actual de diferentes predictores antropogénicos anteriormente discutidos, y en consecuencia mayores tasas de deforestación para la expansión de la frontera agrícola en esa región del Amazonas, esta gestando un círculo vicioso que está trascendiendo a un irreversible “arco de degradación”.

Es bien conocido que el fuego ha sido utilizado durante muchas generaciones como un medio para el manejo de la tierra con fines agrícolas en la Amazonía (Arroyo-Kalin 2012, Roosevelt 2013, Bush *et al.* 2015, Piperno *et al*. 2015), sin embargo son limitados los estudios que demuestren el efecto sobre las propiedades biológicas, físicas, químicas del suelo, y en consecuencia sobre las trayectorias de sucesión secundaria de los bosques en Amazonas, principalmente evaluando la capacidad de recuperación de biomasa y biodiversidad (D´Oliveira *et al*. 2011). En estudios recientes, se concluye que los distintos regímenes de severidad y frecuencia del fuego como práctica agrícola, provocan marcadas diferencias en la regeneración natural de bosques amazónicos, tanto en su composición de especies como en la acumulación de biomasa (D´Oliveira *et al*. 2011, Wandelli y Fearnside 2015). Bajo este escenario, Aragão *et al*. (2014) destaca la importancia de investigar el efecto multifactorial de predictores antropogénicos y biofísicos (por ejemplo fuego y sequía) sobre la deforestación y emisión de carbono, así como sobre la capacidad de recuperación de funciones ecosistémicas (Figura 3). Sin embargo, existe una primera evidencia sobre aumentos abruptos en la mortalidad de árboles (226%) inducidos por incendios anuales durante un evento de sequía en el Suerte de la Amazonía (Brando *et al*. 2016). Por otro lado, estos investigadores observaron como consecuencia una marcada disminución de la cobertura del dosel (23%) y biomasa viva sobre el suelo (12%), favoreciendo la invasión generalizada por gramíneas inflamables a través del área de borde forestal (80%) donde los incendios fueron más intensos.

Predictores antropogénicos

Existen varios estudios desarrollados en algunas áreas de la Amazonía que describen algunos factores que influyen en la deforestación y degradación forestal, basados en criterios ambientales, culturales, sociales, económicos y políticas de desarrollo rural (Laurance 2002, Peres *et al*. 2010, Arroyo-Kalin 2012, Espindola *et al*. 2012, Diniz *et al*. 2013, Nepstad *et al*. 2014, Verburg *et al*. 2014, Piperno *et al*. 2015). No obstante, continua siendo un desafío lograr integrar sus relaciones después de diferentes escenarios de modificación humana a escala de toda la cuenca. La mayoría de estos cambios en el uso de la tierra son el resultado de una combinación de predictores antropogénicos, sin embargo, para entender esta compleja dinámica a escala regional, también es fundamental profundizar en la evaluación de procesos sociodemográficos que actúan a escala local. En este sentido, Godar *et al.* (2014) observaron que casi la mitad (36.158 km^2) de la deforestación en la Amazonía brasileira entre 2004 y 2011 ocurrieron en áreas de productores con propiedades más grandes (> 500 ha), mientras que sólo el 12% (9.720 km^2) ocurrieron en áreas dominadas por propiedades de pequeños productores (<100 ha). Además, los bosques en áreas dominadas por pequeños agricultores fueron menos fragmentadas y degradadas. Sin embargo, aunque las tasas anuales de deforestación disminuyeron durante este período en 68-85% para todos los actores, la contribución de los mayores terratenientes (> 2.500 ha) en la deforestación anual disminuyó a lo largo del tiempo (63% entre 2005 y 2011), mientras que la de los pequeños productores aumentó 69% durante el mismo período. Ahora el mayor desafío es lograr determinar estos patrones de uso de la tierra en los demás países que hacen parte de la cuenca.

Por otro lado, Espindola *et al.* (2012) encontraron notables diferencias en la dinámica de uso de tierras agrícolas en dos años diferentes (1997 y 2007) entre los estados Rondônia, Mato Grosso y Pará, basados en modelos de i) estructura de asentamientos urbanos y vialidad, así como de ii) desarrollo agrario. Estos investigadores concluyen que la distancia a la carretera y el número de nuevas familias asentadas, tuvo mayor impacto en la deforestación y dinámica en el uso de la tierra durante el 2007, lo que indica que esta relación podría ser más fuerte con el transcurso del tiempo. Así mismo, Lapola *et al*. (2013) analizan la ocupación de la Amazonía brasileña cuantificando las relaciones espaciales y temporales de la deforestación y ocupación de la tierra, argumentado que la aplicación de políticas de distribución y tenencia de la tierra debe transcender a la autorregulación del mercado para amortiguar los efectos detrimentales de la intensificación agrícola que privilegia la optimización en el uso de la tierra. Del mismo modo, Perez y Skole (2003) probando modelos matemáticos de distribución de bosques secundarios en la cuenca del Amazonas, usando variables sociales explicativas como los asentamientos humanos sedentarios y las actividades tradicionales para evaluar el efecto sobre la deforestación, encontraron una relación positiva y significativa con las variaciones espaciales entre diferentes subregiones. Sin embargo, en este mismo estudio los nuevos asentamientos y actividades no tradicionales (cultivos anuales y pastizales) tuvieron una fuerte relación en la mayoría de los modelos analizados. La investigación de Perez y Skole (2003) representa un trabajo pionero de referencia regional que demuestra como los predictores antropogénicos son fundamentales para entender el proceso de deforestación en Amazonas, y por lo tanto, conocer la magnitud de las acciones humanas en la demanda de recursos forestales como premisas básicas para la definición de actividades REDD+.

Las altas tasas de inmigración y de crecimiento poblacional han sido considerados predictores antropogénicos determinantes en los cambios en el uso de la tierra de la Amazonía (Laurance *et al*. 2002), principalmente a través de la agricultura, encontrándose que la población mestiza brasileña aumentó aproximadamente de 2 a 20 millones de personas desde el año 1960, debido a la inmigración desde otras regiones de Brasil, y en consecuencia incrementado las áreas agrícolas en esta región (Laurance *et al*. 2001, Diniz *et al*. 2013, Lapola *et al*. 2013). No obstante, la ampliación de las redes viales y pavimentación de las carreteras que ha favorecido la colonización de nuevas áreas, es una de las principales variables que mejor explica cómo la deforestación se está expandiendo paulatinamente hacia la región central de la Amazonía (Verburg *et al*. 2014). De igual modo, se resalta que la pavimentación de carreteras que cruzan el bioma amazónico está permitiendo un mayor flujo de transporte de productos agroforestales a los mercados europeos y asiáticos, así como también proporcionando un mejor acceso para los productores locales de soja (Nepstad *et al*. 2014, Verburg *et al*. 2014, Rodrigues-Filho *et al*. 2015), lo que esta promoviendo simultáneamente un aumento de la inmigración hacia las mismas áreas con mayor deforestación.

La dinámica demográfica depende en gran medida de la inestabilidad de las poblaciones por las demandas sociales y económicas (fuentes de trabajo y medios de vida), ya que la economía rural de la región se basa en gran medida en los sectores de explotación (forestales, agrícolas), a partir de los recursos de la biodiversidad (Aguiar *et al*. 2013) y acceso a los mercados (Lapola *et al*. 2013, Verburg *et al*. 2014). En cualquier caso, se propone hacer una relación directa de los predictores antropogénicos de deforestación, como el efecto de sistemas viales y dinámica de poblaciones sobre la demanda y manejo de bosques para la provisión de bienes y servicios ecosistémicos. Hasta ahora, sólo Lapola *et al*. (2013) y Aguiar *et al*. (2016) incursionaron en el análisis integral de procesos sociodemográficos y socioeconómicos de la deforestación, sobre la emisión de carbono a la atmósfera en el Amazonas brasileño.

Integrando actividades redd+

Hasta ahora es posible identificar, en forma general, los impactos que pueden tener los predictores antropogénicos y biofísicos de deforestación; pero es evidente que todavía falta mucho por investigar sobre la transcendencia e impactos cuantitativos que pueden tener sobre las actividades REDD+ para recuperar y conservar la relación carbono-biodivesidad. Actualmente son reconocidas dos principales estrategias para mitigar el incremento de carbono en la atmósfera a causa de la deforestación, i) controlando la reducción de emisiones a través de la conservación y manejo sustentable de los ecosistemas forestales, e ii) incrementando la producción de biomasa vegetal como importantes reservas de carbono en la biosfera, a través de prácticas de restauración forestal y rehabilitación de áreas forestales degradadas como parte de las actividades integrales REDD+ (figura 5). En estas estrategias esta implícito un impacto positivo sobre la biodiversidad, aunque resultaría más conveniente enfatizar la importancia del balance biodiversidad-función ecosistémica en términos REDD+.

Generalmente los estudios de sucesión forestal en Amazonas se han desarrollado en áreas agrícolas que fueron destinadas para un único ciclo de cultivo. Después del abandono del sistema agrícola, estas áreas son tradicionalmente conocidas como barbechos (tiempo de descanso de la tierra), porque posiblemente podrían ser usadas para nuevos ciclos de cultivos en años posteriores (Figura 4). Sin embargo, se ha demostrado que el uso sucesivo de las mismas áreas agrícolas abandonadas que se encuentran con diferentes tiempos de regeneración, por dos o más ciclos agrícolas adicionales, influye considerablemente en la pérdida de la biodiversidad y biomasa en la Amazonía (Thompson *et al*. 2012, Aragão *et al*. 2014, Villa *et al*. 2015, Wandelli y Fearnside 2015, Aguiar *et al*. 2016). Esta perspetiva comienza a tener mayor preocupación por el incremento de la poblaciones sedentarias, que dependen de los bosques secundarios próximos para el uso sucesivo y ampliación de las áreas agrícolas. En este contexto, se empieza a concebir una agricultura basada en la biodiversidad y carbono, especialmente a través de la agroforestería que ya presenta importantes experiencias con parcelas permanentes en varias subregiones de la cuenca (Porro *et al*. 2012). Cabe indicar, que varios de los sistemas agroforestales (SAF) más antiguos de la cuenca presentan árboles maduros con una disminución de su capacidad productiva, por lo que se resalta la importancia de investigar el impacto de los SAF con manejo de ciclos sucesivos, especialmente en áreas permanentes para evitar la deforestación de nuevas áreas forestales (Figura 6).

