NATHÁLIA VIEIRA HISSA SAFAR

CHANGES IN SOIL AND VEGETATION ATTRIBUTES DURING LOWLAND ATLANTIC FOREST SUCCESSION IN BRAZIL

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

VIÇOSA
MINAS GERAIS - BRASIL
2018

Ficha catalográfica preparada pela Biblioteca Central da Universidade Federal de Viçosa - Câmpus Viçosa

T
Safar, Nathália Vieira Hissa, 1989-
S128c Changes in soil and vegetation attributes during lowland
2018 Atlantic forest succession in Brazil / Nathália Vieira Hissa Safar. – Viçosa, MG, 2018.
ix, 60 f. : il. (algumas color.) ; 29 cm.

Texto em inglês e português.
Inclui anexos.
Orientador: Carlos Ernesto Gonçalves Reynaud Schaefer.
Dissertação (mestrado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Ecologia vegetal. 2. Sucessão florestal. 3. Resiliência (Ecologia). 4. Comunidades vegetais. 5. Sequestro de carbono. 6. Solos - Composição. 7. Formigas. I. Universidade Federal de Viçosa. Departamento de Biologia Vegetal. Programa de Pós-Graduação em Botânica. II. Título.

CDD 22. ed. 581.7

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APROVADA: 09 de março de 2018.

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(Orientador)

Dedico este trabalho aos meus pais, Roberta e Sergei, e a minha irmã Deborah. Vocês me deram forças para chegar até aqui.

AGRADECIMENTOS

Agradeço aos meus pais, Roberta e Sergei, pelo carinho, amor e apoio nas minhas decisões durante toda a minha vida. À minha irmã Deborah por estar sempre ao meu lado, compartilhando de momentos felizes e de aprendizado. Amo vocês.

Agradeço ao meu companheiro Júlio por todo apoio e companheirismo durante todos esses anos, você me ensinou a ver o mundo e a biologia com outros olhos e sem você eu não teria chegado até aqui. À Polinha, sempre muito carinhosa e companheira, sua presença faz toda a diferença na minha vida. Amo vocês.

Ao meu co-orientador Luiz Fernando Magnago pelo apoio durante toda essa jornada, pela sua disponibilidade em me auxiliar em vários momentos chave do meu projeto, desde a construção da ideia, desenho amostral e análises dos dados. Sem suas sugestões e críticas certamente não conseguiria alcançar os meus objetivos.

Meus sinceros agradecimentos ao meu orientador Carlos Schaefer, que sempre esteve disposto a me auxiliar quando eu precisava, pelas diversas oportunidades e viagens que me proporcionou nesses dois anos: Cumuruxatiba, Parque Estadual do Brigadeiro, e a mais incrível de todas: Expedição para Antártica! Muito obrigada pela oportunidade de trabalhar com você, por toda a ajuda e atenção durante estes últimos anos e, por proporcionar a realização deste projeto.

Ao pessoal do Terrantar, especialmente à Claudinha que sempre se mostrou disponível a ajudar no que for preciso; sem você eu não teria conseguido os recursos necessários para realizar esse projeto.

Ao CNPq pela concessão da bolsa de Mestrado. Ao ICMBio pela liberação dos estudos na REBIO do Córrego Grande e na FLONA do Rio Preto. Ao pessoal da REBIO Córrego Grande, Gabriel e Zé, e ao pessoal da FLONA do Rio Preto, Alberto, Murilo e Leandro, pelo apoio logístico e pela atenção. À Suzano Papel e Celulose, pela liberação de estudos em suas reservas. Ao Samir Rolim, por compartilhar os dados de solos das áreas da Reserva Natural da Vale e pelo apoio logístico na mesma.

Ao pessoal que me ajudou nas diversas campanhas de campo que realizei no ano de 2017: Tássio, Matheus, Scarlett e Luca pelo campo no PARNA do Descobrimento; ao Hugo pela coleta na Reserva da Vale; ao pessoal que me ajudou nas coletas nas UCs de Conceição da Barra: Carlinha, Carlos Aquila, Zé, Tosco, Marquito, Moacir, Matheus e seu irmão Gabriel, Natália e Luiz Magnago. Vocês abriram muitas trilhas, montaram muitas parcelas, cavaram diversos buracos, aguentaram mutucas e pernilongos, e fizeram do trabalho de campo algo divertido e descontraído, sem vocês esse projeto não aconteceria, meus sinceros agradecimentos.

Aos companheiros de Antártica e Punta Arenas, minha gratidão pelo mês maravilhoso que vivemos juntos, uma experiência incrível que guardarei para o resto da vida: Flavinha, André Thomazini e Bruno; aos polacas Dasha, Kriztoff e Maciej vocês também fizeram diferença nessa aventura.

Aos meus queridos amigos de Viçosa e da vida que sempre estiveram ao meu lado oferecendo sua companhia, apoio e amizade; sinto-me privilegiada em tê-los por perto. Vocês realmente fizeram e fazem diferença na minha vida, carregarei sempre boas lembranças de todos vocês.

Aos meus companheiros angoleiros da Tribo do Morro, em especial meu Professor Daniel Angoleiro, pelo contato diário e vivência sob os ensinamentos da Capoeira Angola. Com certeza a capoeira foi essencial para a conclusão dessa etapa.

Por fim agradeço à Universidade Federal de Viçosa, em especial ao Departamento de Biologia Vegetal, que me aceitou como mestranda.

SUMÁRIO

RESUMO

SAFAR, Nathália Vieira Hissa, M.Sc. Universidade Federal de Viçosa, março de 2018. **Mudanças nos atributos do solo e vegetação durante a sucessão de florestas de tabuleiro no Brasil.** Orientador: Carlos Ernesto Gonçalves Reynaud Schaefer. Coorientador: Luiz Fernando Silva Magnago.

Distúrbios antrópicos, como a fragmentação e o desmatamento, causam a perda de biodiversidade e estoque de carbono, afetam a produção de serapilheira, causam mudanças drásticas no microclima no chão da floresta o que afeta a dinâmica dos nutrientes do solo, e consequentemente, afetam o funcionamento do ecossistema. Após uma floresta sofrer distúrbio se inicia um processo de sucessão secundária, que envolve mudanças nas comunidades de plantas e animais (principalmente artrópodes), no estoque de carbono, produção de serapilheira e nas propriedades do solo. A Mata Atlântica brasileira é uma das florestas tropicais mais diversas e ameaçadas do mundo, e sua paisagem é composta principalmente por pequenos fragmentos que se encontram em algum estádio de regeneração devido à impactos humanos passados. Esses fragmentos em regeneração desempenham um importante papel na mitigação do carbono e na conservação da biodiversidade. Para investigar as mudanças ao longo da sucessão e a resiliência de florestas de tabuleiro, nós estabelecemos três objetivos principais: (i) avaliar os efeitos do corte raso, com remoção total das árvores, nas propriedades químicas do solo e sua resiliência; (ii) avaliar os efeitos da sucessão na riqueza e composição de árvores e formigas, estoque de carbono total e acima do solo, nos componentes do solo (C orgânico, P, Al^{3+} e soma de bases); e (iii) o tempo que as florestas de tabuleiro em regeneração levariam para atingir os níveis de florestas maduras próximas, para cada parâmetro. Este estudo foi conduzido em florestas preservadas e florestas em regeneração do norte do Espírito Santo, Brasil. Para atingir o objetivo (i) analisamos e comparamos dados de solo (pH, P, Al^{3+}, K^{+}, $Ca^{2+} + Mg^{2+}$), coletados em dois momentos (1978, 2017), de uma floresta madura (controle) e uma floresta próxima que sofreu corte raso como parte de um experimento de longo prazo realizado em 1980, na Reserva da Vale (Espírito Santo, Brasil). Para atingir os objetivos (ii-iii) nós adotamos uma abordagem de cronossequências utilizando duas florestas maduras e onze florestas em regeneração com diferentes idades, distribuídas nas regiões Norte do Espírito Santo e Sul da Bahia, Brasil. Ao avaliar os efeitos do corte raso nas propriedades do solo, nossos resultados mostraram que não houve diferenças significativas entre os tratamentos para nenhum dos componentes do solo

(LMM; $p>0.05$). Sendo assim, ambas as florestas apresentaram a mesma dinâmica do solo ao longo dos 39 anos: aumento de pH (LMM; $p<0.01$) e diminuição de Al^{3+} trocável ao longo dos anos (LMM; $p<0.001$), ausência de mudanças nos níveis de P, K^+ e $Ca^{2+} + Mg^{2+}$ (LMM; $p>0.05$). Estes resultados sugerem que o P disponível e as bases trocáveis, K^+ e $Ca^{2+} + Mg^{2+}$, sejam resistentes ao corte raso de árvores. Outros estudos comparando estes resultados com a dinâmica das árvores das mesmas áreas ajudarão a esclarecer e entender o padrão encontrado. Além disso, ao avaliar os efeitos da regeneração nos atributos florestais, encontramos relações positivas e significativas ($p<0.001$) entre a idade do fragmento e a riqueza e composição arbórea, a composição de espécies de formigas e o estoque de carbono total e acima do solo, sugerindo que estes parâmetros podem ser usados como indicadores de recuperação florestal. No entanto, não encontramos relação entre as propriedades do solo e o avanço da sucessão ($p>0.05$). Este estudo prevê que as florestas de tabuleiro em regeneração levariam cerca de 57-126 anos para recuperar a riqueza e composição de espécies de árvores e formigas, e levariam muito mais, cerca de 188 anos para recuperar o estoque total de carbono. Além disso, essas florestas estão potencialmente sequestrando 1.04 Mg C ha^{-1} yr^{-1}, portanto contribuindo com um importante serviço ecossistêmico que é o sequestro de CO_2. Nossas descobertas sugerem que a riqueza de formigas e os solos de florestais ombrófilas do norte do Espírito Santo podem ser resistentes a distúrbios antrópicos. Por fim, nossos resultados mostram que as florestas de tabuleiro são resilientes, porém levariam aproximadamente de 50 a 200 anos para recuperar o estado original de biodiversidade e funcionamento ecossistêmico, evidenciando a necessidade imediata de desenvolver estratégias para selecionar áreas com maior potencial de regeneração natural.

ABSTRACT

SAFAR, Nathália Vieira Hissa, M.Sc. Universidade Federal de Viçosa, March, 2018. **Changes in soil and vegetation attributes during lowland Atlantic forest succession in Brazil**. Adviser: Carlos Ernesto Gonçalves Reynaud Schaefer. Co-adviser: Luiz Fernando Silva Magnago.

Human disturbances, such as fragmentation and clear-cut logging, cause the loss of biodiversity and carbon stock, affect litter production, cause microclimatic changes at the forest floor, which affect soil nutrient dynamics, and consequently affect the ecosystem functioning. After a disturbance the process of secondary succession begins, which involves changes in plant and animal communities (mainly arthropods), carbon stock, litter production and soil properties. The Brazilian Atlantic forest is one of the most diverse and threatened tropical forest in the world, and its landscapes are mainly composed by small fragments that are in some stage of recovery from past human disturbance. These second-growth fragments have an important role in carbon mitigation and biodiversity conservation. To investigate the changes during forest succession and the resilience of lowland rain forests, we established three main objectives: (i) to assess the effects of whole-tree logging forest clearance on soil properties and their dynamics; (ii) to assess the effects of stand age on tree and ant species richness and composition, aboveground and total C pool, and soil nutrients (organic C, P, Al^{3+} and sum of bases) and (iii) to estimate the time secondary lowland forests take to reach the mature forests levels for each parameter. This study was conducted in old-growth and second-growth lowland rain forests from northern Espírito Santo State, Brazil. To accomplish the objective (i) we analyzed and compared soil data (pH, P, Al^{3+}, K^+, Ca^{2+} + Mg^{2+}), collected in two moments (1978, 2017), from an old-growth forest (control) and one adjacent forest that was cleared as part of a long-term experiment performed in 1980, at the Vale Natural Reserve (Espírito Santo State, Brazil). To accomplish the objective (ii-iii) we adopted a chronosequence approach with two old-growth and 11 second-growth forests at different ages, distributed in the northern Espírito Santo and southern Bahia States, Brazil. When assessing the effects of forest clearance on soil properties, we found no significant differences between treatments for any soil component (LMM; $p>0.05$). Thus, both forests showed the same soil dynamic along the 39 years of interval: increasing pH (LMM; $p<0.01$), and decreasing Al^{3+} over the years (LMM; $p<0.001$), and no changes in P, K^+ and Ca^{2+} + Mg^{2+} (LMM; $p>0.05$). This result suggest that available P, and exchangeable bases K^+, Ca^{2+} + Mg^{2+} may be resistant to whole-tree removal. Further studies comparing our results regarding the effects of forest clearance on soil properties with the long-term tree dynamic of similar forested areas will help to clarify and understand the pattern found. Moreover, when assessing the effects of forest regeneration on forest attributes, we found positive significant relations ($p<0.001$) between stand age and tree species richness and composition, ant species composition and carbon pool (total and aboveground), suggesting that these parameters can be used as indicators of forest recovery. However, we found no relationship between soil properties and forest regeneration ($p>0.05$). This study predicts that secondary lowland rain forests would take several years (57-126 yr) to recover species richness and composition, and much longer, 188 yr to recover C pool, and that these forests are potentially sequestering 1.04 Mg C ha^{-1} yr^{-1}, thus contributing to the important ecosystem service of CO_2 sequestration. Our findings suggest that ant species richness and soils of lowland forests can be resistant to human disturbances. Finally, our results indicate that lowland second-growth forests are resilient, but it would take approximately 50 to 100 years to recover the original state of biodiversity and ecosystem functioning, evidencing that we urgently need to develop strategies for selecting areas with highest natural regeneration potential.

I. Introdução Geral

As florestas tropicais estão sujeitas a diversos distúrbios antrópicos, como o corte seletivo, desmatamento e a fragmentação (Malhi et al., 2014). Estes distúrbios causam a perda de biodiversidade (Laurance et al., 2002; Gibson et al., 2011; Newbold et al., 2015), a diminuição dos estoques de biomassa e carbono das florestas (Magnago et al., 2015; Baccini et al., 2017) e mudanças drásticas no microclima no chão da floresta que afetam as propriedades físicas, químicas e biológicas do solo (Covington, 1981; Johnson et al., 1991; Dahlgren and Driscoll, 1994; Guariguata and Ostertag, 2001). Por essas razões, o desmatamento e a degradação das florestas tropicais são especialmente danosas ao meio ambiente e ao funcionamento ecossistêmico.

Após um distúrbio a floresta inicia um processo de regeneração natural, que envolve mudanças na estrutura e composição das comunidades vegetais (Oliveira-Filho et al., 1997; Liebsch et al., 2008; Magnago et al., 2011; Lasky et al., 2014), na produção de serapilheira (Lohbeck et al., 2015; Huang et al., 2017), nas propriedades do solo (Covington, 1981; Reiners et al., 1994; Magnago et al., 2011; Lewis et al., 2014) que podem ser usadas como indicadores da qualidade do solo e do funcionamento ecossistêmico (Schoenholtz et al., 2000), e nas comunidades de formigas (Dunn, 2004; Schmidt et al., 2013; Solar et al., 2016). Durante a sucessão secundária a riqueza de espécies tende a aumentar (Liebsch et al., 2008; Schmidt et al., 2013), bem como o estoque de biomassa (Lohbeck et al., 2015; Chadzon et al., 2016; Poorter et al., 2016), os nutrientes e a matéria orgânica do solo (Covington, 1981; Brown and Lugo, 1990; Lewis et al., 2014). As florestas em regeneração são consideradas eficientes sumidouros de nutrientes e carbono, devido ao seu alto potencial de produtividade (Gower et al., 1996) e elas apresentam uma alta taxa de produção de serapilheira (Brown and Lugo, 1990) que é a maior fonte de transferência de nutrientes para o solo (Capellesso et al., 2016) através da sua decomposição e lixiviação.

A trajetória de sucessão das florestas pode ser investigada através de duas abordagens: dinâmica e cronossequências (Chadzon et al., 2007). A primeira consiste em monitorar a mesma área ao longo do tempo, e a segunda consiste em ordenar as florestas em regeneração em uma ordem cronológica, florestas estas que diferem quanto ao tempo desde o distúrbio ou abandono, mas que ocorrem em tipos de solos similares e estão sujeitos a condições ambientais similares (Chazdon, 2014). Ordenar as florestas em regeneração em uma ordem cronológica permite comparações ao longo de uma sequência sucessional, portanto essas abordagens têm sido utilizadas em estudos de mudanças temporais em comunidades vegetais (Lohbeck et al., 2012; Buzzard et al., 2016; Poorter et al., 2016; Rolim et al., 2017), comunidades de formigas (Schmidt et al., 2013), produção de serapilheira (Huang et al., 2017) e nas propriedades do solo (Feldpausch et al., 2010; Walker et al., 2010).

Além disso, essas abordagens podem ser usadas para se avaliar a taxa de recuperação, ou resiliência, de atributos florestais, riqueza de espécies e fertilidade do solo, por exemplo, após um distúrbio. Resiliência é a capacidade de um ecossistema de retornar a um estado semelhante ao original, antes do distúrbio, onde sua performance não é significativamente diferente daquela anterior ao distúrbio, em relação à composição de espécies, estrutura florestal e funções ecossistêmicas (Blanco and Lal, 2008; Thompson et al., 2009). A taxa de recuperação e a trajetória de sucessão de uma floresta são influenciadas pelo clima (e.g. precipitação e temperatura), propriedades do solo (e.g. capacidade de retenção de água, porosidade, fertilidade), histórico do uso da terra e a colonização inicial (Lal, 1997; Guariguata and Ostertag, 2001; Chazdon, 2014). No entanto, devido a combinação dos fatores mencionados acima e do nível de degradação, nem todos os ecossistemas são capazes de se recuperar naturalmente quando o distúrbio cessa (Blanco and Lal, 2008).

Em geral, pouco se sabe sobre a resiliência de florestas ombrófilas e, sobre os efeitos de distúrbios como o corte raso nas propriedades químicas do solo e sua resiliência, resistência ou sensibilidade a este tipo de distúrbio. Portanto, objetivo geral deste estudo foi entender a dinâmica das propriedades do solo, do componente arbóreo, do estoque de carbono e da mirmecofauna ao longo da sucessão, avaliando sua fragilidade e resiliência. Para isso nós selecionamos florestas ombrófilas maduras e em regeneração no norte do Espírito Santo, Brasil, que é uma das regiões de Mata Atlântica mais bem preservadas, abrigando uma alta riqueza de espécies e endemismo (Ribeiro et al., 2009). Para uma melhor compreensão dos objetivos propostos, a presente dissertação foi dividida em dois capítulos. No primeiro capítulo nós investigamos os efeitos do corte raso, com remoção total das árvores, nas propriedades químicas do solo e sua resiliência. No segundo capítulo avaliamos a resiliência da riqueza e composição de espécies de árvores e formigas, do estoque de carbono, e de nutrientes solo, e estimamos o tempo que as florestas em regeneração levariam para atingir os níveis de florestas maduras próximas. Dessa forma, cada capítulo traz em detalhes informações sobre cada área de estudo e metodologias aplicadas para coleta, processamento e análise dos dados.

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III. CAPÍTULO I

37 YEARS OF FOREST SUCCESSION AFTER CLEAR-CUTTING A LOWLAND ATLANTIC FOREST SHOWED LITTLE CHANGES ON SOIL PROPERTIES

ABSTRACT – The Atlantic forest has only 7% of its original coverage due to a long history of disturbance, and it has an important role for biodiversity conservation. Clear-cut forest logging can cause microclimatic changes at the forest floor, affect ecosystem functions, forest productivity and, ultimately, the capacity of a forest to recover from it. Hence, it is important to understand how forest clearance can affect the content of nutrients that are important for primary productivity and, hence, for Atlantic forest to regenerate naturally. To assess the long-term (37-yr) effects of forest clear-cut on soil properties, an experiment was performed in 1980 in which one area of an old-growth forest was cleared with full tree logging removal, whereas an adjacent forest area was left intact as control. We also aimed to ascertain if the studied nutrients are sensible, resistant and/or resilient to whole-tree removal. Here we compare data from both areas collected two years before (1978) and 37 years (2017) after the experiment, in order to assess changes in chemical soil properties (pH, available P, exchangeable Al^{3+}, K^{+}, Ca^{2+} and Mg^{2+}) over the years. We found no significant differences between treatments for any soil component (LMM; $p>0.05$) and no significant changes in P, K^{+} and $Ca^{2+} + Mg^{2+}$ (LMM; $p>0.05$) levels over the years, in any area. On the other hand, pH increased (LMM; $p<0.01$) and Al^{3+} decreased over the years (LMM; $p<0.001$) in both areas. Overall, we show that deforestation of a mature lowland forest on very weathered soils do not cause significant apparent effects on chemical soil properties after 37 of regeneration. Our study suggests that P, K^{+} and $Ca^{2+} + Mg^{2+}$ may be resistant to forest clearance. Further studies comparing our results with the long-term tree dynamic of similar forested areas will help to clarify and understand the pattern found.

Keywords: clear-cut; secondary succession; nutrient dynamics; resilient; soil properties

1. Introduction

Human disturbances, such as forest clearing, contribute to forest fragmentation and cause drastic changes in the physicochemical properties of forest soil, affecting soil quality and resilience (Lal and Cummings, 1979; Johnson et al., 1991; Dahlgren and Driscoll, 1994; Guariguata and Ostertag, 2001). Depending on the intensity and frequency of the disturbance, soil properties may be affected in such a way, through compaction, sealing, leaching, salinization, acidification and loss of fertility, that can lead to soil degradation (Oldeman, 1991; Lal, 1997; Islam and Weil, 2000; Blanco and Lal, 2008). In this case, forest productivity and ecosystem functions are affected and, ultimately, the capacity of an ecosystem to recover after disturbance (Oldeman, 1991; Lal, 1997; Wall, 2012; Chazdon, 2014).

Following disturbance, forests begin a process of natural regeneration which involves changes in plant community (e.g., Liebsch et al., 2008) and in soil properties (Covington, 1981; Reiners et al., 1994; Lewis et al., 2014). The initial successional vegetation helps to prevent nutrient losses by taking nutrients from soil and storing part of them into their biomass (Zuazo and Pleguezuelo, 2008). A major portion of absorbed nutrients returns to soil mainly through the decomposition of litter and through leaching (Attiwill and Adams, 1993). Nutrients can also return to soil through stemflow and throughfall (Parker, 1983), contributing to the natural development of forest floor. During secondary succession, the rate of litter production tends to increase while the turnover rates of nutrients decrease (Brown and Lugo, 1990a), leading to the accumulation of nutrients and organic matter in the forest floor and soil (Covington, 1981; Brown and Lugo, 1990b). On the other hand, in preserved mature forests, where only small-scale disturbances occur such as treefalls (Chazdon, 2014), the soil usually retains its natural properties (Osman, 2013).

The properties of forest soil determine the availability of water and nutrients, root penetration, the amount of oxygen and other gases in the soil, and affect the growth and distribution of tree species (Osman, 2013). Hence, soil properties can be used as indicators of soil quality and of ecosystem functioning (Schoenholtz et al., 2000). The pH is an important component of soil solution, since it affects the ion exchange, and the mobilization and availability of nutrients to plants (Schoenholtz et al., 2000; Osman, 2013; McCauley et al., 2017). Nutrients such as P, K^+, Ca^{2+} and Mg^{2+} are used to produce biomass (Vitousek, 1982), and these exchangeable bases, together with Al^{3+} are considered nutrients that might limit net primary production (Vitousek and Sanford, 1986). Hence, as these soil chemical components limit plant growth and distribution, they affect capacity of a forest to regenerate naturally (Laurance et al., 1999; Moran et al., 2000; Osman, 2013; Chazdon, 2014).

Studies on the impacts of clear-cut logging on forest soils, their properties and dynamics are still scarce, but they are of key importance for understanding the long-term implications of forest disturbances on soil quality and forest regeneration, for assessing the fragility and resilience of tropical soils and for promoting sustainable management of soil resources. The Brazilian Atlantic Forest has lost about 88% of its original cover over the last 500 years due to exploitation, and the expansion of agriculture and urban areas (SOS Mata Atlântica, 2017), and it has an important role for the conservation of biodiversity (Myers et al., 2000). In this context, it is important to understand how forest clearance can affect the long-term dynamic of nutrients that might limit primary productivity, and hence, affect the capacity of the Atlantic forest to regenerate naturally.

In this study, we investigate the long-term (37-yr) effects of forest clearance on soil pH, exchangeable cations (Al^{3+}, K^{+}, Ca^{2+} and Mg^{2+}) and available P. For that, we compared soil data from an uncleared old-growth Atlantic forest (control) and a second-growth Atlantic forest (e.g., forest that was clear-cut and left to regenerate naturally), collected in two moments: two years before (1978) and 37 years after the cut (2017). Based on our findings, we also determine if the studied nutrients are sensible, resistant and/or resilient to whole-tree removal.

2. Methods

2.1. Study Area

The study was conducted at the Vale Natural Reserve (VNR) in northern Espírito Santo State, Brazil (19° 9'13.75"S, 40° 4'17.69"W, Fig.S1). This reserve has a total area of ~22000 ha and is one of the largest fragments of Atlantic Forest Coastal Tablelands, or lowland rain forest (IBGE, 2012). The climate is “Af” (tropical rain forest) according to the Köppen system, and the rainy season occurs between October to March, with mean annual precipitation of 1250 mm, and mean maximum temperature about 33.5°C (Engel and Martins, 2005). The predominant soil type is generally deep, acid, highly weathered and nutrient-poor Yellow Argisol (Ultisols) (Embrapa, 2006).

2.2. Experimental design

The experiment was performed in 1980 inside an old-growth forest and consisted in establish five 100x50 m permanent plots (0.5 ha) (A-E) in two treatments: control and clear-cut. The control consisted of five unmanaged plots in an old-growth forest, totalizing 2.5 ha that were left uncut. The clear-cut treatment consisted of clearing five plots (2.5 ha) in an old-growth forest, cutting all trees, lianas and climbers and removing all tree trunks and branches, leaving only debris composed of thin branches and leaves on the forest soil. The forest was then left to regenerate naturally.

2.3. Soil sampling

Soils samples were taken 2 years before (1978) and 37 years (2017) after the experiment. We collected randomly one compound sample of five single samples in each plot, within the depth of 0-20 cm; however, in 1978 the samples were taken from the 0-40 cm depth. Hence, to correct the differences in nutrient content between the depths, we recalculated the nutrients content of the first collection (1978), based on the nutrients proportion found in soil profiles from the study area (Santos et al., 2004); standardizing all samples at the depth of 0-20 cm. The 2017 air-dried samples were sent to the Soil Laboratory of the Federal University of Viçosa for chemical and physical analysis (texture). Soil chemical characteristics were obtained as follows: pH, using on a 1:2.5 soil:deionized water ratio; exchangeable Ca^{2+}, Mg^{2+} and Al^{3+}, by extraction with 1 mol L^{-1} KCl; P and K^{+} by extraction with Melich-1 (Embrapa, 1997).

2.4. Statistical analysis

To verify the effects of treatment and time on soil components, we compared the soil nutrients content from samples taken in 1978 and 2017, in the uncleared old-growth forest and in the cleared forest (second-growth), using Linear Mixed Model (LMM), package ‘lme4’. Forest treatment and time were used as the explanatory variables. As trajectory experiments show problems with time dependence, each plot was considered as the random factor. In order to determine which model were the most important to explain changes in soil nutrient contents, we rank all regression models using the Akaike information criterion corrected for small samples (AICc). For that, we used the R function ‘*dredge*’ from package ‘MuMIn’ to create all possible combinations of variables and rank the models based on their ΔAICc and AICc weights. We only considered the models with $\Delta AICc \leq 2$ as the best supported models. All analyses were performed in the platform R, version 3.3.1 (R Core Team, 2016).