Según Brienen *et al*. (2015) los bosques del Amazonas después de haber sido importantes sumideros de carbono durante los últimos 30 años, podrían perder su capacidad potencial de acumulación de carbono a largo plazo como se esperaba inicialmente, comenzando a ser fuentes de carbono a la atmósfera por el aumento de la tasa de crecimiento y mortalidad de los árboles, contribuyendo en un balance negativo de carbono entre la biosfera y atmósfera. Este resultado indica que si los bosques maduros no garantizan un almacenamiento estable de carbono y la agricultura continúa siendo unas de las principales causas de emisiones de carbono, deberían implementarse actividades REDD+ que vayan más allá de la conservación de bosques y reducción de emisiones; es decir, actividades que también contribuyan con el incremento de las reservas de carbono. Por este motivo, también se proponen cuatro urgentes actividades REDD+ para recuperar e incrementar las reservas de carbono y biodiversidad de bosques en la Amazonía dentro de un sistema de ordenación forestal (Figura 5). Los barbechos mejorados a través de la sucesión controlada, son considerados después de un ciclo de agricultura migratoria como medida de restauración agrosucesional (Tabla 1).

Aún existen pocas experiencias de desarrollo de modelos agrosucesionales en la Amazonía, en particular sobre la sincronización y arreglos espaciales de las especies agroforestales con relación al tiempo de sucesión de especies nativas. En muchas regiones de la Amazonía estos modelos podrían iniciarse a partir de un barbecho tradicional, aprovechando la productividad de los cultivos anuales asociados con arbustos de ciclo corto, en la misma medida que se establecen especies frutales y maderables de ciclo largo, y manejando la cobertura de especies nativas (Villa *et al*. 2015). Sin embargo, estos investigadores discuten que en las comunidades indígenas de Amazonas, los sistemas de barbechos tienen especies nativas que crecen simultáneamente con cultivos tradicionales, pero sin una disposición espacial sistemática para un mejor uso equivalente de la tierra. Por esta razón, se propone un manejo especial para incrementar la densidad de plantas y diversidad de especies agroforestales, conocido también como “barbecho mejorado”, a través del “enriquecimiento de especies”. Este modelo SAF permitiría aumentar los rendimientos de la producción en comparación a monocultivos, bosques secundarios degradados, e incluso que plantaciones forestales, además del potencial para almacenar carbono en el suelo (Figura 6).

Finalmente, es importante resaltar que el establecimiento de sistemas agrosucesionales, y alternativamente los sistemas agroforestales en áreas degradadas, tendrían un impacto importante para la mitigación ambiental desde el momento que estos sistemas sean permanentes por unidad de área (SAF de ciclos sucesivos, figura 6). Para esto es importante el manejo planificado de ciclos sucesivos de los componentes agroforestales, según sus fases fenológicas y productivas, a través de la subdivisión de áreas con diferentes cronosecuencias de desarrollo dentro del mismo sistema agroforestal (ordenación agroforestal). En este sentido, se puede planificar un futuro reemplazo de individuos de especies perennes senescentes, por individuos de fases de desarrollo inicial e intermedio establecidos sistemáticamente (Figura 6). Este sistema tendría la ventaja de mantener la producción de especies anuales asociadas, en cada ciclo de manejo dentro de esas áreas subdivididas, hasta antes del cierre completo del dosel forestal. Adicionalmente, la restauración activa se puede implementar simultáneamente en áreas forestales degradadas dentro de la misma unidad de paisaje, a través de la nucleación con la transposición de banco de semillas provenientes de los bosques maduros circundantes. Esta acción REDD+ también puede implementarse en áreas agroforestales temporales o barbechos que han disminuido su capacidad productiva, pero que han incrementado la acumulación de materia orgánica en el suelo como para crear áreas de amortiguación dentro de la matriz forestal, o también, áreas de conección entre fragmentos y la matriz forestal (Figura 5).

Así mismo, la restauración forestal en Amazonas como parte de las estrategias REDD+ debe trascender a la manipulación de estructura de comunidades ecológicas de acuerdo a sus potencialidades funcionales dentro del ecosistema, porque los servicios ecosistémicos que proporcionan los diferentes tipos de bosques de la región, especialmente el almacenamiento de carbono, también dependen de una restauración funcional. Incluso, en los mismos sistemas agroforestales es posible seleccionar espécies en función de la variación individual del tamaño de los árboles, que podría jugar un papel fundamental en el funcionamiento del ecosistema. Este tipo de enfoque no había sido considerado para SAF; sin embargo, recientemente Arshad y Mattsson (2017) determinaron que la variación de la altura y diámetro de árboles tienen un efecto positivo sobre la biomasa aérea, seguido por un efecto no significativo de la diversidad de especies. Estos investigadores concluyen que la forma de manejo de la estructura de los SAF podría ser un enfoque efectivo para mejorar la productividad en estos sistemas, lo que a su vez dependerá del manejo integral de recursos forestales (Tabla 1).

Conclusiones

Para incrementar la eficiencia en la aplicación de estrategias REDD+ en bosques de la Amazonía, es fundamental entender simultáneamente la relación de patrones y procesos de los ecosistemas forestales con el sistema socioecológico, a través del análisis de predictores biofísicos y antropogénicos, desde una escala local hasta una escala regional. Por lo tanto, además de conocer las características funcionales y estructurales de estos ecosistemas a través de predictores biofísicos que describen los gradientes climáticos y relación BEF, también se propone comenzar a comprender mejor el efecto multifactorial de predictores antropogénicos como la frecuencia, duración e intensidad de diferentes actividades asociadas con los cambios en el uso de la tierra, principalmente a través de la deforestación para la expansión de la frontera agrícola. Así mismo, evaluar simultáneamente los predictores antropogénicos que repercuten directamente sobre la demanda actual y futura de los bienes y servicios ecosistémicos, principalmente bajo escenarios dinámicos de migración, colonización y crecimiento poblacional. Estos predictores de evaluación de acciones REDD+ representan nudos críticos actuales para aumentar la eficiencia de conservación y manejo de ecosistemas forestales en la Amazonía. Por este motivo, se debe comenzar a evaluar la magnitud de los efectos que tienen los predictores de deforestación, especialmente los relacionados con la agricultura, para la integración de acciones REDD+ a través de la rehabilitación de áreas degradadas con sistemas agroforestales sucesionales y permanentes, así como con la aplicación de diferentes métodos de restauración (pasiva y activa) y de manejo integral de recursos forestales.

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Tabla 1. Importancia de los diferentes tipos de manejo del bosque sobre las cinco actividades REDD+ propuestas para la cuenca Amazónica: reducción de emisiones de deforestación (A) y degradación forestal (B), incremento de reservas de carbono (C), manejo sustentable del bosque (D), conservación de reservas de carbono (E). Se indican acciones que tienen una directa y fuerte influencia (**), y acciones con menor potencial (*). Adaptado de Kapos *et al.* (2012).

Tipo de manejo del bosque y acciones potenciales para la conservación.	Actividades REDD+				
	A	B	C	D	E
Conservación de bosques					
Áreas naturales protegidas	**	**	*	*	**
Proteger bosques maduros y secundarios	**	**	**	*	**
Agricultura sustentable					
Recuperación de áreas degradadas	*	*	**	*	
Sistemas Agroforestales	*	*	*	*	*
Barbechos mejorados	*	**	*	*	*
Manejo de recursos forestales					
Reducir tala selectiva		**		*	
Ordenación forestal	**	**	*	**	**
Restauración forestal					
Recuperación de áreas degradadas	*	*	**	*	
Restauración activa			**		
Restauración pasiva	*	*	**	*	

Lista de figuras

multiestratos dominado por cacao (líneas de trazos) con cosechas sucesivas cada 30 años (a), multiestratos con especies frutales, maderables, y cacao, con cosechas cada 25 años (b). Se indican tendencias comparativas para plantaciones forestales más comunes en el trópico y Amazonas (líneas continuas), como *Swietenia macrophylla* King. (c), y *Tectona grandis* L.f. (d), con cosechas aproximadamente cada 20 años para cada especie (Adaptado de De Costa y Suranga 2012, Porro *et al*. 2012).

Fig. 1.

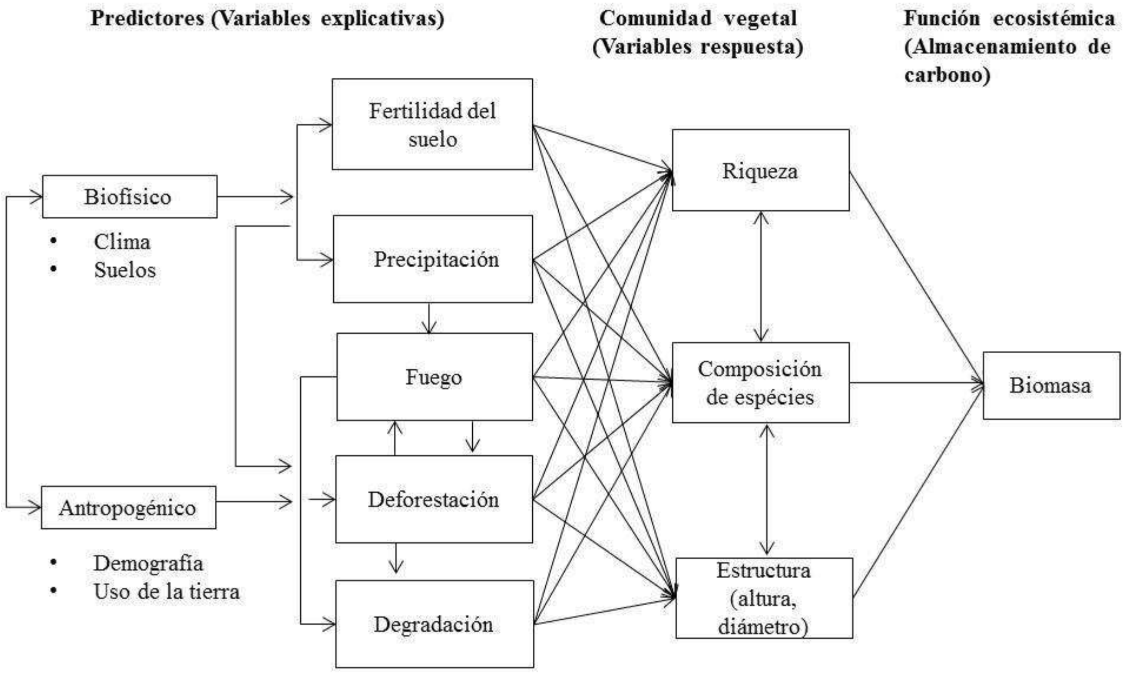
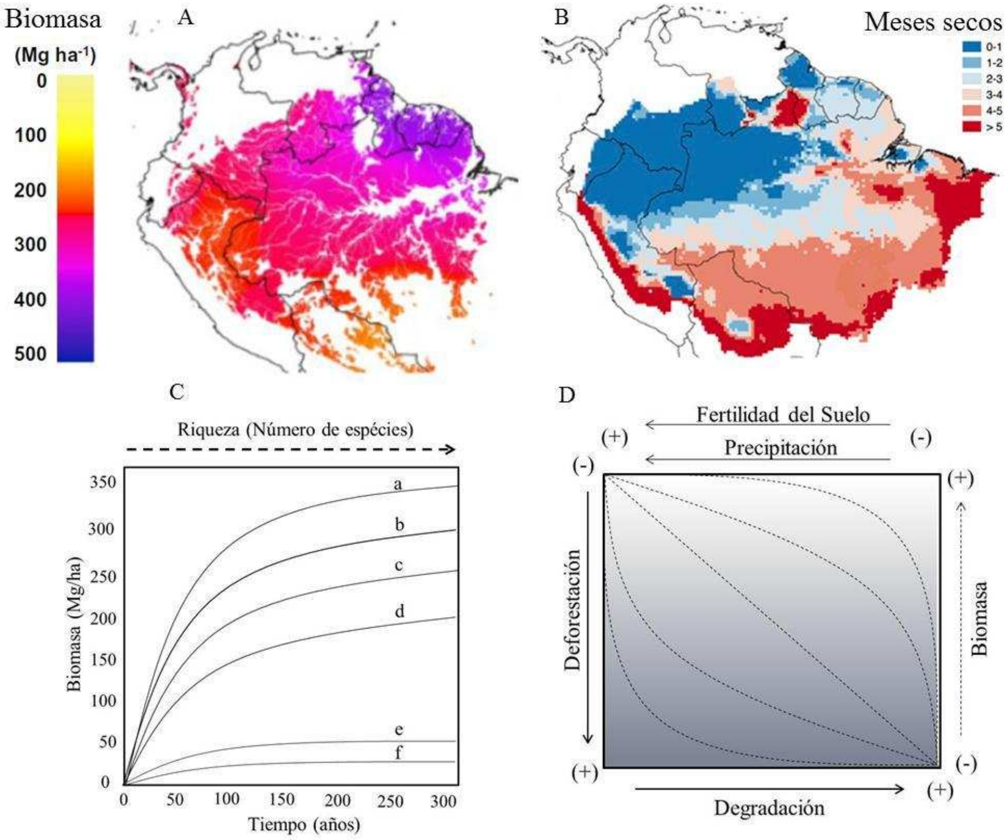