3. Results

The soil texture samples of 2017 from both areas, control and clear cut, showed a low content of silt (~2%), clay (~ 11%), and fine sand (~14%), and a high content of coarse sand (~73%), indicating that the natural soil of these areas varies from sandy to loamy sandy soil (Table S1). Overall, the K^+ content did not change, Al^{3+} content decreased and the pH increased over the years, regardless forest treatment; whereas the contents of P and $Ca^{2+} + Mg^{2+}$ showed a decrease in the control and an increase in the clear-cut area after 39 years (Table 1).

Table 1: Analytical results of soil analyses for both treatments in a Lowland rain forest at the Vale Natural Reserve – ES, Brazil.

	Control				**Clear-cut**			
	1978		**2017**		**1978**		**2017**	
	Mean	**± S.D.**	**Mean**	**± S.D.**	**Mean**	**± S.D.**	**Mean**	**± S.D.**
pH H_2O	4.72	0.22	5.02	0.39	4.72	0.31	5.11	0.36
P (mg/Kg)	2.20	1.35	1.82	0.48	1.32	0.49	1.98	0.87
Exchangeable soil components ($cmol_c$/kg soil)								
Al^{3+}	0.34	0.22	0.08	0.13	0.29	0.14	0.04	0.05
$Ca^{2+} + Mg^{2+}$	2.24	0.99	1.46	0.75	1.56	0.91	1.66	0.71
K^+	0.05	0.05	0.05	0.02	0.05	0.03	0.05	0.01

We present the best-supported linear mixed models for each soil chemical response variable, selected based on the ΔAICc (≤ 2) (Table 2). Overall, we have found no significant differences between treatments for any nutrient content, neither pH. The content of Al^{3+} decreased (LMM; $F_{1,18} = 28.00$, $P < 0.001$, Fig.1A) and the pH increased (LMM; $F_{1,18} = 10.97$, $P < 0.01$, Fig.1B) over the years. On the other hand, despite the observed changes in all nutrients levels over the years, the content of P, K^+ and $Ca^{2+} + Mg^{2+}$ did not change significantly over the years.

Table 2: Linear mixed model results for the impact of forest clearance and time on soil properties in a mature and second-growth lowland forest (northern Espírito Santo State, Brazil). Only models with ΔAICc lower than 2 are shown.

Best Model	Intercept	Treatment	Year	df	logLik	F	AICc	weight
Al~year+(1|rep)	0.32		-0.257*	4	13.23	28.00	-15.8	0.761
pH~year+(1|rep)	4.72		0.345*	4	-2.27	10.97	15.2	0.766
P+(1|rep)~null	1.83			3	-24.97		57.4	0.609
K+(1|rep)~null	0.05			3	42.89		-78.3	0.683
Ca_Mg+(1|rep)~null	1.73			3	23.80		55.1	0.574

*=p<0.05

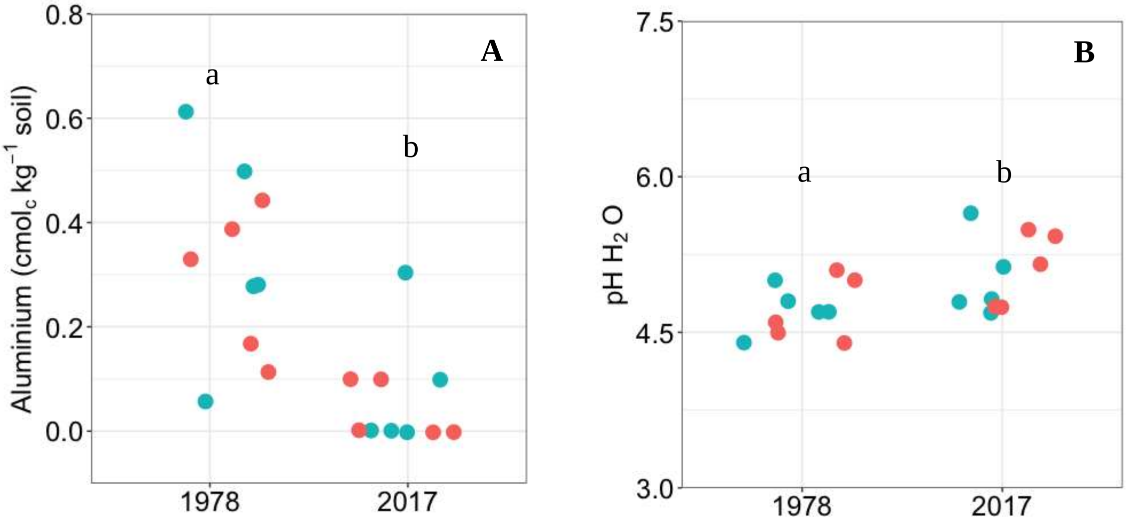

Figure 1. Soil nutrient contents (**A.** Aluminium; **B.** pH H_2O) sampled in five 100 x 50 m plots in one second-growth forest patch (treatment clear-cut) and one mature forest stand (control) in the Vale Natural Reserve, northern Espírito Santo State, Brazil. The control is represented by the blue circle and the clear-cut treatment by the red circle.

4. Discussion

Understanding the resistance and or resilience of soil properties after disturbance in tropical forests is important due to the relation with forest productivity (REFS). Here we are showing for the first time, using a robust and long-term data (after 37 years of cutting), that the local deforestation of a mature lowland forest on nutrient-poor soils caused no significant effects on chemical soil properties, after 37 years of cutting. We found that the amounts of P, K^+ and Ca^{2+} + Mg^{2+} did not change over the years, whereas the Al^{3+} decreased and pH increased over the years in both areas. This results are consistent with those reported in other studies elsewhere, such as the increasing pH (Allen, 1985; Reiners et al., 1994), decreasing Al^{3+} (Silver et al., 1996), and no changes in available P (Allen, 1985), exchangeable K^+ (Covington, 1981) and Ca^{2+} + Mg^{2+} levels (Reiners et al., 1994) along forest regeneration. Hence, these results together with those reported here suggest that P, K^+, Ca^{2+} and Mg^{2+} levels can be resistant to whole-tree removal.

The exchangeable bases (K^+, Ca^{2+}, Mg^{2+}) did not change along the years in the control, probably because in preserved mature forests only small-scale disturbances occur, such as tree falls, causing little or no soil disturbances (Chazdon, 2014). In the cleared forest, an initial loss of nutrients probably occurred through leaching, due to vegetation removal (Zuazo and Pleguezuelo, 2008). However, the initial establishment of rapidly-growing species that quickly accumulates biomass was crucial to prevent further nutrient losses (Zuazo and Pleguezuelo, 2008; Chazdon, 2014). In very infertile sandy soils like the one studied, a large part of the nutrient stock is concentrated, not in the mineral soil, but in the plants (Moran 2000). Besides, the decomposition of easily decomposing early litterfall (Covington, 1981), produced by the early successional species, contribute to the input of organic matter and nutrients on forest soil. During the first 30-40 years following clear-cutting, occur an exponential increase of living biomass (Whittaker et al., 1974), the recovery of the biogeochemical cycles, due to the increasing capacity of an ecosystem to trap and hold nutrients (Odum, 1969), increasing litter production and decreasing turnover rates of nutrients (Brown and Lugo, 1990a). Therefore, the initial nutrient loss in the cleared forest was probably balanced by inputs via the decomposition of litter, what may explain why K^+, Ca^{2+}, Mg^{2+} did not change after 37 years of cut. Moreover, although a considerable amount of P is release to the soil when a forest is cleared, the available P pool is short lived (Allen, 1985), so that this input is hardly detected, helping to explain why P levels did not change significantly over the years.

The increasing pH indicate that acidity decreased over the years in both areas. Although we did not compare the dynamics of soil organic matter (SOM) in this study, due to lack of information regarding organic matter in the first sampling (1978), it is known that it can affect both pH and Al^{3+} levels. Hence, understanding how the SOM affects these components may help to explain the dynamic found. Several studies have showed that the amount of SOM increases during forest regeneration (Brown and Lugo, 1990a; Reiners et al., 1994; Rhoades et al., 2000; Silver et al., 2000; López-Ulloa et al., 2005; Marín-Spiotta et al., 2008; Lewis et al., 2014). The addition of organic matter (OM) decreases the soil solution acidity, probably due to the release of more organic anions during plant residues decay, causing an increase in soil pH (Ritchie and Dolling, 1985; Xu et al., 2006). This suggest that the increasing pH may be attributed mostly to SOM increment.

Exchangeable aluminium increased over the years in both areas. At a given pH, the addition of OM contributes to the formation of Al-organic matter complexes causing a reduction of aluminium in soil solution (Bloom et al., 1979; Wong and Swift, 1995), suggesting that Al^{3+} decreased due to an OM increment. On the other hand, aluminium solubility is very sensitive to pH alterations, so that Al^{3+} solubility greatly decreases when pH reach values close to 5.2 (Walker et al., 1990), thus any variation in pH in the range of 5.2 will lead to an increase or decrease of Al^{3+}. More specifically, pH influences the binding between Al^{3+} and OM, which has a strong affinity for each other (Bloom et al., 1979), in a way that higher pH values decrease the aluminium capacity to bind to OM (Tipping, 2002), resulting in precipitation of soluble Al^{3+} forms. Therefore, the reduction of Al^{3+} in the present study over the years may be due to increased pH, following the presumed accumulation of SOM.

5. Conclusions

Deep weathered sandy soils of the Atlantic lowland rain forest have very low nutrient availability, which can limit the absorption of nutrients and the regeneration of the second-growth forest. Further studies comparing our results with the long-term tree dynamic of the same forests, will provide a better understanding of the pattern found. The low nutrient mobilization after the 37 years of succession suggests that a whole-tree removal in these lowland forests does not result in large inputs of nutrients to the soil. Finally, in terms of nutrient supply, our long-term data showed that deforestation of a mature lowland forest on nutrient-depleted soils causes no apparent drastic effects on chemical soil properties after 37 years of regeneration. This suggests the very low phosphorus, potassium, calcium and magnesium background on lowland rain forest soils may be resistant to forest clearance.

Acknowledgements

We thank Hugo Cândido for field support; Celso Antônio and Matheus Manso Cóser for laboratory assistance; Vale Natural Reserve for allowing us to conduct research within the reserve and Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq for funding support. This paper is part of the Masters (Honours) thesis of NS with Federal University of Viçosa (Brazil).

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SUPPLEMENTARY MATERIAL

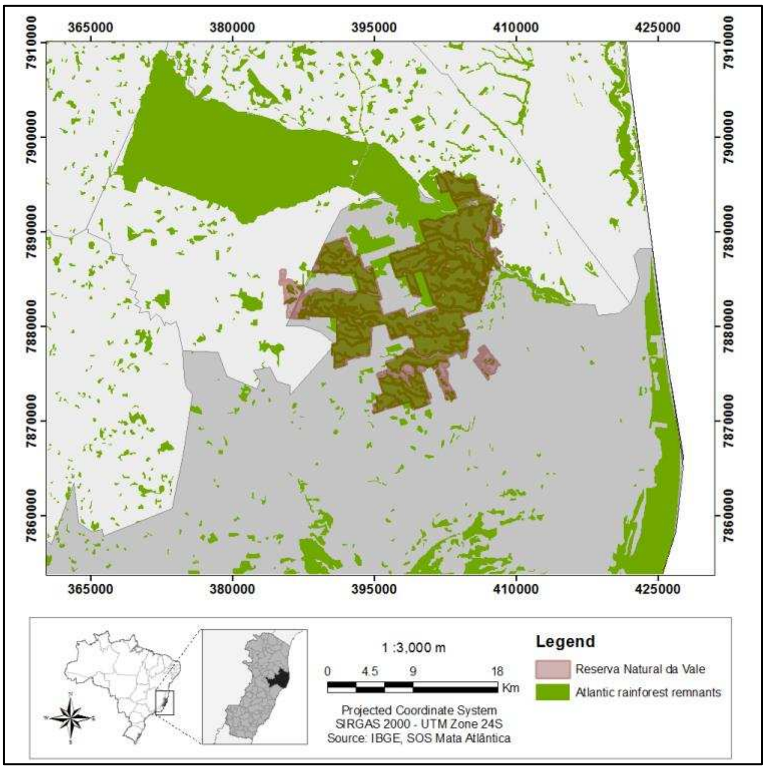

Figure S1. Geographic location of the Vale Natural Reserve in the municipality of Linhares, Espírito Santo State, Brazil.

Table S1: Texture analysis of soil collected in 2017 in an old-growth stand (control) and a second-growth patch (clear-cut) of a Lowland rain forest at the Vale Natural Reserve – ES.

Site	**Silt (%)**	**Clay (%)**	**Fine sand (%)**	**Coarse sand (%)**	**Soil type**
Control					
A	2.8	7.4	26	63.8	sand
B	1.7	10.1	9.6	78.6	loamy sand
C	1.2	19.5	15.9	63.4	sandy loam
D	1.8	12.9	10.8	74.5	loamy sand
E	1	9.6	11	78.5	loamy sand
mean; ± S.D.	1.7; ± 0.7	11.9; ± 4.7	14.7; ± 6.8	71.8; ± 7.6	
Clear-cut					
A	1.1	8.5	17.8	72.6	sand
B	1.3	7.4	17	74.3	sand
C	2.9	12	8.7	76.4	loamy sand
D	2.8	11.3	8	77.9	loamy sand
E	1.9	10.1	12.2	75.9	loamy sand
mean; ± S.D.	2.0; ± 0.8	9.9; ± 1.9	12.7; ± 4.6	75.4; ± 2.0	

IV. CAPÍTULO II

RESILIENCE OF LOWLAND RAIN FORESTS: AN ABOVEGROUND BIOMASS, EDAPHIC AND MULTI-TAXA ASSESSMENT

ABSTRACT – The Atlantic forest is one of the most diverse and threatened tropical forest ecosystem in the world, and its landscapes are mainly composed by small fragments that are in different stage of recovery from past human disturbance. These second-growth fragments of varying sizes have an important role in carbon mitigation and biodiversity conservation. Here we analyse the resilience of second-growth lowland forests through a chronosequence approach, by assessing the effects of stand age on the recovery of tree coupled with ant species richness and composition, aboveground and total C pool, and soil nutrients (organic C, P, Al^{3+} and sum of bases), and estimating the time needed to recover to mature forests level for each parameter. We analysed data collected in two old-growth and 11 second-growth lowland forests at different ages, about 130 plots (1.3 ha). We measured and identified all trees with diameter-at-breast-height (dbh) $\geq$ 15 cm; and collected littler and soil samples (0-20 cm), and leaf-litter ants using Winkler extractor. The studied secondary forests are potentially sequestering 1.04 Mg C ha^{-1} yr^{-1}, thus contributing to the important ecosystem service of CO_2 sequestration. Second-growth lowland forests would take several years (57-126 yr) to recover species richness and composition, and much longer, 188 yr to recover C pool. These results indicate that both tree species richness and composition, ant species composition and aboveground C pool could be used as indicators of forest recovery. Yet, we found no relationship between soil properties and forest regeneration. Our findings suggest that ant species richness and soils from lowland forest can resist disturbances, and suggest a general resilience of lowland second-growth forests, although they take a long time to recover the original state of biodiversity and forest structure. This, in turn, highlight the urgent need to plan strategies for selecting areas with high potential for natural regeneration.

Keywords: Atlantic forest; disturbance; resilience; trees; carbon; soil properties; ants

1. Introduction

Forest ecosystems represent the largest terrestrial carbon reservoir (Gibbs et al., 2007) and are a crucial component of the global carbon cycle through photosynthetic processes (Malhi et al., 2002). Among all forest ecosystems, tropical forests stand out for being hostpots for biodiversity conservation (Myers et al., 2000) and carbon stocks (Bonan, 2008; Beer et al., 2010). Yet, tropical forests are subject to several anthropic impacts, such as fragmentation, deforestation and selective logging (Malhi et al., 2014), which result in the loss of biodiversity (Laurance et al., 2002; Bihn et al., 2007; Gibson et al., 2011; Newbold et al., 2015; Barlow et al., 2016) and the loss of large amounts of carbon in the form of the greenhouse gas CO_2, which is reflected in the decrease in forest biomass storage (Magnago et al., 2015; Baccini et al., 2017). For these reasons, deforestation and degradation of tropical forests are especially harmful to the environment and ecosystem functioning.

These impacts trigger the process of natural regeneration that involves changes not only in the structure and composition of plant community (Oliveira-Filho et al., 1997; Liebsch et al., 2008; Magnago et al., 2011; Lasky et al., 2014), but also in litter production (Lohbeck et al., 2015; Huang et al., 2017), soil properties (Brown and Lugo, 1990; Magnago et al., 2011; Lewis et al., 2014) and arthropods assemblages such as ants (Dunn, 2004; Schmidt et al., 2013; Solar et al., 2016). During secondary succession, species richness tends to increase (Dunn, 2004; Silver et al., 2004; Liebsch et al., 2008;), as well as the aboveground biomass (Lohbeck et al., 2015; Chadzon et al., 2016; Poorter et al., 2016), soil fertility (Brown and Lugo, 1990) and soil organic C concentrations (Brown and Lugo, 1990; Lewis et al., 2014); but the net primary productivity tends to decrease with stand age (Gower et al., 1996; Ryan et al., 2004). The rate of forest recovery and the succession trajectory are influenced by climate (e.g., precipitation, temperature), soil properties (e.g., water retention, porosity, fertility), land use history and initial colonization (Guariguata and Ostertag, 2001; Chazdon, 2014). Thus, not all ecosystems are able to recover naturally after disturbances cease due to the combination of the factors mentioned above (Blanco and Lal, 2008).

Forest successional trajectories can be investigated through a chronosequence approach (Buzzard et al., 2016; Chazdon et al., 2016; Huang et al., 2017; Poorter et al., 2016). This approach consists in arranging second-growth forests that differ in the time since disturbance or abandonment, but occur on similar soil types and are subject to similar environmental conditions (Chazdon, 2014), in a chronological sequence. This arrangement allows comparisons across a successional sequence, based on changes in parameters that are affected by disturbance, such as stand attributes (e.g. aboveground biomass), species richness and soil fertility. The chronosequence approach has been used to study temporal changes in plant communities (e.g., Lohbeck et al., 2012; Buzzard et al., 2016; Poorter et al., 2016), ant communities (e.g., Bihn et al., 2007; Schmidt et al., 2013), litter production (e.g., Huang et al., 2017) and soil properties (e.g., Feldpausch et al., 2010; Walker et al., 2010). Hence, this approach can also be used to evaluate the recovery rate, or resilience (i.e., the capacity of an ecosystem to recover after a disturbance, returning to a state that it is not significantly different from the pre-disturbance state, in relation to forest structure and ecosystem functions) (Blanco and Lal, 2008; Thompson et al., 2009) of those parameters following disturbance.

Little is known about the resilience of second-growth forests and the studies are usually focused on one factor (e.g. aboveground biomass) or *taxon* (e.g. plants or ants) (Liebsch et al. 2008; Schmidt et al., 2013; Poorter et al., 2016). We believe that different organisms respond differently to environmental disturbances, hence studies involving a larger number of groups (e.g. plants, animals, forest structure and soil development) (e.g., Dunn, 2004; Silveira et al., 2016; Solar et al., 2016) are recommended for a more precise and broad understanding of the resilience and resistance of the ecosystem functioning. Hence, investigating the capacity of secondary forests to recover after a disturbance or clear cut could help to establish safe predictions about what would happen to these fragments in different scenarios of environment impacts. Effective conservation and management plans can therefore be better designed and put into practice.

Several forest parameters are important for ecosystem functioning, and in this study we selected the following: tree and ant assemblages, carbon stock and soil properties. Soil properties determine the availability of water and nutrients, the amount of oxygen and other gases in the soil, affect water uptake by plants, and the growth and distribution of tree species (Vitousek and Sanford, 1986; Schoenholtz et al., 2000; Osman, 2013). Biodiversity is important for the maintenance of ecosystem processes and functions (Lefcheck et al., 2015; Brockerhoff et al., 2017). Trees, in addition to their importance for biodiversity, they contribute to nutrient cycling, through nutrients uptake and return to soil by the decomposition and leaching of litter and wood-debris (Attiwill and Adams, 1993), and they store carbon in their biomass, releasing it if disturbed, and for this reason they are a crucial component for the regulation of global carbon cycle (Bonan, 2008). Carbon sequestration is an important ecosystem service on the global scale, and it is essential for the balance between atmosphere and biosphere (Lal, 2008). Moreover, ants can act as ecosystem engineers, influencing soil quality and nutrient cycling, and playing an important role in seed dispersal and herbivory (Folgarait, 1998; Del Toro et al., 2012). Besides, as they are influenced by the vegetation and soil types (Hoffmann and Andersen, 2003), they can be highly sensitive to environmental changes and therefore, they have been used as biological indicators (Ribas et al., 2012).

In this study we aimed to evaluate the resilience of the Atlantic forest, which harbor a large number of species and high levels of endemism, but it is one of the most endangered forests in the world, remaining only 12.4% of forest remnants above 3 hectares (SOS Mata Atlântica, 2017). Here we evaluated the changes along succession and the resilience of lowland rain forests of northern Espírito Santo State, Brazil, by comparing second-growth forests of various ages with mature forests data (tree and ant assemblages, carbon storage and soil properties), using a chronosequence approach. Specifically, we aimed to answer the following: what happen with these parameters during forest succession? Is there a relationship between each parameter and the forest age? How long do these forests would take to reach the values of each parameters found in a reference forest (i.e., mature forest)?

2. Material and Methods

2.1. Study region

This study was conducted in old- and second-growth lowland rain forests located within and nearby the Biological Reserve of Córrego Grande and the National Forest of Rio Preto, both located in the municipality of Conceição da Barra, northern Espírito Santo State, Brazil (Figure 1). The study sites are part of one of the best preserved regions of the Atlantic Forest, holding 17.7% of its original vegetation (Ribeiro et al., 2009). The vegetation in the study sites is classified as Lowland rain forest or Coastal Tableland forest (IBGE, 2012). The regional climate is tropical rain forest “Af” (Köppen classification) with annual temperature and rainfall averaging more than 22ºC and ~1200 mm, respectively, and rainy season occurring between October to

March (Souza and Resende, 1999). The predominant soil type is characterized as Yellow Argisols (Ultisols) (Embrapa, 2006).

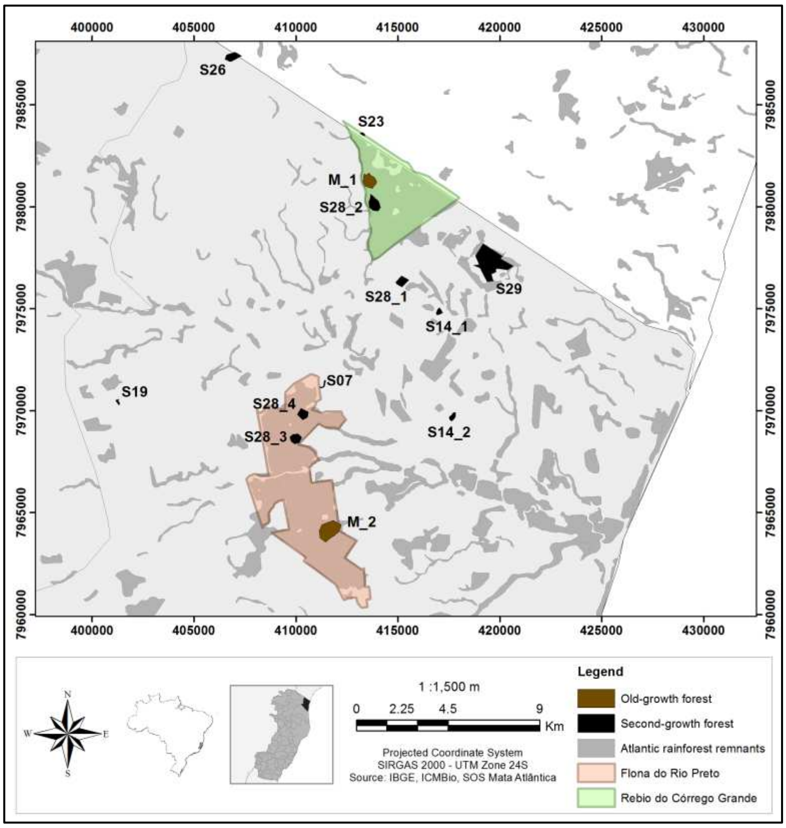

Figure 1. Geographic location of the areas sampled in the northern region of Espírito Santo State, Brazil. Second-growth forests (S) in black and Old-growth forests (M) in brown. The number following the letter S refers to the age of the secondary forests.

2.2. Data sampling

We established ten 10x10 m permanent plots (0.1 ha) equidistant 20 m in 13 areas of lowland rain forest, totalizing 130 plots. We sampled two old-growth forests (M) and 11 second-growth forest (S) patches of different ages, ranging from 7 to 29 years of natural regeneration (Table S1). The distance between the old-growth forests and the regenerating forests ranged from 1.5 to 12.3 km, with an average distance of 6.9 km. The study areas were chosen and the approximately age of the second-growth forests (i.e., time since disturbance or abandonment) were both determined based on Landsat images from Google Earth complemented with information from landowners. The Atlantic forest landscape is highly complex in terms of physiography and history (Ribeiro et al., 2009), which makes it difficult to select areas that have undergone the same type of disturbance and intensity of land-use. Besides, since there are no satellite images available from before 1970’, we only selected fragments that underwent a disturbance after this period, so that we could more accurately estimate the age of the fragments.

In each plot all living trees with a circumference at breast height (CBH) $\geq$ 15 cm – corresponding to a diameter (DBH) $\geq$ 4.8 cm – were tagged, measured and identified to species. The updated nomenclature of the specimens was checked at the database Flora do Brazil (Reflora), following the Angiosperm Phylogeny Group IV guidelines (APG IV, 2016). Furthermore, we classified species as endemic or not to the Brazilian Atlantic, and in threatened categories determined by the National Centre for Flora Conservation (CNCFlora) following the IUCN convention (data obtained from http://www.plantminer.com/).

Soil was sampled between April/May 2017. In each plot, we collected one compound sample of three single sampling points, at the 0–20 cm depth, taken in three equally spaced points in a diagonal transect across the plot, totalizing 10 soil samples per area. The soil samples were air-dried, sieved through a 2 mm sieve and sent for chemical and physical analysis at the Soil Laboratory of the Federal University of Viçosa. Exchangeable Al^{3+} was determined by extraction with 1 mol L^{-1} KCl; available P by extraction with Melich-1 (Embrapa, 1997) and soil organic carbon by the Walkley-Black method (Walkley and Black, 1934). The sum of bases was calculated by the sum of Ca^{2+}, Mg^{2+}, Na^{+} and K^{+}. Finally, samples texture was determined by separating them, using the pipette method, into clay (particles <0.002 mm diameter), silt (0.002-0.05 mm), fine sand (0.05-0.2 mm), and coarse sand (0.2-2 mm) fractions.

Litter was sampled using a quadrant of 30 x 30 cm that was positioned in the center of each plot. We collected all the litter (leaves, stems, roots, seeds) within the perimeter defined by the quadrant. Afterwards the litter samples were dried at the Herbarium's (VIC) greenhouse of the Federal University of Viçosa, with temperature ~30ºC and weighed to obtain litter dry biomass (Mg ha^{-1}).