Predictores (Variables explicativas)
Comunidad vegetal (Variables respuesta)
Función ecosistémica (Almacenamiento de carbono)
Fertilidad del suelo
Biofísico
• Clima
• Suelos
Precipitación
Fuego
Antropogénico
Deforestación
• Demografia
• Uso de la tierra
Degradación
Riqueza
Composición de espécies
Estructura (altura, diámetro)
Biomasa

Fig. 2.



Biomasa
(Mg ha-1)
0
100
200
300
400
500
A
B
Meses secos
0-1
1-2
2-3
3-4
4-5
> 5
C
Riqueza (Número de espécies)
Biomasa (Mg/ha)
350
300
250
200
150
100
50
0
a
b
c
d
e
f
0
50
100
150
200
250
300
Tiempo (años)
D
Fertilidad del Suelo
Precipitación
(+)
(-)
(-)
(+)
Deforestación
Biomasa
(+)
(-)
Degradación
(+)

Fig. 3.

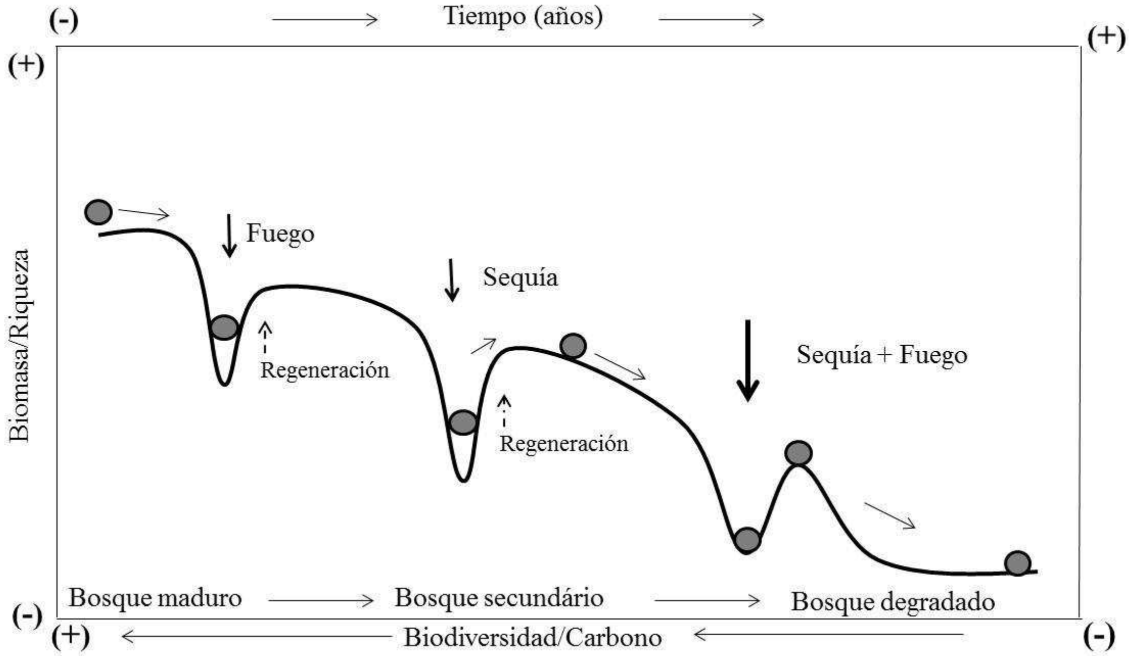

(-)
Tiempo (años)
(+)
(+)
Biomasa/Riqueza
Fuego
Sequía
Regeneración
Sequía + Fuego
Regeneración
(-)
Bosque maduro
Bosque secundário
Bosque degradado
(+)
Biodiversidad/Carbono
(-)

Fig. 4.

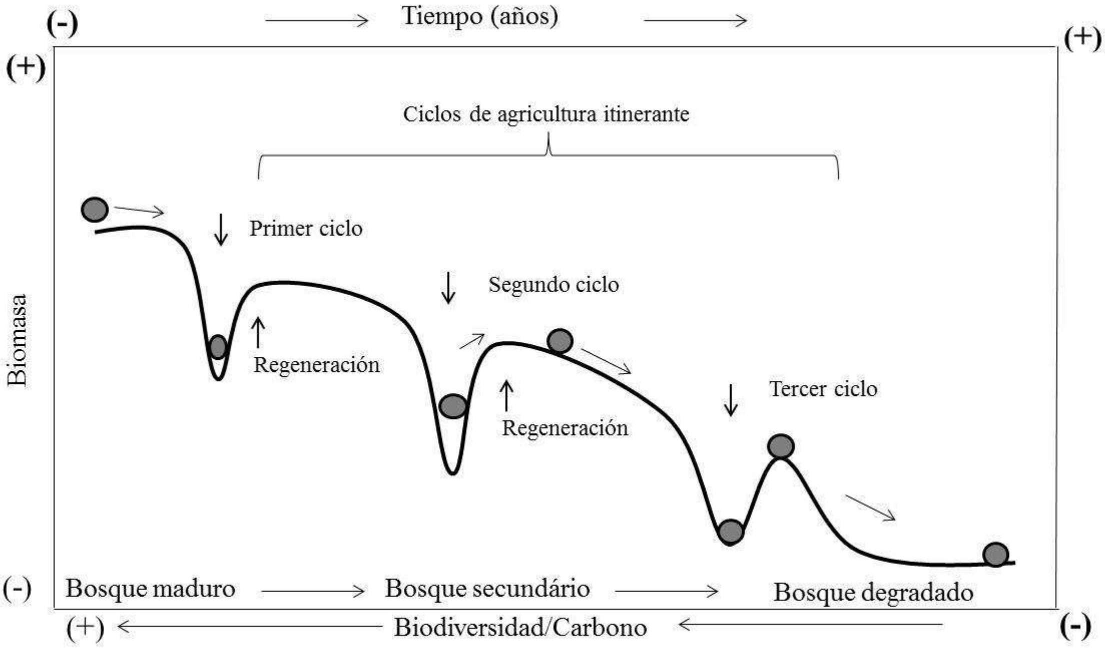

(-)
Tiempo (años)
(+)
(+)
Ciclos de agricultura itinerante
Biomasa
Primer ciclo
Segundo ciclo
Regeneración
Regeneración
Tercer ciclo
(-)
Bosque maduro
Bosque secundário
Bosque degradado
(+)
Biodiversidad/Carbono
(-)

Fig. 5.

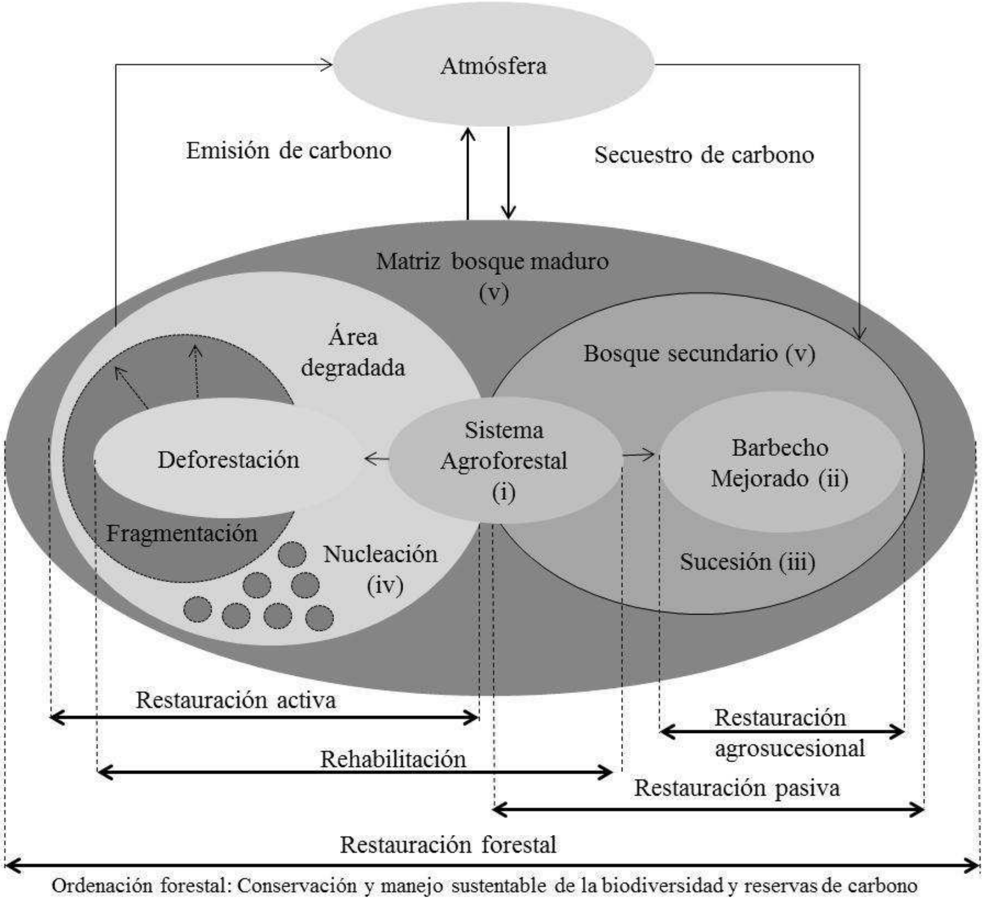
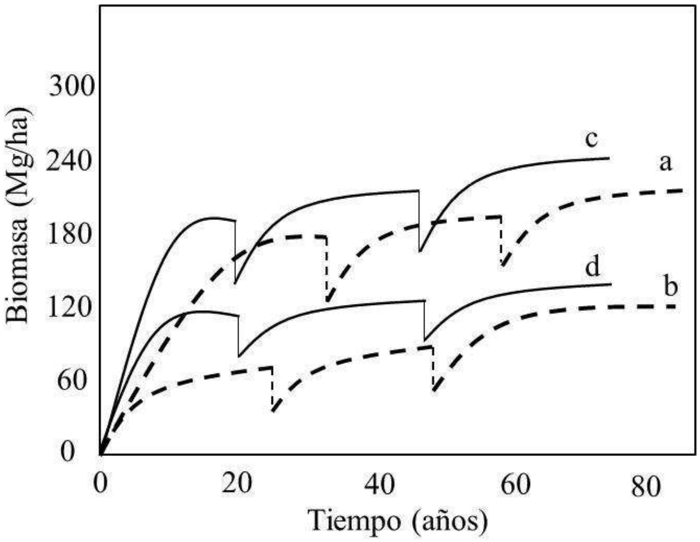