Finally, we sampled leaf-litter ants (Hymenoptera: Formicidae) using a modified version of the Winkler/Moczarski collector, a technique that improves extraction of litter-dwelling insects (Besuchet et al., 1987). Here we also used the 30 x 30 cm quadrant in the center of the plot where litter was collected to be sifted. The litter was hit repeatedly to break twigs where ants might be nesting. Then, a layer of 2 cm of soil (topsoil) beneath the litter was scratched and all the material was added to the sifter. We took one sample for each plot, totalizing 130 for all areas. Each sample was left to dry in the "Winkler bags" for two days during which the insects were collected in an alcohol pot tied at the bottom of the bags. Ant species were identified using specific keys for each collected *genera*. To unnamed specimens we gave number codes (sp. 1 etc.) or morphospecies codes following those from the ant collection of the Community Ecology Laboratory (Labecol) at the Federal University of Viçosa, which are available on the online platform AntWeb (accessed in https://antweb.org/). That is, whenever a given specimen sampled in this work matched an existing morphospecies in the Labecol's ant collection, we gave it the same code. If a given specimen was not represented by any morphospecies from Labecol, we created a new *ufv-xx* code. At least one specimen of each morphospecies was databased on the platform AntWeb.

2.3. Aboveground carbon stock estimation

To estimate the aboveground biomass (AGB) of trees we used Chave et al.'s (2014) allometric equation for moist forests (eq.1-2). The AGB of trees were summed to obtain live plot AGB and the total AGB (Mg ha^{-1}) was given as the sum of trees AGB and litter dry biomass.

$$\ln(AGB) = [-1.803 - 0.976E + 0.976\ln(\rho) + 2.673\ln(DBH) - 0.0299[\ln(DBH)]^2] \quad \text{(eq.1)}$$

$$E = (0.178 \text{ x } TS - 0.938 \text{ x } CWD - 6.61 \text{ x } PS) \text{ x } 10^{-3} \quad \text{(eq.2)}$$

where ρ is wood density (g.cm^{-3}); E is an environmental variable; PS is precipitation seasonality; TS is temperature seasonality; and CWD is climatic water deficit. Both PS and TS were obtained from WorldClim and CWD (in millimeters per year) (accessed in http://chave.ups-tlse.fr/pantropical allometry.htm). The species wood density (g.cm^{-3}) were obtained from the neotropical data of The Global Wood Density (GWD) data base (http://hdl.handle.net/10255/dryad.235). For species that we could not find wood density information we used the average of the genus or family; and for unidentified individuals we used the average wood density of the plot.

To convert AGB into aboveground C storage (AGC) we assumed that 50% of biomass is made up by carbon (Houghton et al., 2000). The total C stocks in the forests was calculated as the sum of AGC and soil organic C (SOC).

2.4. Statistical Analysis

To determine whether species composition of second-growth forests tend to become more similar to species composition of mature forests along succession, we computed Chao's Abundance-based Sørensen similarity index (Chao et al., 2005) for tree and ant species composition using the EstimateS version 9.1.0 (Colwell, 2013). The Chao-Sørensen similarity index has good qualitative and quantitative properties

(Barwell et al., 2015), takes into account the relative abundance of species, is sensitive to rare species (Chao et al., 2005; Jost et al., 2011). Ant abundance was given in terms of number of colonies and quantified by the frequency of occurrence in the area, which means that we counted as one occurrence each time a given species (i.e., colony) was found in a sample (i.e., plot) within the area. This was so because ants are social insects and many individuals of a species in a sample does not necessarily mean that there is more than one colony of that species on that same spot (Dunn et al., 2010). We then evaluated the similarity of tree and ant species composition between each secondary forest and the mature forests. The species composition of the two mature forests together is the reference composition to be achieved (100%) along succession.

We obtained the recovery rate of tree species richness (total, endemic, threatened) and composition, ant species richness and composition, aboveground and total carbon stock of second-growth forests to verify whether these parameters are resilient and to assess the time that these forests take to reach the values found in the mature forests (ecosystem reference). First, each parameter in each second-growth forest was measured as a percentage of the mean of the mature forest parameters (i.e., the 100%), as performed by Poorter et al. (2016). Then, to check if these parameters are recovering during forest regeneration, we performed a logistic regression using Generalized Linear Models (GLMs) with quasibinomial to correct the overdispersion. Finally, the recovery rate, or resilience, was estimated based on the regression line coefficients, as follows: $\boldsymbol{y = exp(\alpha + \beta x) / (1 + exp(\alpha + \beta x)}$; where y is the reference value, α is the intercept, β is the slope and x is the time to achieve y.

There is a greater variability of the forest soil properties among fragments, and for this reason we performed Generalized Additive models (GAMs), which are more flexible models, to assess the effects of stand age on these soil properties. All statistical analyses were performed using the platform R, version 3.3.1 (R Core Team, 2016).

3. Results

3.1. Tree communities

We sampled a total of 1273 trees classified in 224 species of 53 families, of which 87 species (39%) are endemic to the Brazilian Atlantic Forest and 51 (23%) are threatened to some degree (Table S2). The most representative families were Annonaceae (158 trees), Fabaceae (136 trees) and Anacardiaceae (126 trees). The Fabaceae family showed the highest tree species richness with 32 species, followed by

Myrtaceae with 25 species, Sapotaceae with 17 species and Annonaceae with 10 species. In addition, the most abundant species were *Annona dolabripetala* Raddi (67 trees) and *Xylopia frutescens* Aubl. (51 trees).

The number of species recorded in the old-growth forest stands (OGF) varied from 67 to 72, whereas in the second-growth forests (SGF) varied from 8 to 63 species. We found a significant increase in the total species richness ($\chi^2_{(1, N=11)} = 189.02$; $P < 0.001$, Fig.2a), in the endemic species richness ($\chi^2_{(1, N=11)} = 85.06$; $P < 0.001$, Fig.2b) and in the similarity of species composition ($\chi^2_{(1, N=11)} = 1.31$; $P < 0.001$, Fig.2c) with forest age; however, we found no relationships between threatened species richness and forest age ($\chi^2_{(1, N=11)} = 6.14$; $P = 0.0578$, Fig.2d). Therefore, late successional forests harbor more endemic species than initial forests. Based on the regression line coefficients, we predict that these second-growth forests would take ~56 yr to reach the total species richness (α= -3.62; β= 0.16), ~55 yr to reach endemic species richness (α= -5.04; β= 0.19) and ~65 yr to recover species composition (α= -5.1; β= 0.16).

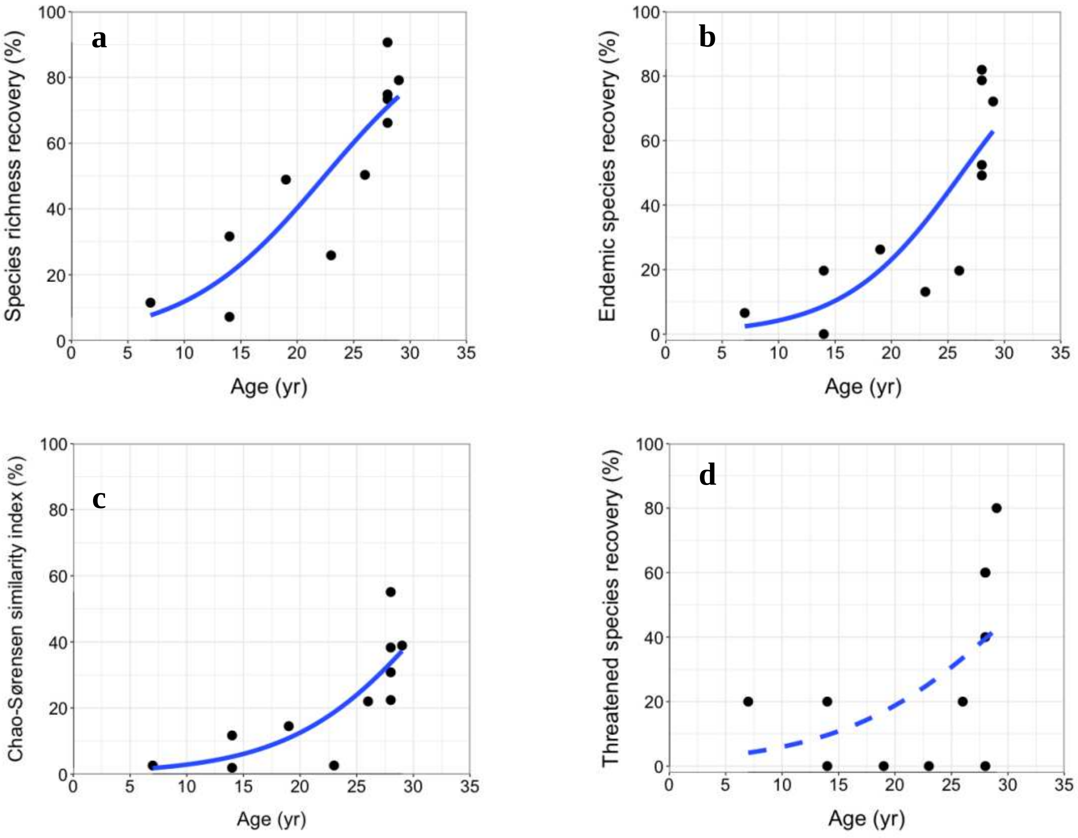

Figure 2. Relationship between tree species richness and composition, and stand age using chronosequence of secondary lowland rain forests. Resilience of total species richness (**a**); endemic species richness (**b**); species composition based on Chao-Sørensen similarity index (**c**); and threatened species richness (**d**). Higher values indicate a greater similarity to species richness and composition of mature forests (maximum, 100). Significant relationships ($P \leq 0.05$) are indicated by continuous lines; non-significant relationships ($P > 0.05$) are indicated by dashed line.

3.2. Aboveground and total carbon stock

AGC estimates varied more than four-fold among the second-growth forests, from 15.0 to 68.4 Mg C ha^{-1}, and varied from 205.9 to 363.2 Mg C ha^{-1} among the mature forests. Total C pool, which include the total AGC and SOC, varied from 37.1 to 90.9 Mg C ha^{-1} in second-growth forests and from 230.3 to 395.1 Mg C ha^{-1} in mature forests (Table S3). We found that total AGC increases with forest age ($\chi^2_{(1, N=11)} = 73.58$; $P < 0.001$, Fig.3a) and that, based on the regression line coefficients, the secondary lowland rain forest would take ~123 yr to recover the same amount of AGC ($\alpha = -3.29$; $\beta = 0.07$) stored by mature forests. Similarly, the total C pool also increase with forest age ($\chi^2_{(1, N=11)} = 51.23$; $P < 0.001$, Fig.3b), and the secondary lowland rain forest would take ~188 yr to recover total C pool ($\alpha = -2.22$; $\beta = 0.04$) of mature forests.

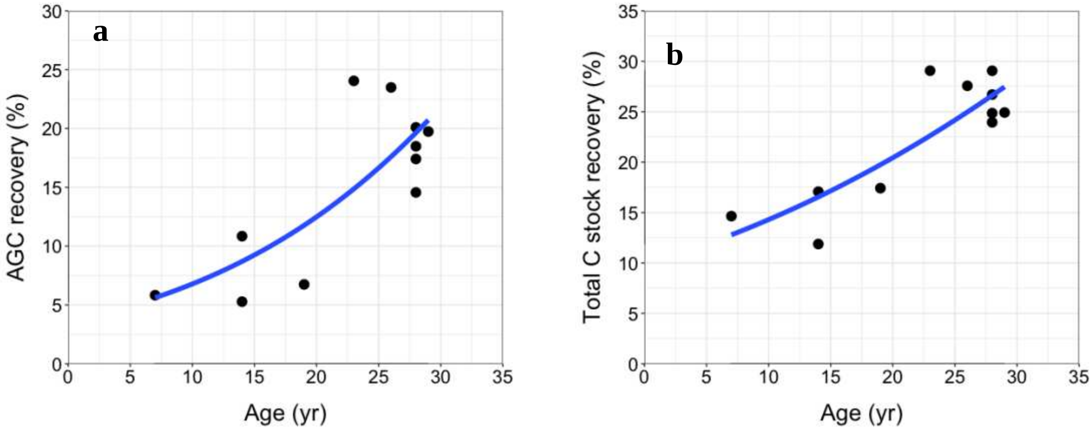

Figure 3. Relationship between total aboveground C stock (**a**) and total C stock (**b**), and stand age using chronosequence of secondary lowland rain forests. Higher values indicate a greater similarity to carbon storage of mature forests (maximum, 100). Significant relationships ($P \leq 0.05$) are indicated by continuous lines.

3.3. Ant assemblages

We collected a total of 115 ant species or morphospecies from 42 genera and 9 subfamilies (Table S4). The most speciouse subfamily was Myrmicinae (78 species), followed by Ponerinae (17 species), Formicinae (7 species), Ectatomminae (5 species), Dolichoderinae (2 species), Dorylinae (2 species), Proceratiinae (2 species), Amblyoponinae (1 species) and Pseudomyrmecinae (1 species). The four richest genera were *Solenopis* (17 species), *Pheidole* (14 species), *Strumigenys* (10 species) and *Hypoponera* (8 species). The species *Wasmannia auropunctata* was the most frequent species (collected in 49.2% of the plots), followed by *Solenopsis* sp.2 and

Solenopsis sp.1 (45.4 and 39.2%, respectively), the latter two being the only species collected in all fragments. Among all species, 42 were found in only one plot and 11 were exclusive to the mature forests, which are: *Carebara* sp.1, *Cryptomyrmex* sp.1, *Discothyrea neotropica*, *Ectatomma edentatum*, *Hypoponera* alw06, *Mayaponera constricta*, *Odontomachus* sp.1, *Rhopalothrix* ufv-04, *Rogeria* sp.4, *Solenopsis* sp.5, *Solenopsis* ufv-32.

We found a significant increase in compositional similarity of ant species assemblages ($\chi^2_{(1, N=11)} = 0.364$; $P < 0.001$; Fig.4a) with stand age, however, we found no significant relationships between ant species richness and forest age ($\chi^2_{(1, N=11)} = 15.05$; $P = 0.068$, Fig.4b). Based on the regression line coefficients, we predict that these second-growth forests would take ~126 yr to recover ant species composition ($\alpha = -0.98$; $\beta = 0.05$) found in mature forests (ecosystem reference).

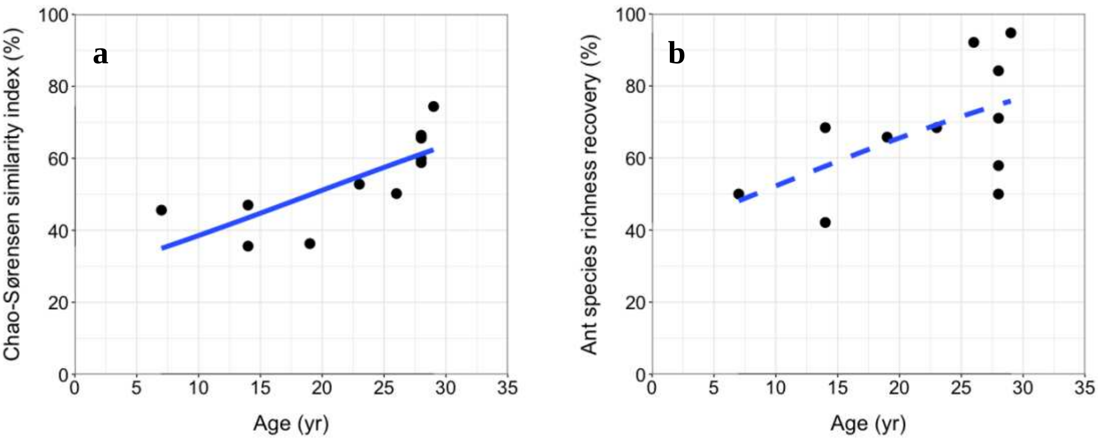

Figure 4. Relationship between ant species richness and composition with stand age using chronosequences of secondary lowland rain forests. Resilience of species composition based on Chao-Sørensen similarity index (**a**) and resilience of ant species richness (**b**). Higher values indicate a greater similarity to species richness and composition of mature forests (maximum, 100). Significant relationships ($P \leq 0.05$) is indicated by continuous lines and non-significant relationships ($P > 0.05$) is indicated by dashed line.

3.4. Soil properties

The studied soils have textures ranging from sand to sandy clay, and the contents of available P, exchangeable Al and SB varied greatly among the fragments, showing no significant increase or decrease pattern with succession progress (Table S3). Moreover, SOC in the top 20 cm varied from 17.7 Mg ha^{-1} to 42.0 Mg ha^{-1} in the second-growth forests, and from 24.3 Mg ha^{-1} to 31.9 Mg ha^{-1} in the mature forests (Table S2). We did not find significant effects of stand age on any soil parameter evaluated ($P > 0.05$ for all variable; Fig. 5a-d).

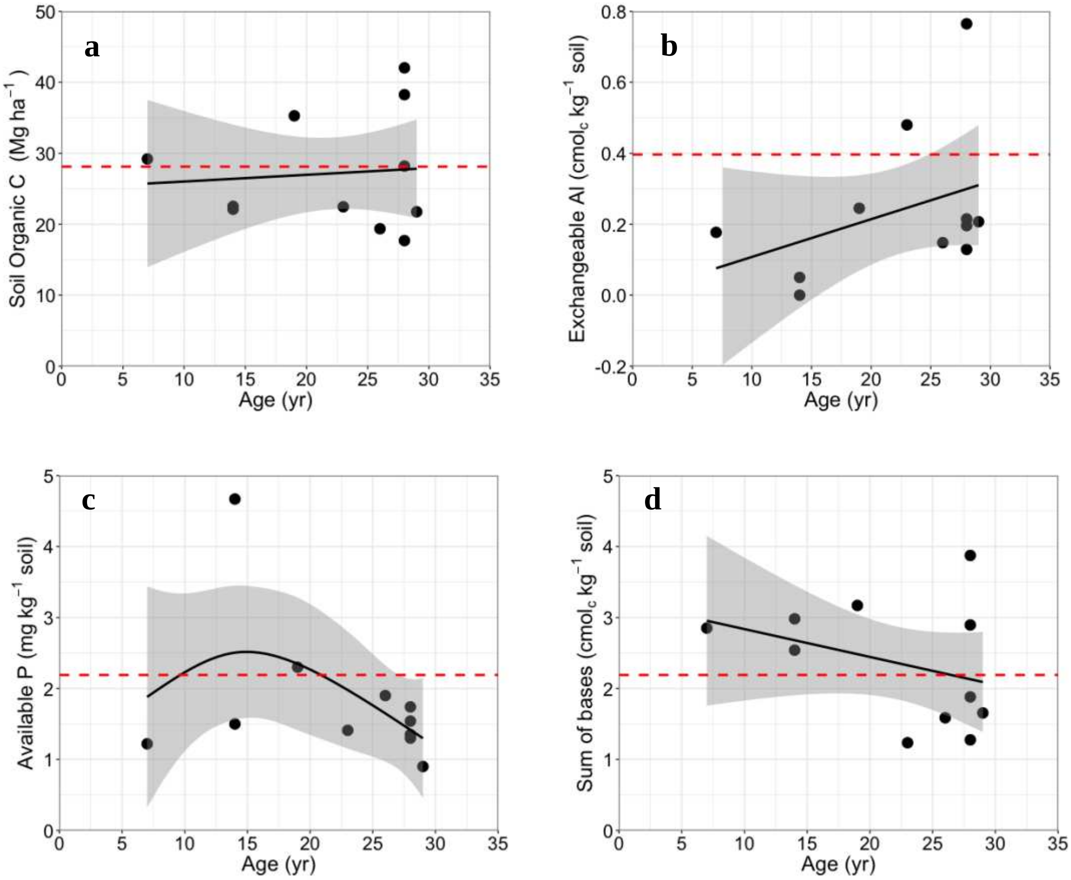

Figure 5. The effects of stand age on the (**a**) soil organic carbon stock ($F_{1,9}$ = 0.07, P = 0.798), (**b**) exchangeable Al^{3+} ($F_{1,9}$= 1.493, P = 0.252), (**c**) available P ($F_{1,9}$= 1.323, P = 0.284) and (**d**) sum of bases ($F_{1,9}$ = 1.169, P = 0.308). Trend lines were constructed using GAM and red dashed horizontal lines represent the mean of mature forests.

4. Discussion

Our assessment of the resilience of different taxa along with carbon stock and soil properties, is the first empirical and regional-scale research in tropical forests, and represent a crucial step in understanding the behavior of a forest ecosystem along regeneration. Our findings show that lowland rain forests can gradually recover during forest succession and suggest that ant species richness and soil properties can be resistant to disturbance at regional-scale. Since they have not changed significantly over the years, showing no tendency during regeneration. We consider the implications of our results for the conservation of biodiversity and carbon in human-modified landscapes.

4.1. Forest parameters: resilience and changes during succession

We found that species richness and floristic composition of the regenerating forests are becoming similar to that of old-growth forests throughout natural succession, as also found in other tropical forests studies (e.g., Saldarriaga et al., 1988; Brown and Lugo, 1990; Guariguata and Ostertag, 2001; Liebsch et al., 2008; Norden et al., 2009). Under optimal conditions (i.e., lack of disturbances or extreme climatic effects, such as drought events), secondary forests may recover relatively rapidly in terms of tree species richness and composition, in approximately 55-56 and 65 yr, respectively. Our prediction for species richness recovery is lower than the 80 yr reported by Brown and Lugo (1990a) in a compilation of tropical forests from different regions of the globe. While the prediction for endemic species recovery found here is 35 times lower than that estimated by Liebsch et al. (2008) for the Atlantic forest. This huge difference may be attributed to the fact that Liebsch et al. (2008) studied different regions of Brazil, encompassing different types of Atlantic forests (e.g., Semi- or Deciduous Seasonal, Ombrophilous), which are slightly distinct in terms of forest structure and composition (IBGE, 2012). Whereas we studied sites that are relatively close or adjacent to potential sources of propagules (i.e., old-growth forest remnants) (Chazdon, 2014), restricted to the Atlantic lowland forests of northern Espírito Santo State. The colonization and return of species on disturbed areas depends heavily on seed dispersal (Uhl and Clark, 1983; Guariguata and Ostertag, 2001) specially in forests growing in large disturbed areas. Hence, we believe that the fact that we studied one type of forest (i.e., lowland rain forest) and sampled relatively close sites in the landscape, may contribute to a faster return of species composition and number of species to the disturbed areas.

Here we show that secondary lowland forests can be resilient and recover the AGC and total C stocks of the reference forests in approximately 123 to 188 years, much longer than tree species richness. Our predictions are consistent with that of Saldarriaga et al. (1988) and de Paula et al. (2015), who reported 190 yr and 150 yr of recovery, respectively, and with that of Brown and Lugo (1990a), who reported that in 80 yr the second-growth forests would still not reach the C storage found in the mature forests. On the other hand, this estimation is greater than the 100 yr of recovery estimated by Fearnside and Guimarães (1996) in secondary Brazilian Amazon forests, and the 66 yr for tropical forests to recover 90% of old-growth forest storage estimated by Poorter et al. (2016). This differences may be influenced by the soil properties of the studied sites, which are highly weathered and poor in nutrients, thus tree assemblages grow more slowly (Guariguata and Ostertag, 2001), taking a longer time to reach a mature forest structure (i.e., biomass storage).

We did not find significant relationship between ant species richness and recovery time, as also reported by other studies (Belshaw and Bolton, 1993; Schmidt et al., 2013). The recolonization of disturbed areas may occur rapidly due to the short distance between our study areas and the "source forest" of ants for recovery (i.e., large and preserved forests), so that regenerating forests can have similar species richness, regardless their successional stage. On the other hand, we found that ant species composition does recover along forest regeneration, as also found in other studies (Dunn, 2004; Schimdt et al., 2013), and that it would take 126 years to reach the species composition of the mature forests. This indicates an increased biotic homogenization in late-successional fragments. Overall, our results show that during forest regeneration the species similarity showed a tendency to increase, while the number of species did not. This suggests that disturbances can induce changes in species composition, but it may not affect the number of species (Hoffmann and Andersen, 2003).

We found no relationships between any of the studied soil properties and stand age, which was also not found in other studies (de Camargo et al., 1999; Marín-Spiotta et al., 2008; Schedlbauer and Kavanagh 2008; Neumann-Cosel et al., 2011; Marín-Spiotta and Sharma, 2012; Paz et al., 2016). This suggests that other factors than forest age might explain the variability in exchangeable Al^{3+}, available P, sum of bases and soil C pool. Although some global-scale studies have shown that soil properties are affected by disturbance and tend to recover during forest succession (López-Ulloa et al., 2005; Marín-Spiotta et al., 2008; Lewis et al., 2014), our findings suggest that lowland Atlantic forest soils can be resistant to disturbance at regional-scale. That is, they resist drastic changes and are able to maintain its functions after a disturbance and along forest regeneration (Lal, 1997).

4.2. Implications for biodiversity and carbon conservation

In this study, we found 11 ant species and 51 tree species exclusive to the preserved forests. The number of tree species recorded in the old-growth forest stands varied from 67 to 72, whereas in the second-growth forests varied from 8 to 63 species. Ant species richness also varied greatly between fragments. In general, the secondary forests presented lower ant species richness than the mature forests, as also found in another study (Silva et al., 2007), with some forests presenting half the richness of mature forests (see also Solar et al., 2016). While others presented similar richness to that of mature forests. This suggests that, in terms of number of species, disturbed and undisturbed forests can have similar values, although the assemblage will most likely be different (Hoffmann and Andersen, 2003; Devictor et al., 2008; Alonso, 2010). Our results reveal the unique biodiversity values of undisturbed forests, but also show that regenerating forests can be an effective complement to primary forests in supporting tropical biodiversity.

The studied lowland forests store large amounts of carbon in their aboveground biomass (average 284.6 ± 78.7 Mg C ha^{-1}), which is almost twice the carbon stock reported for other South American rain forests (Sullivan et al., 2017) and the reported in IPCC global carbon map for tropical rain forests (Ruesch and Gibbs, 2008). This suggests that local assessments may reveal a greater potential of carbon storage by tropical rain forests than predicted from IPCC-based assessments. The total C pool varied more than four-fold among second-growth forests, from 15.0 to 68.4 Mg C ha^{-1}, also comparable to the storage found in other secondary tropical forests (Poorter et al., 2016), showing that different secondary forests have different capacities to store carbon. These results highlight the importance of both mature and secondary forests for the regulation of global carbon cycle (Bonan, 2008).

The regenerating forests studied are potentially stocking 1.07 Mg C ha^{-1} yr^{-1} in their aboveground biomass, less than the net carbon uptake reported in other secondary forests (3.05 Mg C ha^{-1} yr^{-1} by 20 yr-old secondary neotropical forests, Poorter et al., 2016; 5 Mg C ha^{-1} yr^{-1} by secondary forests the Philippines, Lasco et al., 2004). Yet, it is consistent with the rates reported in other studied (1.1 Mg C ha^{-1} yr^{-1} by tropical forests from America, Baccini et al., 2017; 1.4 Mg C ha^{-1} yr^{-1} by secondary forests from Puerto Rico, Silver et al., 2004). Although second-growth forests are described to have a high productivity potential (Gower et al., 1996), which makes them an efficient nutrient and C sink, old-growth forests also play a major role in C sequestration (Silver et al., 2004), and thus, in carbon cycle. Therefore, it is important to highlight the importance of regenerating forests, not only for biodiversity conservation, but also for regulating the global carbon cycle, due to their high carbon sink potential and also because they represent a low-cost alternative for carbon sequestration (Bongers et al., 2015; Chazdon et al., 2016; Poorter et al., 2016).