Atmósfera
Emisión de carbono
Secuestro de carbono
Matriz bosque maduro (v)
Área degradada
Bosque secundario (v)
Deforestación
Sistema Agroforestal (i)
Barbecho Mejorado (ii)
Fragmentación
Nucleación (iv)
Sucesión (iii)
Restauración activa
Restauración agrosucesional
Rehabilitación
Restauración pasiva
Restauración forestal
Ordenación forestal: Conservación y manejo sustentable de la biodiversidad y reservas de carbono

Fig. 6.


Biomasa (Mg/ha)
300
240
180
120
60
0
0
20
40
60
80
Tiempo (años)
c
a
d
b

CAPITULO VI: La agroforestería como estrategia para la recuperación y conservación de reservas de carbono en bosques de la Amazonía

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Resumen

Durante los últimos años los continuos cambios en el uso de la tierra en la Amazonía, principalmente a través de la conversión de bosques por prácticas agropecuarias y de extracción, han generado graves transformaciones en la estructura y funcionamiento de los ecosistemas con impactos a escala regional y global. La deforestación para establecer sistemas agrícolas itinerantes es uno de los principales factores que contribuyen con las emisiones de carbono a la atmósfera como uno de los servicios de mayor repercusión ambiental. Sin embargo, existen reconocidos mecanismos de reducción de emisiones de carbono por deforestación y degradación (REDD+), i) bien sea controlando la reducción de emisiones de las fuentes a través de la conservación y manejo sustentable de los bosques, y ii) recuperando e incrementando la biomasa vegetal como importantes sumideros a través de estrategias de rehabilitación y restauración forestal. Con la finalidad de incrementar la eficiencia en la recuperación y conservación de carbono en áreas vulnerables de deforestación y degradación forestal en la Amazonía, se propone como objetivo desarrollar un análisis de los impactos ambientales potenciales de la Agroforestería como alternativa REDD+, a través de i) la rehabilitación de áreas degradadas sometidas a ciclos sucesivos de fuego y cultivos, ii) la restauración pasiva de bosques secundarios, e iii) implementación de barbechos mejorados con el manejo de especies agroforestales. La agroforestería representa una importante alternativa para recuperar y conservar reservas de carbono a través de las principales actividades REDD+ frente a la presión generada por la agricultura itinerante en la Amazonía.

Palabras clave: barbecho mejorado, deforestación, degradación forestal, rehabilitación, restauración pasiva

Introducción

La degradación de los bosques tropicales tiene consecuencias negativas significativas sobre diferentes componentes estructurales y funcionales de los ecosistemas, por lo tanto, también en su capacidad de proporcionar bienes y servicios ambientales con impactos regionales y globales; como es el caso de las reservas de carbono en el suelo y biomasa vegetal, regulación de procesos climáticos, y mantenimiento de la biodiversidad (Thompson *et al.* 2012, 2013). Por esta razón, actualmente los esfuerzos de investigación, ajustes de políticas ambientales y estrategias de gestión a nivel mundial, están dedicando especial atención a la importancia de la conservación y manejo de los bosques tropicales con el propósito de reducir las emisiones de carbono por deforestación y degradación forestal, y mantener un uso sustentable de la tierra para fines agrícolas. En este contexto, existe una particular preocupación por la cuenca amazónica como una de las mayores extensiones de bosques tropicales con mayor capacidad de secuestro y almacenamiento de carbono a nivel mundial (Malhi *et al.* 2006, Pan *et al*. 2011, Saatchi *et al.* 2011, Aragão *et al*. 2014), debido a que presentan alarmantes tasas de deforestación actual y acumulada, siendo una de las mayores en comparación a otras regiones tropicales (Margulis 2004, Laurance *et al*. 2004, Cerri *et al.* 2007, Nepstad *et al*. 2009, INPE 2013).

Se estima que los bosques tropicales pueden almacenar aproximadamente 247 Pg de carbono en la biomasa aérea y subterránea (Saatchi *et al*. 2011), mientras que existen otras estimaciones actuales de carbono que están en el orden de 471 ± 93 Pg, almacenado en la biomasa y otros compartimientos como el suelo, necromasa y hojarasca acumulada (Pan *et al*. 2011). No obstante, debido a los continuos cambios en el uso de la tierra, principalmente a causa de la deforestación y quema para la expansión de la frontera agrícola, una gran parte del carbono almacenado en la biomasa se libera a la atmósfera como dióxido de carbono, en consecuencia el carbono almacenado en los suelos, en el mantillo de hojarasca y materia orgánica, también puede convertirse en una fuente de emisiones debido al incremento de la respiración derivada de la descomposición (Lal 2008, Thompson *et al*. 2012).

La Amazonía ha sido un importante sumidero de carbono durante las últimas tres décadas, pudiendo llegar a almacenar aproximadamente 93 Pg en la biomasa aérea y subterránea; además existen resultados consistentes sobre su alto potencial para el secuestro de carbono como uno de los servicios ambientales de mayor repercusión global (Malhi *et al*. 2006, Cerri *et al.* 2007, Saatchi *et al*. 2011), siendo Brasil el país que presenta la mayor extensión de área, con más del 60 % de toda la cuenca, convirtiéndolo en una región estratégica para la conservación del carbono y mitigación al cambio climático (Soares-Filho *et al*. 2006, Soares-Filho *et al.* 2010, INPE 2013). Sin embargo, un estudio reciente revela que los bosques de la Amazonía están presentando una tendencia a incrementar la tasa de mortalidad de árboles repercutiendo sobre la capacidad de almacenamiento de carbono, por eso también se presume que los impactos del cambio climático pueden tener un efecto preponderante. Así mismo, se conoce que las regiones tropicales han contribuido significativamente como sumidero mundial de carbono entre los años 1980 y 1990, mientras que los resultados actuales muestran que el carbono neto total almacenado en la biomasa de bosques intactos de la Amazonía ha disminuido en un 30 %, desde 0,54 Pg año^{-1} de carbono en la década de 1990, hasta 0,38 Pg año^{-1} en la década de 2000 (Brienen *et al*. 2015).

En las últimas dos décadas, las emisiones netas de carbono derivadas de la deforestación y la degradación tropical eran casi iguales a las emisiones totales procedentes de los cambios en el uso de la tierra a escala global (1,11 Pg año^{-1} de carbono), porque los efectos de estos cambios fueron más o menos equilibrados en zonas tropicales, influyendo en el papel que desempeñan los bosques tropicales como sumideros de carbono a largo plazo (Pan *et al*. 2011). La agricultura de tala y quema también ha contribuido de manera significativa a las emisiones globales de carbono en los países tropicales (Thompson *et al*. 2012), pero aún no existen suficientes estimaciones razonables de las emisiones causadas por este tipo de agricultura itinerante a nivel de la cuenca amazónica, y que actualmente representa un modelo de uso de la tierra no sustentable. A pesar de la reducción de hasta un 80 % de la deforestación en la cuenca amazónica entre los años 2005 y 2013 (INPE, 2013), donde Brasil sigue siendo responsable de aproximadamente el 40 % de los bosques lluviosos tropicales que quedan en el mundo, teniendo un papel vital en el mantenimiento de reservas de carbono terrestre (Laurance *et al*. 2001), aún prevalece una constante degradación forestal debido a la tala selectiva, deforestación para la agricultura, e incendios forestales (Nobre y Borma 2009, Boucher *et al*. 2013, INPE 2013, Aragão *et al*. 2014).

Varios investigadores han analizado diferentes escenarios ambientales frente a los continuos cambios en el uso de la tierra causados por la deforestación en la cuenca amazónica, observando que dichas transformaciones en los ecosistemas repercuten en la pérdida significativa de sumideros de carbono, además de considerables impactos negativos sobre el balance a escala global (Laurance *et al*. 2001, Laurance *et al*. 2004, Aragão *et al.* 2014, Gatti *et al*. 2014). La deforestación en esta región es causada principalmente para la ampliación de áreas cultivadas e incremento de los rendimientos de producción agrícola para cubrir las demandas a escala familiar y mercados locales, así como para mercados nacionales e internacionales (Soares-Filho *et al*. 2006, Porro *et al*. 2012, Boucher *et al*. 2013). Además de las áreas destinadas para cultivos extensivos de soya y la ganadería que ocupa más del 85 % de las tierras agrícolas en la región (Soares-Filho *et al*. 2006, Boucher *et al.* 2013), el tipo de agricultura más practicada se ha caracterizado por ser itinerante, tradicionalmente conocido en diferentes países que conforman la cuenca, como *conuco*, *coivara* o *chakra*, y del cual se desconoce la proporción de área total utilizada en toda la cuenca. Este modelo agrícola consiste en la deforestación de 0,5 a 1,5 ha de bosques primarios o secundarios como parte de la preparación del terreno para el establecimiento de cultivos durante un corto período de tiempo, generalmente de dos a tres años hasta su abandono cuando disminuye la fertilidad de los suelos (D'Oliveira *et al*. 2011, Arroyo-Kalin 2012). Por este motivo, la conservación y manejo sustentable de los bosques en la Amazonía también ha cobrado más importancia durante la última década, frente a la necesidad de prevenir y mitigar el efecto de la acelerada deforestación y degradación forestal causada por diferentes cambios en el uso de la tierra y efectos del cambio climático, principalmente para reducir las emisiones de carbono a la atmósfera (Soares-Filho *et al*. 2006, Nobre y Borma 2009, Nepstad *et al.* 2009, Soares-Filho *et al*. 2010, Porro *et al*. 2012, Aragão *et al*. 2014).