Here we show that secondary and old-growth forests have both high conservation value, so they play an important role in regional conservation planning. Hence, ending tropical deforestation and forest degradation, and letting these second-growth forest to naturally regenerate in human-modified landscapes would contribute to biodiversity conservation and to reduce carbon emissions. Therefore, they should represent a priority for conservation strategies based on carbon stocks payment under REDD+. We also show that tree and ant species composition, tree species richness and forest carbon pool tend to recover to mature forest levels along succession, but this was not observed for ant species richness and soil properties, suggesting they are more resistant to disturbance at landscape scale. The full recovery of lowland rain forests in regeneration can be slow, taking approximately 50 to 200 years, which is far beyond any recurrent conservation strategies agreements (e.g., Aichi Targets, COP 21, COP 22). Hence, we urgently need to develop strategies for selecting areas with high potential for natural regeneration. This highlight the importance of government's commitment in creating assisted regeneration strategies and carbon mitigation plans for a much longer period than what has been done.

5. Conclusions

Here we show evidences that secondary and old-growth forests have both high conservation (e.g., biodiversity and carbon) value, and therefore they play an important role in regional conservation planning. We conclude that disturbed lowland forests are able to recover naturally and gradually over time, without needing an active reforestation. Our study predicts that these forests would take about 50 to 200 years to recover completely, in terms of tree species richness and composition, ant species composition and carbon storage. Hence, we urgently need to develop strategies for selecting areas with high potential for natural regeneration, and guarantee the creation of assisted regeneration strategies for a much longer period than what has been done.

Acknowledgements

Many thanks to Júlio Chaul for the identification of specimens and for the comments about the species collected; Carlos Aquila, Carla S. Guimarães, João Paulo Gusmão, Marco Antônio Peixoto, Moacir Rocha, Hugo Galvão, Natália Silva, Matheus Cóser and Gabriel Cóser for fieldwork support; Celso Antônio for laboratory assistance; Suzano Papel e Celulose Company for allowing our access to the study areas; REBIO do Córrego Grande and FLONA do Rio Preto for providing accommodation and transportation to the study areas; Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq for funding support.

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SUPPLEMENTARY MATERIAL

Table S1: Total area, age, type of disturbance and geographical coordinates from each of the 13 studied fragments of Atlantic lowland rain forest sampled in the northern Espírito Santo, Brazil. (NA = information not available)

Fragment	Area (ha)	Age (years)	Type of disturbance	Geographical Coordinates
S07	3.4	7	NA	18°20'50.64"S; 39°50'21.09"W
S14_1	10.4	14	pasture	18°18'50.81"S; 39°47'4.61"W
S14_2	7	14	pasture	18°21'35.70"S; 39°46'42.05"W
S19	4.5	19	pasture	18°21'13.66"S; 39°56'2.67"W
S23	2.3	23	human occupation	18°14'6.69"S; 39°49'12.02"W
S26	12.8	26	NA	18°12'4.64"S; 39°52'53.41"W
S28_1	708	28	NA	18°18'3.71"S; 39°48'6.52"W
S28_2	101	28	fire	18°15'58.57"S; 39°48'53.66"W
S28_3	278	28	fire	18°22'17.35"S; 39°51'3.78"W
S28_4	4.5	28	fire	18°21'35.96"S; 39°50'54.60"W
S29	118	29	NA	18°17'48.23"S; 39°45'40.23"W
M_1	72.7	preserved	preserved	18°15'18.30"S; 39°49'4.00"W
M_2	649	preserved	preserved	18°24'31.35"S; 39°50'0.92"W

Table S2: List of tree species found and their abundance in the 13 fragments of Atlantic lowland rain forest sampled in the northern Espírito Santo, Brazil, with their threat status according to CNC and IUCN Red List for Threatened species. Endemic species are in bold and with ** when information about endemism was not found. The number following the letter S refers to the age of the secondary forests. (LC = least concern; NT = near threatened; VU = vulnerable; EN = endangered; CR = critically endangered, NA = not available)

FAMILY	**Second-growth forests**											**Old-growth forests**		**CNC/ IUCN status**
Species	**S07**	**S14_1**	**S14_2**	**S19**	**S23**	**S26**	**S28_1**	**S28_2**	**S28_3**	**S28_4**	**S29**	**M_1**	**M_2**	
ACHARIACEAE														
Carpotroche brasiliensis (Raddi) A Gray	-	-	-	-	-	-	1	-	1	1	-	-	1	NA
ANACARDIACEAE														
Anacardium occidentale L.	-	-	-	-	1	-	-	-	-	-	-	-	-	NA
Anacardium sp.	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
Astronium concinnum Schott	-	-	-	5	-	-	-	-	12	10	-	-	-	NA
Astronium graveolens Jacq.	-	-	-	3	1	1	2	-	3	-	-	-	-	LC
Mangifera indica L.	-	-	-	-	2	-	-	-	-	-	-	-	-	NA
Schinus terebinthifolia Raddi	6	3	-	-	2	-	-	-	-	-	-	-	-	NA
Tapirira guianensis Aubl.	-	-	1	6	2	9	12	5	1	-	1	-	-	NA
Thyrsodium spruceanum Benth.	-	-	-	-	-	6	8	6	12	2	1	1	1	NA
ANNONACEAE														
***Annona acutiflora* Mart.**	-	-	-	-	-	-	-	1	-	-	2	-	-	NA
***Annona cacans* Warm.**	-	-	-	-	-	-	-	3	-	-	1	-	-	LC
***Annona dolabripetala* Raddi**	-	-	-	1	2	2	5	9	13	16	15	-	-	NA
***Duguetia chrysocarpa* Maas**	-	-	-	-	-	-	-	-	1	-	-	-	-	NA
Guatteria australis A. St.-Hil.	-	-	-	5	-	4	1	2	-	6	-	1	-	LC

***Guatteria ferruginea* A.St.-Hil.**	-	-	-	-	-	-	-	-	-	-	1	-	-	NA
Guatteria sellowiana Schltdl.	-	-	-	-	-	-	1	1	-	-	3	-	-	LC
***Pseudoxandra spiritus-sancti* Maas**	-	-	-	-	-	-	-	-	-	-	-	5	5	NA
Xylopia frutescens Aubl.	-	-	-	-	18	4	20	-	-	1	8	-	-	NA
***Xylopia ochrantha* Mart.**	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
APOCYNACEAE														
Aspidosperma discolor A.DC.	-	-	-	-	-	-	-	1	-	-	-	-	-	NA
***Aspidosperma illustre* (Vell.) Kuhlm. and Piraja**	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
***Aspidosperma pyricollum* Müll. Arg.**	-	-	-	-	-	-	1	-	-	-	-	-	-	NA
Geissospermum laeve (Vell.) Miers	-	-	-	1	-	-	-	-	1	-	1	-	-	NA
***Himatanthus bracteatus* (A. DC.) Woodson**	-	-	-	-	2	1	8	4	1	-	-	-	-	NA
Malouetia cestroides (Nees ex Mart.) Müll.Arg.	-	-	1	-	-	-	2	-	-	-	6	1	-	LC
***Rauvolfia capixabae* I.Koch and Kin.-Gouv.**	-	-	1	-	-	-	-	2	-	-	1	1	1	NA
Tabernaemontana salzmanni A.DC.	-	-	-	-	-	-	-	3	-	-	1	3	3	NA
ARALIACEAE														
***Dendropanax brasiliensis* (Seem.) Frodin**	-	-	-	-	-	-	-	-	-	-	-	1	1	NA
Schefflera morototoni (Aubl.) Maguire et al.	-	-	-	-	-	-	1	1	1	-	1	-	-	NA
ARECACEAE														
***Allagoptera caudescens* (Mart.) Kuntze**	-	-	3	-	-	-	-	-	4	3	-	-	3	NA
***Astrocaryum aculeatissimum* (Schott) Burret**	-	-	-	-	-	1	-	1	2	1	1	6	1	LC
***Attalea burretiana* Bondar**	1	-	1	-	-	-	-	-	3	9	-	-	-	NA
***Elaeis guineensis* Jacq.**	-	-	-	-	2	-	-	-	-	-	-	-	-	NA
BIGNONIACEAE														
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	-	-	-	2	-	-	-	-	-	-	-	-	-	NA

Handroanthus heptaphyllus (Vell.) Mattos	-	-	-	-	-	-	-	-	-	-	-	-	2	LC
Handroanthus serratifolius (Vahl) S.Grose	-	-	-	1	-	2	2	1	-	1	-	-	-	NA
Jacaranda puberula Cham.	-	-	-	2	-	-	-	-	-	-	-	-	-	LC
Sparattosperma leucanthum (Vell.) K.Schum.	-	-	-	1	-	-	-	-	-	-	-	-	-	NA
***Tabebuia elliptica* (DC.) Sandwith**	-	-	-	-	-	-	-	2	-	-	-	-	-	NA
Tabebuia obtusifolia (Cham.) Bureau	-	-	-	-	-	-	-	-	-	-	-	-	1	LC
Tabebuia roseoalba (Ridl.) Sandwith	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
BORAGINACEAE														
Cordia sericicalyx A.DC.	2	-	-	2	-	1	-	1	-	3	-	-	-	NA
BURSERACEAE														
***Crepidospermum atlanticum* Daly**	-	-	-	-	-	-	-	2	-	-	-	-	-	NA
Protium aracouchini (Aubl.) Marchand	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
Protium heptaphyllum (Aubl.) Marchand subsp. heptaphyllum	-	-	2	-	8	5	2	1	-	-	9	2	-	NA
Protium warmingianum Marchand	-	-	-	-	-	-	-	7	-	2	-	3	9	NA
CARDIOPTERIDACEAE														
Citronella paniculata (Mart.) R.A.Howard	-	-	-	-	-	-	-	1	-	-	-	3	1	NA
CARICACEAE														
***Jacaratia heptaphylla* (Vell.) A.DC.**	-	-	-	-	-	-	-	-	-	-	-	-	1	NA
CARYOCARACEAE														
***Caryocar edule* Casar.**	-	-	-	-	-	-	-	-	-	-	1	1	-	LC
CHRYSOBALANACEAE														
***Couepia schottii* Fritsch**	-	-	-	-	-	-	-	-	-	-	1	-	-	EN
Hirtella hebeclada Moric. ex DC.	-	-	-	-	-	-	-	1	-	1	-	-	1	NA
***Hirtella insignis* Briq. ex Prance**	-	-	-	-	-	-	-	-	-	1	-	-	-	EN
Licania kunthiana Hook.f.	-	-	-	-	-	1	-	1	-	-	1	2	-	NA
Parinari excelsa Sabine	-	-	-	-	-	1	-	-	-	-	-	-	-	NA

Parinari parvifolia Sandwith	-	-	-	-	-	-	-	-	1	-	-	-	-	NA
DICHAPETALACEAE														
***Stephanopodium blanchetianum* Baill.**	-	-	-	-	-	-	-	-	-	-	-	-	2	NA
EBENACEAE														
Diospyros hispida A.DC.	-	-	3	-	-	-	-	-	-	1	-	-	-	LC
ELAEOCARPACEAE														
Sloanea eichleri K.Schum.**	-	-	-	-	-	1	-	-	-	1	-	-	-	NA
ERYTHROXYLACEAE	-	-	-	-	-	-	-	-	-	-	-	1	-	
***Erythroxylum columbinum* Mart.**	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
EUPHORBIACEAE														
Joannesia princeps Vell.	-	-	2	1	-	-	1	1	-	13	-	-	4	LC
***Pausandra morisiana* (Casar.) Radlk.**	-	-	-	-	-	-	-	-	-	-	-	7	-	NA
***Senefeldera verticillata* (Vell.) Croizat**	-	-	-	-	-	-	-	3	2	11	-	6	-	NA
FABACEAE														
Albizia polycephala (Benth.) Killip ex Record	-	-	1	1	-	-	-	-	-	-	-	-	-	NA
Andira fraxinifolia Benth.	-	-	1	-	-	1	-	-	-	-	-	-	-	NA
***Bauhinia forficata* Link**	-	-	-	-	-	-	-	-	1	-	-	-	-	NA
Centrolobium sclerophyllum H.C.Lima	-	1	-	-	-	-	-	-	-	-	-	-	-	LC
Chamaecrista ensiformis (Vell.) H.S.Irwin and Barneby	-	-	1	-	-	-	-	-	-	-	-	-	-	NA
Dialium guianense (Aubl.) Sandwith	-	-	-	-	-	-	-	2	-	-	-	-	2	NA
***Diplotropis incexis* Rizzini and A.Mattos**	-	-	-	-	-	-	1	-	-	-	-	-	-	NA
Fabaceae **														NA
Goniorrhachis marginata Taub.	-	-	-	1	-	-	-	-	1	2	-	-	1	NA
Inga capitata Desv.	-	-	-	-	-	-	-	-	-	-	-	-	1	NA
Inga cylindrica (Vell.) Mart.	-	-	-	1	-	-	-	-	3	2	1	-	-	NA
***Inga hispida* Schott ex Benth.**	-	-	-	-	-	-	-	2	-	1	-	-	-	LC

Inga striata Benth.	-	-	-	-	-	-	-	1	1	-	-	-	-	NA
***Inga subnuda* Salzm. ex Benth. subsp. subnuda**	-	-	1	-	2	-	3	1	-	-	2	-	-	NA
Inga thibaudiana DC. subsp. thibaudiana	-	-	3	-	-	-	-	-	-	-	-	-	-	NA
Lonchocarpus cultratus (Vell.) A.M.G.Azevedo and H.C.Lima	-	-	3	-	-	-	-	-	-	-	-	1	-	NA
***Machaerium fulvovenosum* H.C.Lima**	-	-	-	2	-	-	4	-	4	5	-	-	-	LC
Machaerium ovalifolium Glaz. ex Rudd	-	-	-	1	-	-	-	1	-	1	-	-	-	NA
Machaerium sp.**	-	-	-	1	-	-	-	-	-	-	-	-	-	NA
***Macrolobium latifolium* Vogel**	-	-	-	-	-	-	-	-	-	-	1	1	1	NA
Melanoxylon brauna Schott	-	-	-	-	-	3	1	-	-	3	5	-	1	VU
Ormosia arborea (Vell.) Harms	-	-	-	-	-	-	-	2	-	-	1	-	-	NA
***Ormosia nitida* Vogel**	-	-	-	-	-	-	-	-	-	-	-	-	1	NA
***Parapiptadenia pterosperma* (Benth.) Brenan**	-	-	-	-	-	-	-	-	2	-	-	-	1	NA
Pterocarpus rohrii Vahl	-	-	-	-	-	-	2	2	2	-	2	-	3	NA
Swartzia apetala Raddi var. apetala	-	19	-	1	-	2	1	-	-	-	1	-	-	NA
Swartzia apetala var. glabra (Vogel) R.S.Cowan	-	-	-	1	-	-	-	-	-	-	-	-	-	NA
***Swartzia simplex* var. continentalis Urb.**	-	-	-	-	-	-	-	-	-	-	1	-	2	NA
Swartzia sp.**	-	-	-	-	-	3	-	-	-	-	-	-	-	NA
***Vatairea heteroptera* (Allemão) Ducke**	-	-	-	-	-	-	-	1	-	-	-	2	-	NA
Zollernia ilicifolia (Brongn.) Vogel	-	-	-	-	-	-	-	-	1	-	-	-	-	NA
***Zollernia modesta* A.M.Carvalho and Barneby**	-	-	-	-	-	-	-	-	-	-	-	1	-	NT
HYPERICACEAE														
***Vismia martiana* Reichardt**	-	-	-	-	-	-	-	-	-	-	4	-	-	LC
ICACINACEAE														