Por estos motivos, la conservación de los bosques amazónicos depende en gran parte de un conjunto de estrategias y acciones orientadas a optimizar el uso y manejo de bienes y servicios ecosistémicos, que simultáneamente garanticen la conservación de reservas de carbono, primordialmente a través de la agricultura. En esa búsqueda de un equilibrio entre desarrollo y conservación, la agroforestería ha sido implementada como una propuesta de agricultura sustentable basada en conocimientos tradicionales e innovaciones tecnológicas, incluso con destacadas experiencias exitosas en comunidades indígenas y rurales (Porro *et al.* 2012, Tremblay *et al*. 2015). La agroforestería como un tipo de manejo de bosque, también es conocida como un modelo de agricultura climática inteligente, porque puede contribuir a incrementar la productividad agrícola basada en la biodiversidad, generando medios de vida sustentables en la misma medida que se controla la deforestación y degradación forestal, como las dos principales actividades para reducir las emisiones de carbono a la atmósfera (REDD). Por otra parte, también es considerada como una estrategia que comprende tres actividades complementarias para la conservación, manejo sustentable e incremento de las reservas de carbono en los bosques (REDD+) a través de la rehabilitación de áreas degradadas (Nair *et al*. 2010, Kapos *et al*. 2012). En todo caso, a pesar de que la discusión sobre el impacto derivado de los diferente tipos de manejo de bosques asociados a las cinco actividades REDD+ no es un asunto nuevo, y que la agroforestería es una práctica antigua y ampliamente conocida a través de numerosas experiencias de campo y publicaciones de diferentes índole, desafortunadamente no existe una propuesta integral que analice simultáneamente las potencialidades y relaciones existentes para la conservación e incremento de reservas de carbono como estrategia alternativa de mitigación ambiental frente a la deforestación para el establecimiento de sistemas agrícolas itinerantes que traen como consecuencia la formación de paisajes forestales fragmentados y con diferentes niveles de degradación, así como la emisión de carbono a la atmósfera.

Por esta razón, se presenta una revisión descriptiva y analítica donde se contextualiza sistemáticamente aspectos teóricos y conceptuales sobre algunos impactos ambientales potenciales de la agroforestería sobre el manejo de bosques en la Amazonía, como alternativa para incrementar la eficiencia en la conservación y recuperación de carbono en áreas vulnerables de deforestación y degradación forestal a causa de la agricultura itinerante. En la primera sección de este trabajo, se justifica como la agroforestería representa un modelo que integra diferentes actividades REDD+ de agenda mundial, y posteriormente se describen dichas estrategias basadas en métodos de restauración forestal. De este modo, se discute cómo la agroforestería puede representar un modelo de gestión de referencia a escala de toda la cuenca, aun cuando se reconocen que otros tipos de uso de la tierra siguen siendo las causas de mayor impacto de deforestación y degradación. Esta revisión está fundamentada en los criterios actuales considerados por la Unión Internacional de Organizaciones de Investigación Forestal (*International Union of Forest Research Organizations,* IUFRO) sobre la relación existente entre bosques y carbono como aspecto clave para alcanzar los objetivos REDD+ a escala global.

La agroforestería como estrategia redd+

Es bien conocido que el carbono es un elemento fundamental en diferentes procesos biológicos, ecológicos y biogeoquímicos desde una escala de organismos vivos hasta una escala global, el cual puede ser almacenado y transferido constantemente entre reservorios distribuidos en la biósfera, atmósfera, hidrósfera y litósfera. En este sentido, los océanos representan el compartimiento que almacena la mayor cantidad, con aproximadamente 38.400 Pg de carbono, mientras que las reservas orgánicas del suelo oscilan entre 1.550 Pg, la atmósfera con 760 Pg, y el componente biótico con 560 Pg. El ciclo biológico consiste en el intercambio de gases entre la biomasa viva y la atmósfera, donde la absorción del CO_2 por las plantas ocurre a través de la fotosíntesis, y cerca del 50 % del total absorbido es liberado inmediatamente por la respiración autotrófica; así también, la respiración heterotrófica que ocurre en el suelo durante el proceso de descomposición representa una fuente de retorno a la atmósfera (Lal 2008, Ciais *et al*. 2013).

Lal (2008) y Ciais *et al*. (2013) mencionan que las actividades humanas producen una emisión anual aproximada de 8 Pg de carbono, de los cuales 6,4 Pg provienen de combustibles fósiles, y 1,6 Pg de la deforestación como parte de los cambios en el uso de la tierra, siendo la segunda fuente global más importante de emisiones de CO_2 a la atmósfera. Los bosques con sus suelos contienen hasta tres veces la cantidad de carbono contenida actualmente en la atmósfera, y procesan anualmente a través de la fotosíntesis y la respiración una cantidad equivalente de 15 a 20 % de ese total. Estos procesos biogeoquímicos son fundamentales para mantener los patrones climáticos globales y regionales, evidenciando la importancia de los bosques para el mantenimiento de flujos y reservorios. Frente a este escenario, es relevante indicar que la transformación de los bosques tropicales debido a la deforestación ha sido un proceso continuo a partir del periodo pre agrícola hace unos 8.000 años, estimándose una pérdida del 50 % de la cobertura forestal original del planeta principalmente a causa de la agricultura, siendo la mayor parte durante las últimas tres décadas. Hasta hace un poco más de una década se estimó que cerca de un 40 % de los bosques del mundo se encontraban poco intervenidos, pero que de igual forma eran áreas vulnerables de deforestación para la agricultura (Bryant *et al*. 1997, Roosevelt 2013). En el caso de los bosques de la Amazonía, estudios arqueológicos demuestran que han estado sometidos a la deforestación y uso del fuego para el establecimiento de sistemas agrícolas itinerantes durante toda la era antropocénica (Arroyo-Kalin *et al*. 2012, Roosevelt 2013).

Por otra parte, es importante destacar que los bosques lluviosos tropicales poseen una considerable capacidad de almacenamiento de carbono, que oscila entre 100 y 300 Mg ha^{-1}, y la producción de biomasa puede variar entre 70 y 400 Mg ha^{-1} (Baker *et al*. 2004, Saatchi *et al*. 2011), mientras que los bosques de la Amazonía como mayor reserva de carbono del planeta puede presentar una capacidad aproximada de almacenamiento de 200 Mg ha^{-1}; aunque todavía se conoce muy poco sobre el nivel de variación a causa de los cambios actuales en el uso de la tierra, variación de los patrones climáticos, y efecto de los incendios forestales (Malhi *et al*. 2006, Pan *et al*. 2011, Saatchi *et al.* 2011, Aragão *et al*. 2014, Gatti *et al*. 2014). Otras investigaciones explican que durante las últimas tres décadas ha estado ocurriendo un incremento en la biomasa vegetal de los bosques húmedos neotropicales, observándose el mismo patrón en diferentes bosques amazónicos, por eso se discute que la principal causa ha sido la elevada concentración de carbono en la atmósfera que estimula la producción primaria neta (Baker *et al*. 2004, Malhi *et al*. 2006, Pan *et al*. 2011, Saatchi *et al.* 2011); aunque resultados de una investigación actual indican que los sumideros de carbono están declinando debido a una disminución de la tasa de cambio de biomasa neta y un aumento de las tasas de mortalidad cuando se analizan a una escala de tiempo de largo plazo, representando un incremento de 30 % de las reservas de necromasa desde 1983 hasta 2012 (Brienen *et al*. 2015). Bajo estos escenarios actuales y futuros, queda evidente de que las diferentes estrategias de conservación y manejo sostenible de los bosques de la Amazonía, no son suficientes alternativas para la conservación, recuperación e incremento de las reservas de carbono, y que deben implementarse actividades REDD complementarias como medios de mitigación ambiental. Frente a esta perspectiva, se destacan las ventajas de los sistemas agroforestales para la recuperación de áreas forestales degradadas e incremento de las reservas alternativas de carbono a corto plazo, a partir de 10 hasta 30 años, e incluso también podría ser a largo plazo cuando se mantienen ciclos agroforestales sucesivos en la misma unidad de producción.

Este incremento significativo de emisiones de carbono a la atmósfera, han generado cambios importantes en el patrón de acumulación y dinámica del mismo a escala global, lo que simultáneamente ha influido sobre alteraciones en el clima a un ritmo alarmante (Ciais *et al*. 2013). A pesar de atravesar este escenario ambiental, son bien conocidas dos estrategias propuestas para mitigar el incremento de carbono en la atmósfera, i) controlando la reducción de emisiones a través del manejo de las fuentes, e ii) incrementando la biomasa vegetal como sumideros a través de prácticas de forestación, reforestación, y rehabilitación, siendo esta última relevante con el establecimiento de sistemas agroforestales. De este modo, con la agroforestería se pueden conservar bosques primarios con mayores reservorios de carbono, limitando la demanda de áreas forestales para el establecimiento de nuevos ciclos de cultivos itinerantes, y en consecuencia reduciendo la deforestación y degradación forestal (Kapos *et al*. 2012), o través del manejo de bosques secundarios durante las primeras etapas de sucesión, después que es abandonado un sistema agrícola itinerante, también conocidos como barbechos mejorados o sistemas agroforestales sucesionales (Vieira *et al*. 2009, Kapos *et al*. 2012).

Es conveniente resaltar que en la actualidad los sistemas agroforestales representan el modelo agrícola más apropiado para la recuperación y conservación de bosques tropicales (Vieira *et al*. 2009, Kapos *et al.* 2012), por ser un sistema de uso de la tierra donde se cultivan especies agrícolas y arbóreas en la misma unidad de producción durante un prologando periodo de tiempo, con arreglos espaciales y temporales específicos en función de las características biológicas y ecológicas de cada especie, y de las condiciones ambientales de cada localidad. También es necesario señalar que la descripción funcional de los sistemas agroforestales aún se encuentra en constante evaluación para comprender mejor la relación existente entre producción y conservación de bosques tropicales. Además, se destaca que más allá de la cosecha de productos agroforestales y conservación de reservas de carbono, estos sistemas también podrían generar otros tipos de servicios ambientales, como la conservación de suelos para aumentar la productividad y mitigar los procesos erosivos, aumentar la biodiversidad de organismos descomponedores y mantener los niveles de fertilidad.

Conservación de reservas de carbono

Los bosques son los ecosistemas que secuestran y almacenan mayor cantidad de carbono en la biomasa vegetal y en el suelo, por lo que es bien reconocido tienen una función importante en el intercambio de carbono entre la biosfera y la atmósfera, siendo los bosques de la Amazonía los más importantes desde el punto de vista de conservación de reservas de carbono (Lal 2008, Pan *et al*. 2011, Saatchi *et al*. 2011). Buena parte de las reservas de carbono en la región, hasta un 50% de almacenamiento y productividad, depende de los árboles con mayor abundancia que está fuertemente sesgada hacia relativamente pocas especies *hiperdominantes*, representando apenas 1% del total de especies (Fauset *et al*. 2015). Sin embargo, se ha determinado que las tasas de deforestación en el Amazonas brasileño han sido una de las más rápidas del mundo, especialmente entre los bosques tropicales, con un promedio de pérdida de 17.486 km^2 año^{-1} (Espindola *et al*. 2012). Por lo tanto, comprendiendo los principales patrones y procesos determinantes en la estructura y funcionamiento de los bosques amazónicos, principalmente los relacionados con la dinámica del carbono en el mantenimiento de la productividad y biodiversidad, será posible tener mejores aproximaciones en la estimación de los impactos generados por la agroforestería con estrategia REDD+ frente a la deforestación para el establecimiento de sistemas agrícolas itinerantes. Además de la agroforestería, se reconoce que existen diferentes tipos de acciones de manejo de bosques que también pueden contribuir con las cinco actividades REDD+, destacándose la importancia del i) manejo del fuego, ii) la reducción de la tala selectiva, iii) la aplicación de métodos de restauración y reforestación, iv) así como la ordenación ambiental para delimitar dichas acciones.

Frente a este contexto ambiental, los patrones espaciales y temporales de pérdida de bosques en la Amazonía también han sido variables y heterogéneos que dificultan su entendimiento, aunque es evidente que las áreas con mayor tasa de deforestación ocurren en Brasil, entre el este y sur de la cuenca, en los estados de Pará, Mato-Grosso y Rondonia, considerados también como zonas calientes de deforestación (Laurance *et al*. 2001, Espindola *et al*. 2012, Porro *et al*. 2012, Diniz *et al*. 2013, Verburg *et al*. 2014) con poca potencialidad para la conservación de reservas de carbono. En la Amazonía brasileña, las tasas de deforestación estimadas oscilan entre 1,1 hasta 2,9 millones ha año^{-1}, mientras que el área total deforestada ha alcanzado aproximadamente 85 millones ha, aproximadamente el 14 % de la superficie total (INPE 2013). Aunque existe un escenario negativo, también se cuenta con estrategias esperanzadoras para reducir la deforestación, y con los esfuerzos recientes se ha logrado ampliar la red de áreas protegidas de 1,26 a 1,82 millones Km^2 adicionales, que contienen el 51 % de área restante de bosque en la región (Nepstad *et al*. 2009, Soares-Filho *et al*. 2010, INPE 2013). A pesar de todo, la reducción de la deforestación en los últimos años ha tenido lugar frente a las continuas presiones en el uso de la tierra, especialmente por los impactos causados por la ampliación de las plantaciones de soya y áreas ganaderas de Brasil como actividades de alta rentabilidad económica (Soares-Filho *et al*. 2006, Boucher *et al*. 2013, Verburg *et al*. 2014).

Una primera aproximación consistente sobre algunos criterios ambientales que permiten evaluar la dinámica de la deforestación de algunas regiones de la Amazonía ha sido analizando la variabilidad climática, como el efecto que tienen las bajas precipitaciones, las severas y prolongadas estaciones de déficit hídrico, y suelos con baja fertilidad, principalmente sobre la vulnerabilidad de los bosques deciduos y semideciduos de la cuenca (Nobre y Borma 2009, Aragão *et al*. 2014, Gatti *et al.* 2014), que muy probablemente repercute en la productividad en términos de ganancia de carbono y en la capacidad de regeneración después que ocurre una perturbación. Así mismo, los incendios antropogénicos se están convirtiendo en una causa cada vez más común en la degradación forestal, especialmente en las zonas con mayor deforestación y fragmentación (Nobre y Borma 2009, Aragão *et al*. 2014). En consecuencia, se presume que el sur y este de la Amazonía, con dominancia de bosques estacionales, seguiría siendo la región más vulnerable a la degradación forestal por su alta sensibilidad a la incidencia de incendios antropogénicos y condiciones climáticas extremas, y en consecuencia una menor capacidad para la recuperación y conservación de reservas de carbono.

Es evidente que para controlar la deforestación causada por diferentes actividades de envergadura dentro de la cuenca amazónica, se necesitará de mayor esfuerzo en el ajuste, conciliación y aplicación rigurosa de políticas agrarias de desarrollo rural y políticas de conservación ambiental, especialmente por el impacto causado por la ganadería extensiva, plantaciones de soya, la minería, y tala selectiva para fines industriales. Estas tendencias actuales de uso de la tierra, con probabilidades de expansión en la Amazonía, permiten presumir que se está gestando un círculo vicioso de degradación forestal con autoperpetuantes consecuencias ecológicas que afectaría la resiliencia de los ecosistemas y capacidad de secuestrar y almacenar carbono. Sin embargo, la agroforestería como estrategia REDD+ frente a la situación actual, puede contribuir a conservar y recuperar las reservas de carbono, por lo menos mitigando la presión por deforestación de nuevas áreas para fines agrícolas, a través de la implementación de métodos comprobados de rehabilitación de áreas forestales degradadas en relación a los gradientes climáticos y potencialidades ecológicas de las especies. Estas actividades REDD+ deben ser planificadas desde una escala local hasta una regional, bajo diferentes escenarios actuales y futuros de cambios en el uso de la tierra que permitan ordenar y clasificar áreas potenciales para la conservación y manejo sustentable de bosques, así como de acuerdo a la capacidad de resiliencia y vulnerabilidad de degradación. Además de la importancia de integrar las actividades REDD+ en todos los escenarios, también se destaca la relevancia potencial que podrían tener las especies hiperdominantes para la restauración y rehabilitación forestal.

Recuperación de reservas de carbono

La recuperación de las reservas de carbono en una matriz de paisaje forestal de la Amazonía, donde existen áreas con diferentes estados de conservación y manejo para el establecimiento de sistemas agrícolas itinerantes, es posible a través de la implementación de diferentes actividades REDD+. De acuerdo a este patrón generalizado de uso de la tierra en la cuenca, y según las potencialidades de la agroforestería a escala regional, en esta revisión se presentan tres acciones para recuperar e incrementar las reservas de carbono en los diferentes tipos de bosques. En este sentido, se propone i) la rehabilitación de áreas degradadas sometidas a ciclos sucesivos de uso del fuego y cultivos, y con poco tiempo de barbecho, que afecta la capacidad de regeneración del bosque. Con la rehabilitación de áreas forestales degradadas también se contribuye con ii) la restauración pasiva evitando el uso continuo de bosques secundarios durante diferentes etapas de sucesión después de un ciclo de cultivo itinerante, y evitando la deforestación de bosques primarios. En este caso, también se podría implementar un manejo sustentable de los bosques secundarios a través de iii) barbechos mejorados, aumentando la incorporación y densidad de siembra de especies arbóreas agroforestales de ciclo largo durante la sucesión controlada, después de un sistema agrícola itinerante.

Rehabilitación de áreas forestales degradadas. Existen reportes generalizados de que el tiempo y capacidad de recuperación de carbono de los bosques después de una perturbación, dependen de la escala, intensidad y las formas de degradación (Thompson *et al*. 2012, 2013), como ha sido descrito para bosques de Borneo bajo una agricultura itinerante por más de 200 años, y donde la acumulación de biomasa fue significativamente menor en los sitios sometidos a seis o más ciclos de cultivo, debido a una pérdida de bancos de semillas y capacidad de rebrote de especies (Lawrence *et al*. 2004). Pero en todos los casos dependerá del efecto multifactorial entre la resiliencia de los ecosistemas y métodos de rehabilitación agroforestal implementados. En la cuenca Amazónica, el fuego ha sido utilizado durante muchas generaciones como un medio para el manejo de la tierra con fines agrícolas (Arroyo-Kalin 2012, Roosevelt 2013), del mismo modo ha sido identificado como un agente físico que ha estado influyendo en varios procesos ambientales responsables de la degradación forestal, aunque se desconoce la magnitud de sus consecuencias a escala regional. También se conoce que el fuego tiene un fuerte efecto negativo sobre la acumulación de carbono en bosques secundarios, debido a que con cinco o más ciclos de fuego en una misma área, se puede reducir significativamente en más del 50 % del total, además de acelerar la degradación forestal (Zarin *et al*. 2005, Thompson *et al*. 2012, 2103). Por lo tanto, es de esperarse que el proceso de rehabilitación agroforestal pueda ser más complejo y difícil en áreas sometidas a excesivos e intensos ciclos de fuego, donde los bosques secundarios disminuyen su capacidad de recuperar su carbono original dentro del intervalo promedio de retorno. Esto también ocurre por la continua mortalidad post-incendio y baja fertilidad de los suelos, además de la reducción de las tasas de acumulación de biomasa por la dominancia de especies ruderales herbáceas y arbustivas con baja densidad de la madera.

En cualquier escenario, se espera que los sistemas agroforestales establecidos en áreas forestales degradadas puedan llegar a secuestrar y almacenar mayores cantidades de carbono en la biomasa vegetal y suelos en comparación con los sistemas agrícolas itinerantes sin árboles y de corto periodo de tiempo. Por eso, la plantación de árboles en áreas degradadas podría ser relativamente eficiente comparada con otras estrategias de uso del bosque, debido a que producen mayor cantidad de hojarasca que mejora paulatinamente la fertilidad de los suelos y favorece la acumulación de carbono a corto plazo (Nair *et al.* 2010, Kapos *et al.* 2012). Con este modelo es posible conservar cantidades importantes de carbono en la biomasa mientras se producen alimentos y se conserva la biodiversidad local durante largos periodos de tiempo bajo ciclos sucesivos de cultivos perennes en la misma unidad de producción, donde cada ciclo agroforestal puede comprender entre dos y tres décadas. En ese aspecto, se estima que el establecimiento de sistemas agroforestales a escala global puede capturar cerca de 38 billones Mg de carbono, lo que equivaldría aproximadamente a 15 % del total de las emisiones fósiles del mismo período, con una capacidad de almacenamiento de carbono que oscila entre 12 y 200 Mg ha^{-1}, y aproximadamente 95 Mg ha^{-1} en zonas tropicales (Albrecht y Kandji 2003, Nair *et al*. 2010). Además, Albrecht y Kandji (2003) considerando el carbono en la biomasa aérea y en el suelo, y estandarizando los valores a 50 años de rotación, indican que los sistemas agroforestales podrían acumular entre 1,1 y 2,2 Pg de carbono en todo el mundo, con lo que podría reducir la tasa de acumulación del mismo en la atmósfera. Así mismo, las diferentes prácticas silvícolas como la selección, asociación y densidad de plantación de las especies, deben ser criterios técnicos determinantes en los procesos asociados con la captura de carbono en sistemas agroforestales, lo que debe ser considerado para las diferentes condiciones ambientales y ecológicas de la cuenca amazónica.

Restauración pasiva. Es bien conocido que existe un impacto negativo significativo de la deforestación y el fuego sobre la capacidad de regeneración del bosque secundario en la Amazonía. No obstante, es importante resaltar que después del primer ciclo de uso de la tierra las tasas de acumulación de carbono en la biomasa aérea suelen ser mayores a corto plazo durante las dos primeras décadas de sucesión debido a una mayor demanda para el rápido crecimiento, aunque a largo plazo después de 30 años tiende a estabilizarse hasta alcanzar paulatinamente niveles de un bosque primario (Feldpausch *et al*. 2004). Además, la productividad primaria neta en bosques secundarios puede llegar a ser de tres a cinco veces mayor que la de los bosques primarios, aunque las reservas de carbono en los bosques primarios son mucho mayores. Por esta razón, los bosques secundarios representan un destacado sumidero de carbono a escala mundial que compensa parcialmente las emisiones causadas por las altas tasas de deforestación en las mismas regiones tropicales, incluyendo la cuenca amazónica (Luyssaert *et al*. 2008, Feldpausch *et al*. 2004). Cabe destacar que, hasta ahora no existen estudios que consideren el efecto sinérgico de la intensidad, frecuencia y duración de la agricultura itinerante sobre los procesos biogeoquímicos de bosques amazónicos, especialmente sobre la dinámica del carbono; aunque es razonable presumir como patrón general, que los repetidos ciclos de tala y quema están afectando la capacidad de recuperación de la biomasa y por lo tanto repercute en la pérdida progresiva de carbono.

La dinámica de sucesión natural del bosque secundario, es también conocida como una estrategia de restauración forestal, que consiste en comenzar a conservar permanentemente áreas que fueron previamente deforestadas. Sin embargo, una vez que los bosques alcanzan la madurez cuando la acumulación de carbono comienza a estabilizarse, es posible que haya una disminución de este importante sumidero al punto que podría mantener un balance neutro entre la acumulación y pérdida de biomasa, incluso no se descarta un escenario futuro donde el balance neto de biomasa presente valores significativamente negativos si no se colocan en práctica diferentes acciones sinérgicas de mitigación ambiental a través de las actividades REDD+. En este sentido, el balance neto de carbono de los bosques amazónicos depende de la contribución relativa de los sumideros actuales en proceso de regeneración, y de las pérdidas por deforestación. Por esta razón, estimando los niveles de déficit de sumideros que podrían generar diferentes escenarios de desequilibrio, sería posible ejecutar acciones integrales REDD+ en función de la cantidad necesaria de carbono que debería ser recuperado y almacenado en sumideros potenciales y alternativos, como por ejemplo a través de diferentes modelos agroforestales.

D´oliveira *et al*. (2011) evalúan la regeneración de bosques amazónicos después de diferentes severidades de quema y concluyeron que los resultados fueron consistentes con otros estudios realizados en la misma región, donde los distintos regímenes de severidad pueden producir fuertes diferencias en la regeneración natural, en la estructura, composición, y acumulación de biomasa. Generalmente, la práctica de la restauración pasiva ocurrirá en áreas que fueron usadas anteriormente para el establecimiento de sistemas agrícolas, y donde el uso del fuego puede generar cambios significativos en la dinámica de sucesión vegetal. Así mismo, es importante tener presente que el uso del fuego es sólo una de las principales prácticas de manejo de la agricultura itinerante, por lo que el efecto ponderando de todas las posibles prácticas implementadas previamente causaría un mayor impacto sobre los procesos de restauración pasiva. Finalmente, es importante señalar que la recuperación de reservas de carbono también podría comenzar desde los mismos sistemas agrícolas itinerantes recientemente establecidos, a través de la agroforestería sucesional, bajo la condición de que sea el último ciclo de manejo tradicional de tala y quema.

Restauración agrosucesional. Existe una limitada investigación sobre el desarrollo de sistemas agroforestales regenerativos análogos (SAFRA) y barbechos mejorados en la Amazonía como alternativas de manejo de los bosques secundarios con relación a la dinámica de ganancia de carbono, en particular sobre la fenología reproductiva de las especies, y por lo tanto en la sincronización y arreglos espaciales. No obstante, existen otras razones importantes y conocidas para su adopción que en muchas regiones de la cuenca puede iniciar a partir de un sistema agrícola itinerante, o también después del abandono durante la etapa de barbecho cuando inicia la sucesión de especies de árboles nativos, e incluso en cualquiera de las etapas durante la dinámica conuco-barbecho a través de una restauración planificada. En estos sistemas es posible establecer diferentes especies agroforestales para simular la dinámica de la sucesión natural del bosque secundario; es decir, considerando la cronosecuencia de establecimiento de acuerdo con los ciclos de vida de las mismas y controlando el crecimiento de las especies nativas, por lo que durante la primera etapa se aprovecha la productividad de los cultivos anuales combinados con arbustos de ciclo corto, mientras se establecen y desarrollan las plántulas de frutales de ciclo largo.

Los barbechos mejorados, como modelo de restauración agrosucesional, comienzan cuando nuevos cultivos de ciclo medio y largo, generalmente frutales, son plantados durante la etapa inicial de sucesión natural de especies nativas, a veces justo después de la cosecha de especies anuales y bianuales cuando el sistema agrícola es abandonado. Los sistemas de barbechos mejorados pueden ser productivos por un rango de tiempo comprendido entre 5 y 20 años de cosecha (Vieira *et al*. 2009). Estos modelos agroforestales son a veces más productivos que sistemas de sucesión sin especies agroforestales conocidos como barbechos improductivos, presentando mayor acumulación de hojarasca en el suelo, y mayor almacenamiento de carbono en la biomasa aérea. Según diferentes experiencias de campo en Amazonas, se ha observado que en las comunidades indígenas los sistemas de cultivo generalmente están asociados con especies nativas de los bosques creciendo simultáneamente sin una disposición espacial sistemática, pero en términos de producción puede ser mayor que los monocultivos o bosques secundarios degradados.

En el caso de la Amazonía brasileña, la agroforestería es fundamental para mantener un desarrollo sustentable en áreas de preservación permanente y áreas de reserva legal a través de la creación de áreas productivas en pequeñas propiedades indígenas o rurales (Schroth *et al*. 2006). En estas unidades de conservación la agroforestería tiene la ventaja de contar con una alta biodiversidad y recursos locales, en la misma medida que se protegen otras áreas de bosques primarios o secundarios con diferentes etapas de sucesión. Por lo tanto, de conformidad con las normas legales y criterios técnicos y ambientales de cada tipo de área protegida, se propone el modelo SAFRA para áreas de preservación permanente, que también son conocidos con otros nombres como *Forest Garden* o barbechos mejorados; y para las áreas de reserva legal, se propone adoptar el modelo conocido como *Taungya* que se caracteriza por el uso de especies arbóreas asociadas con cultivos agrícolas (Schroth *et al*. 2006, Vieira *et al*. 2009).

En general, los dos modelos agroforestales propuestos pueden tener un impacto considerable en relación a i) la conservación y recuperación de reservas de carbono en la biomasa aérea y subterránea, aumentando la densidad de siembra de árboles, y ii) mejorando la gestión sustentable de los productos forestales no maderables, iii) la conservación de la biodiversidad a través de la restauración pasiva y rehabilitación de áreas degradadas. Las principales razones para la adopción de sistemas agroforestales en Amazonas, son principalmente de carácter ambiental que también pueden tener repercusiones en el ámbito social y económico bajo un enfoque de sustentabilidad.

Conclusiónes

La agroforestería representa una importante alternativa para el manejo sustentable de los bosques con el propósito de recuperar y conservar reservas de carbono a través de las principales actividades REDD+ frente a la presión generada por la agricultura itinerante en la Amazonía. Por lo tanto, se proponen como acciones REDD+ i) la rehabilitación de áreas forestales degradadas, que al mismo tiempo contribuye directamente con ii) la restauración pasiva de bosques secundarios, o también a través de iii) barbechos mejorados con la incorporación de especies agroforestales durante la sucesión controlada. Finalmente, la iii) conservación permanente de bosques primarios debería ser parte clave de la estrategia integral de conservación de carbono.

Una de las premisas más relevantes para proponer a la agroforestería como un tipo de acción REDD+, surge frente a la preocupación del incremento de las emisiones de carbono a la atmósfera y disminución del potencial de los sumideros de carbono que tienen los bosques de la Amazonía a largo plazo, después de alcanzar el equilibrio e incremento de las tasas de mortalidad de árboles (Brienen *et al*. 2015). Por esta razón, se sugiere que a través de la agroforestería se podrían recuperar reservas de carbono a corto plazo con las propuestas indicadas en este estudio, del mismo modo es necesario evaluar el impacto potencial a largo plazo de los de ciclos agroforestales sucesivos sobre los posibles déficits de sumideros. En un escenario futuro optimista, se espera que las tasas anuales de conservación y almacenamiento del carbono obtenidas mediante el conjunto de actividades REDD+ deberían aumentar con el tiempo, principalmente a través de la reducción de la deforestación y degradación forestal, pero posiblemente también los sistemas agroforestales sucesivos podrían alcanzar su máxima acumulación de carbono con cantidades similares a las de bosques secundarios en regeneración.

En base al conocimiento existente sobre las ventajas de los sistemas agroforestales, aún se necesita profundizar mucho más sobre el análisis de los impactos ambientales potenciales bajo escenarios actuales y futuros en la cuenca, frente a los patrones de uso de la tierra en las diferentes unidades ecológicas existentes, que además se convertiría en una acción REDD+ clave para la planificación del manejo y conservación de las reservas de carbono a escala regional. Además de las acciones asociadas con los impactos positivos derivados de la agroforestería, no se debe descartar la integración de los diferentes tipos de manejo de bosques que permiten contribuir con las cinco actividades REDD+. Así mismo, se destaca la importancia de evaluar simultáneamente el impacto sobre los componentes ambientales y sociales relacionados con la conservación de la biodiversidad, seguridad alimentaria y medios de vida sostenibles de pobladores locales como aspectos determinantes para mantener un desarrollo sustentable en esta trascendental región tropical.

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CAPÍTULO VII. Exchanges of Agroforestry Experiences between the Piaroa Communities in the Venezuelan State of Amazonas: Public Relations for the Agroforestry Sciences

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Backgrounds of the Case Study

There is enough evidence on itinerant agriculture among growing settler indigenous populations, being one of the causes for forests loss in the Orinoco-Amazon Region ((Llambí & Llambí, 2000; Villa *et al* 2012). Thus, the agroforestry systems are considered an alternative of sustainable production for the region from a social and environmental point of view (Brown, 1996; Torres & Villa, 2014). Given the need to contribute with the conservation and sustainable use of the forests in the Venezuelan State of Amazonas, the PROBIODIVERSA Foundation for the biodiversity conservation, and the National Institute for Agricultural Research (INIA- Instituto Nacional de Investigaciones Agrícolas) started a management project for the development of Agroforestry systems with the Piaroa indigenous communities in 2009, as a way to recover degraded areas, preserving the forests, producing food and creating means of subsistence for these families. After a complex process of addressing the communities, taking actions for the project, attaining accomplishments and obtaining some products, there is now a good deal of interest among new indigenous families and communities in participating in the initiative. There is no doubt that inducing and strengthening collective abilities with the help of bilingual indigenous interpreters was the key to the success of the Project in those communities. Since then, the exchange of experiences between participant Piaroas has been fundamental, and it has become true through didactic fieldwork as means to promote Agroforestry activities and to practice conservation and forest sustainable management among new Piaroa communities.

Strategic Planning

In order to have an effective communication between the indigenous communities who were responsible for implementing the project and those that felt interested in participating in the conservation and sustainable management of the forest initiative, the main objective was to promote the dialogue and the exchange of knowledge regarding local experiences with Agroforestry systems among the Piaroa communities of the Cuao and Cataniapo Rivers, in the State of Amazonas, Venezuela. The participation of public and private institutions was very important as well. There were also guided visits and demonstrations along with an external and direct communication on Agroforestry experiences, as means of performing comparative analysis on the setting up and management of the systems, as well as on the given advantages and disadvantages. It was expected that the institutions in the Amazonas State had a direct relation with the communities, so that a synergic work of communication could be possible in the Agroforestry field, through participant research, strengthening of skills and knowledge exchanging.

The general structure of the demonstrative fieldwork of each experience in each one of the visited communities, included three main steps, i) induction and awareness, ii) fieldwork: visiting the Agroforestry systems, iii) General discussions: positive and negative aspects of the analysis, and local planning of important further steps.

Target Group

The basin of the Cuao River is inhabited mainly by the ethnic group of Piaroa and it is considered to be the habitat of their ancestors. There have been some important transformations for this settler population and the forest ecosystems surrounding them. On the other hand, if compared to the creole populations, the Piaroa People remaining near the Upper Cuao show the most traditional and native traits of the Piaroa culture due to their greater isolation (Zent; 1997).

During each fieldwork and its demonstrations, each community linked to the project has participated with nearly 40 people, and, up to now, there are 153 people in all, representing different families within each of the six Piaroa communities. Also, during the fieldworks, there have been public servants from the INIA and PROBIODIVERSA, as well as members of other Piaroa communities from the Autana Municipality such as Piedra Tonina, Pendare, Caño Veneno, and a special participation of the farmers from the Gavilán and Sardi communities in the basin of the Cataniapo River (Atures Municipality, Amazonas State). In the same way, male and female Piaroa farmers coming from over 15 families living in the communities of Coromoto de Cuao, Raudalito Picure, Raudal de Danto and Raudal de Perro, have actively participated. They had a main role at the events taking place there because of their relevant experiences in traditional crops.

Key Messages

The key message being delivered through sharing knowledge and exchanging intercultural experiences between indigenous communities and every actor involved in the managing of the forests, is a growing sense of sensitivity towards conservation and sustainability of the goods and services provided by those forests and through the products obtained so far. This has produced new academic outcomes and papers on the perspectives of the current and future situations of the management and use of the soil in the basins of the Cuao and Cataniapo Rivers in the State of Amazonas. Furthermore, the achievements of the organization of the community to meet the demands of their systems of agricultural production could be replicated, having in mind the relations between the social and environmental realities.

Communication Tools Used

It is important to stress that during the course of all the demonstrations held along the fieldwork as part of the exchanges of Agroforestry experiences, the indigenous people of the mentioned communities have actively participated, gaining a more advanced technical profile and carrying out roles as bilingual interpreters from Spanish to Huottöja and from Huottöja to Spanish because most of the participants and families from the Piaroa communities do not manage to communicate in Spanish. Within the external and direct communication methods held in those demonstrative Agroforestry lands, there is no doubt that the bilingual communication tool was key to meet the goal of attracting the interest and facilitating the understanding of the participant indigenous, who felt at the end like wanting to engage in the management project and in the breaking down of a communication barrier that had jeopardized previous projects that ended up being unsuccessful.

Lessons learned

Such communication method implemented, including demonstrative fieldwork through experience exchanges, is presumed to be the most suitable one for the particular target group, characterized by its Spanish understanding limitations, and lack of professional training, or even schooling. Thus, the key message had to be transmitted through bilingual interpreters, for the better comprehension and acceptance of the management processes, since the very moment of approaching to the communities, and until the time to start working on the technical implications for the maintenance of the plots of Agroforestry land and on the measures taken for the management and conservation of the secondary and primary forests -specially their biodiversity-. Similarly, it is to be emphasized that these experience exchanges made the encounter of different key actors possible (INIA, PROBIODIVERSA and indigenous communities) when crucial debates on subjects of a worldwide interest are taking place, such as the Climate change’s impact mitigation, the adaptation to it, or the restoration of degraded areas and their biodiversity by doing and learning directly through close experiences.

Recommendations

The workshops held with the Piaroa communities from the Venezuelan Amazonia, need to be inclusive and, above all, they must take into account the importance of the participation of the women, who, through generations have been responsible for the transmission of the awareness of their cultural values. In fact, among the Piaroa, women are in charge of many daily subsistence activities for the family's sake, as well as of the management of the biodiversity of the forests, besides working for the raising of their children. Now, assuming that men and women have different ways of relating to the environment, it has been necessary to evaluate the existing link between gender and biodiversity, especially during the realization of activities of the Agroforestry management project. This gender approach has shaped a lot the ways to transmit the information about the means of using, conserving and managing the biodiversity to the Piaroa's present and future generations. Women generally devote a great deal of the time in their lives managing biodiversity and raising their children simultaneously, most of the times.

The network collaborative works has been an important key to manage and replicate this Agroforestry initiative. PROBIODIVERSA has held this team work with the INIA, with Piaroa communities from the basin of the Cataniapo River, and under the formal consent of the Environment Ministry (MPPAMB- Ministerio para el Ambiente), with the purpose of promoting the participative model of the Agroforestry management, as a friendly way to treat the environment, also capable of locally generating important social, economic and environmental benefits. The initiative started under the PPD/GEF, and was coordinated by the PNUD in Venezuela. The foundation takes action in this initiative by articulating its work with researchers from the INIA who have offered a consistent contribution, also in community management, while the indigenous people have given significant amounts of natural resources, physical or hand labour, and willingness to maintain and replicate experiences. In the meantime, the MPPAMB has been monitoring activities in order to guarantee a legal framework. Thus, more and more key allies have come to make part of the team, like the Foundation for the Development of the Sciences (FUDECI- Fundación para el Desarrollo de las Ciencias) and its participation in different events and logistical support for commuting. At the same time, professors from the ULA (Universidad de Los Andes), the UCV (Universidad Central de Venezuela), and students from still other universities have been invited for the same purposes. Finally, two nutrition cooperatives have been set for the phase of food transformation.

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CONCLUSÕES GERAIS

Nossos resultados demostraram que a intensificação da agricultura itinerante, reduzindo o tempo de pousio e aumentando o número de ciclos, reduz a recuperação da riqueza, composição de espécies e área basal de florestas secundárias após de períodos produtivos (**Capítulo I**). De forma contrária, depois de um único ciclo de agricultura itinerante, ocorre um padrão contrastante, onde duas décadas após o abandono do cultivo a recuperação da riqueza de espécies em uma floresta secundária atinge aproximadamente um 70% da riqueza de uma floresta madura. No entanto, a recuperação da composição das espécies nesse mesmo período atingiu uma média de 25% em relação à floresta madura. A alta diversidade beta é presumivelmente um fator determinante para a rápida recuperação da riqueza de espécies em florestas secundárias nesta região (**Capítulo II**).

Nosso estudo mostra que a diversidade beta explica até 70% da variação na riqueza total de espécies entre os sítios, provavelmente devido a que as manchas desmatadas estão inseridas dentro de uma matriz de floresta madura, com maior abundância de dispersores potenciais e com menor distância de fontes de sementes para a colonização e estabelecimento de espécies arbóreas. Este contexto ecológico também justifica o elevado *turnover* taxonômico observada durante a sucessão. No entanto, a similaridade da comunidade mostrou divergências marcadas através da sucessão (diversidade beta taxonômica e funcional), indicando que as espécies pioneiras estão dominando essas florestas secundárias, quando comparadas às florestas maduras com maior riqueza e dominância de espécies tolerantes à sombra. Assim, a diversidade funcional foi menor do que a diversidade beta taxonômica, provavelmente devido a um menor *turnover* funcional em comparação com o *turnover* taxonômico (**Capítulo III**).

Nossos resultados proporcionam importantes evidencias sobre relação BEF durante a sucessão secundaria de uma floresta tropical Assim, os modelos de equação estruturais testados sobre dominância funcional (CWM) e diversidade funcional (FD), permitiram explicar variações na biomassa acima do solo de forma individual. O modelo integral para explicar o efeito conjunto, só CWM dos traços funcionais analisados tiveram efeitos diretos significativos sobre a biomassa cima do solo. Isto indica que CWM da densidade da madeira e diâmetro do caule são bons preditores, corroborando a hipóteses de razão de biomassa como principal modelador do funcionamento ecossistêmico na floresta semidecidual estudada. O tempo de sucessão foi o melhor preditor para explicar variações da biomassa acima do solo em todos os modelos SEM explorados, seguidamente da textura solo que teve afeitos significativos positivos sobre a biomassa acima do solo, em comparação à fertilidade do solo que apresentou efeitos negativos e não significativos (**Capítulo IV**).

Nosso estudo contribui no entendimento da relação BEF ao longo da sucessão secundária, e pode ajudar a predizer como as florestas tropicais respondarão aos cenários futuros de mudanças climáticas. Por esse motivo, discutimos que para aumentar a eficiência na implementação de estratégias REDD+ em florestas da Amazônia, é necessário compreender simultaneamente a relação de padrões e processos dos ecossistemas florestais com o sistema sócio-ecológico, através da análise de preditores biofísicos e antropogênicos, a partir de um nível local para uma escala regional. Por conseguinte, além de conhecer as características funcionais e estruturais destes ecossistemas através preditores biofísicos que determinam a relação BEF, nós também propomos avaliar o efeito multifactorial dos preditores antropogênicos como a frequência, duração e intensidade de diferentes atividades associadas às mudanças no uso do solo, principalmente através do desmatamento para a expansão da fronteira agrícola. Por esta razão, devemos começar a avaliar a magnitude dos efeitos das mudanças no uso da terra, especialmente os relacionados à agricultura, para propor medidas de integração de ações REDD+ através da reabilitação de áreas florestais degradadas com sistemas agroflorestais permanentes, bem como com a aplicação de diferentes métodos de restauração (passiva e ativa) e gerenciamento integral de recursos florestais (**Capítulos V e VI**).