Emmotum nitens (Benth.) Miers	-	-	-	-	-	-	-	2	3	2	-	-	-	NA
LACISTEMATACEAE														
Lacistema recurvum Schnizl. **	-	-	-	-	-	1	1	-	1	2	-	-	-	NA
LAMIACEAE														
Vitex orinocensis Kunth	-	-	-	1	-	-	-	-	-	-	-	-	-	NA
LAURACEAE														
Lauraceae sp. **	-	-	-	-	-	-	-	-	-	-	1	-	-	NA
Lauraceae sp.2 **	-	-	-	-	-	-	-	1	-	-	-	-	-	NA
***Licaria bahiana* Kurz**	-	-	-	2	-	-	-	-	1	1	-	-	-	NA
***Ocotea beulahiae* J.B. Baitello**	-	-	-	-	-	-	-	-	-	-	-	-	2	EN
***Ocotea confertiflora* (Meisn.) Mez**	-	-	-	-	-	-	-	1	-	3	-	2	-	VU
***Ocotea prolifera* (Nees and Mart.) Mez**	-	-	-	-	-	-	-	-	-	1	-	-	-	NA
Ocotea sp. **	-	-	-	-	-	-	2	-	-	-	-	1	-	NA
LECYTHIDACEAE														
***Cariniana legalis* (Mart.) Kuntze**	-	-	1	-	-	-	-	-	-	-	-	-	-	EN
***Cariniana parvifolia* S.A.Mori, Prance and Menandro**	-	-	-	-	-	-	-	1	-	-	-	-	-	EN
Couratari macrosperma A.C.Sm.	-	-	-	3	-	-	-	-	-	2	-	-	-	NA
Eschweilera ovata (Cambess.) Mart. ex Miers	3	3	7	-	-	-	2	-	-	-	10	1	2	NA
***Lecythis lanceolata* Poir.**	-	-	2	1	-	-	-	-	1	1	-	-	1	LC
Lecythis lurida (Miers) S.A.Mori	-	-	1	1	-	1	5	-	-	-	-	-	-	LC
Lecythis sp. **	-	-	-	-	-	-	-	-	-	-	1	-	-	NA
MALPIGHIACEAE														
Byrsonima crispa A.Juss.	-	-	-	-	1	-	-	-	-	-	-	-	-	NA
Byrsonima sericea DC.	1	-	2	4	16	1	10	1	-	-	-	-	-	NA
Byrsonima stipulacea A.Juss.	-	-	-	-	-	-	-	-	-	-	4	-	-	NA
MALVACEAE														

Eriotheca macrophylla (K.Schum.) A.Robyns	-	-	-	-	-	-	2	5	2	-	-	5	-	NA
Hydrogaster trinervis Kuhlm.	-	-	-	-	-	-	1	-	-	-	-	3	-	NA
Luehea mediterranea (Vell.) Angely **	-	-	-	-	-	-	2	1	1	-	-	-	-	NA
Pachira endecaphylla (Vell.) Carv.-Sobr.	-	-	-	-	-	-	-	-	1	1	-	2	-	NA
Pseudobombax grandiflorum var. majus A.Robyns	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
Sterculia excelsa Mart.	-	-	-	-	-	-	-	-	-	-	2	10	6	NA
MELASTOMATACEAE														
Miconia cinnamomifolia (DC.) Naudin	-	-	-	-	-	-	3	-	1	-	-	-	-	NA
MELIACEAE														
Trichilia lepidota subsp. schumanniana (Harms) Pennington	-	-	-	-	-	-	-	-	-	-	-	-	1	LC
Trichilia pseudostipularis (A.Juss.) C.DC.	-	-	-	-	-	-	-	-	-	-	-	-	1	NT
Trichilia silvatica C.DC.	-	-	-	-	-	-	-	-	-	-	-	1	-	LC
MORACEAE														
Artocarpus heterophyllus Lam.	-	-	-	-	5	-	-	-	-	-	-	-	-	NA
Brosimum glaucum Taub.	-	-	-	5	-	2	1	10	2	2	2	-	1	NT
Brosimum glaziovii Taub.	-	-	-	1	-	-	-	5	4	-	2	3	1	LC
Clarisia ilicifolia (Spreng.) Lanj. and Rossberg	-	-	-	-	-	-	-	-	3	2	-	1	1	NA
Clarisia racemosa Ruiz and Pav.	-	-	-	-	-	-	-	2	-	-	-	2	1	NA
Helicostylis tomentosa (Poepp. and Endl.) Rusby	-	-	-	-	-	-	-	1	-	-	1	2	3	LC
Sorocea guilleminiana Gaudich.	-	-	-	-	-	-	-	3	1	-	-	2	-	LC
MYRISTICACEAE														
Virola gardneri (A.DC.) Warb.	-	-	-	-	-	-	-	1	1	-	-	-	4	NA
Virola officinalis Warb.	-	-	-	-	-	-	3	8	1	-	-	6	3	NA

MYRTACEAE														
Calyptranthes lucida Mart. ex DC.	-	-	-	-	-	-	-	-	-	-	-	2	1	NA
***Campomanesia espiritosantensis* Landrum**	-	-	-	-	-	-	-	-	-	-	-	-	1	CR
Campomanesia guazumifolia (Cambess.) O.Berg	-	-	-	-	-	-	-	-	1	1	-	-	1	NA
***Eugenia beaurepairiana* (Kiaersk.) D.Legrand**	-	-	-	1	-	-	-	-	-	-	-	-	-	NA
***Eugenia fusca* O.Berg**	-	-	-	-	-	-	-	1	-	-	-	1	1	NA
***Eugenia itapemirimensis* Cambess.**	-	-	-	-	-	-	-	-	-	-	-	2	2	NA
Eugenia ligustrina (Sw.) Willd.	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
***Eugenia macrosperma* DC.**	-	-	-	-	-	-	-	-	1	-	-	-	-	NA
***Eugenia pisiformis* Cambess.**	-	-	-	-	-	-	-	-	-	-	1	-	-	LC
***Eugenia platyphylla* O.Berg**	-	-	-	-	-	1	1	-	1	-	-	-	-	NA
Eugenia sp. **	-	-	-	-	-	-	-	-	-	-	-	-	1	NA
Eugenia sp.2 **	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
Eugenia sp.3 **	-	-	-	-	-	-	-	1	-	-	-	-	-	NA
***Gomidesia crocea* O.Berg**	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
***Marlierea excoriata* Mart.**	-	-	-	-	-	-	-	-	-	-	-	1	1	NA
Myrcia amazonica DC.	-	-	-	-	-	-	-	-	1	-	-	-	-	NA
***Myrcia lineata* (O.Berg) Nied.**	-	-	-	-	-	-	-	-	-	-	-	2	-	EN
Myrcia splendens (Sw.) DC.	-	-	-	-	-	1	8	-	-	-	-	-	-	NA
***Myrcia sucrei* (G. M. Barroso and Peixoto) E. Lucas and C. E. Wilson**	-	-	-	-	-	-	-	-	-	1	-	-	-	NA
***Myrcia vittoriana* Kiaersk.**	-	-	-	-	-	-	1	-	-	-	-	-	-	NA
Myrciaria floribunda (H.West ex Willd.) O.Berg	-	-	-	-	-	-	-	-	-	-	-	1	-	LC
Myrtaceae sp **	-	-	-	-	-	-	-	-	-	-	1	-	-	NA
Myrtaceae sp.2 **	-	-	-	-	-	-	-	-	-	-	-	-	1	NA

Psidium guajava L.	-	-	-	-	2	-	-	-	-	-	-	-	-	NA
Psidium guineense Sw.	-	-	1	-	-	-	-	-	-	-	-	-	-	NA
NYCTAGINACEAE														
Guapira noxia (Netto) Lundell	-	-	-	1	-	1	1	1	-	1	-	3	9	NA
Guapira opposita (Vell.) Reitz	-	-	-	-	-	-	-	-	1	-	-	-	2	NA
PERACEAE														
Pera glabrata (Schott) Poepp. ex Baill.	1	-	-	-	-	1	3	1	-	1	1	-	-	NA
Pera heteranthera (Schrank) I.M.Johnst.	-	3	-	-	-	5	2	-	-	-	1	-	-	NA
Pera sp. **	-	-	-	-	-	-	-	-	-	-	1	-	-	NA
Pogonophora schomburgkiana Miers ex Benth.	-	-	4	-	-	2	-	4	1	-	1	2	-	NA
PHYLLANTHACEAE														
Hyeronima oblonga (Tul.) Müll.Arg.	-	-	-	-	-	-	2	-	-	-	-	-	-	NA
Margaritaria nobilis L.f.	-	-	-	-	-	-	2	-	-	-	-	-	-	LC
POLYGALACEAE														
***Acanthocladus pulcherrimus* (Kuhlm.) J.F.B.Pastore and D.B.O.S.Cardoso**	-	-	-	-	-	-	-	-	-	1	-	-	-	NT
POLYGONACEAE														
Coccoloba tenuiflora Lindau	-	-	-	-	-	-	-	-	-	-	-	-	2	NA
PRIMULACEAE														
Myrsine umbellata Mart.	1	-	-	-	-	-	-	-	-	-	-	-	-	NA
PUTRANJIVACEAE														
Drypetes sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	NA
QUIINACEAE														
Lacunaria crenata subsp. decastyla (Radlk. J.V. Schneid. and Zizka **	-	-	-	-	-	-	1	1	-	-	1	-	-	NA
RUBIACEAE														

Amaioua intermedia var. brasiliana (DC.) Steyerm.	-	-	-	-	-	-	-	-	-	1	1	-	-	NA
Ferdinandusa guainiae Spruce ex K.Schum.	-	-	-	-	-	-	-	1	-	-	-	-	-	NA
Guettarda angelica Mart. ex MÃ¼ll.Arg.	-	-	-	-	-	-	-	-	-	1	-	-	-	NA
Psychotria sp.	-	-	-	-	-	-	-	-	-	-	-	2	-	NA
Rubiaceae **	-	-	-	-	-	-	-	-	-	-	-	-	1	NA
***Simira glaziovii* (K.Schum.) Steyerm.**	-	-	-	-	-	-	-	1	-	-	-	-	1	NA
Tocoyena brasiliensis Mart.	-	-	-	-	-	1	-	-	-	-	-	-	-	NA
RUTACEAE														
Dictyoloma vandellianum A.Juss.	-	-	-	-	-	-	-	-	-	1	-	-	-	NA
***Neoraputia alba* (Nees and Mart.) Emmerich ex Kallunki**	-	-	-	-	-	-	-	-	1	-	-	-	-	NA
***Rauia nodosa* (Engl.) Kallunki**	-	-	-	-	-	-	-	-	-	-	1	-	-	NA
SALICACEAE														
Casearia commersoniana Cambess.	-	-	-	-	-	2	-	-	1	1	2	-	-	NA
Casearia oblongifolia Cambess.	-	-	-	-	-	-	-	-	-	1	-	-	-	NA
Casearia sp.	-	-	-	-	-	1	-	-	-	1	-	-	-	NA
Casearia sp. Nov.	-	-	-	2	-	-	-	-	-	-	-	-	-	NA
Casearia ulmifolia Vahl ex Vent.	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
***Macrothumia kuhlmannii* (Sleumer) M.H.Alford**	-	-	-	-	-	-	-	-	-	-	-	-	2	NA
Xylosma prockia (Turcz.) Turcz.	-	-	-	-	-	-	-	-	-	1	-	-	1	NA
SAPINDACEAE														
Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl.	-	-	-	2	-	-	4	-	-	1	-	-	1	NA
***Cupania emarginata* Cambess.**	-	-	-	-	-	-	2	-	-	-	-	-	-	NA
Cupania rugosa Radlk.	-	-	-	-	-	-	-	-	-	3	-	-	-	NA
Cupania scrobiculata Rich.	-	-	-	1	3	15	8	4	1	1	3	-	1	NA

Toulicia patentinervis Radlk.	-	-	-	-	-	-	-	-	-	-	-	-	1	NA
SAPOTACEAE														
***Chrysophyllum januariense* Eichler**	-	-	-	-	-	-	-	-	-	-	2	3	-	VU
***Chrysophyllum lucentifolium* Cronquist subsp. lucentifolium**	-	-	-	1	-	-	-	-	-	-	-	-	2	NA
Ecclinusa ramiflora Mart.	-	-	-	-	-	1	1	-	1	3	-	2	-	NA
Manilkara salzmannii (A.DC.) H.J.Lam	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
Manilkara sp.nov. **	-	-	-	-	-	-	-	-	-	-	-	-	3	NA
***Micropholis crassipedicellata* (Mart. and Eichler) Pierre**	-	-	-	-	-	-	-	-	-	-	-	1	-	LC
Micropholis gardneriana (A.DC.) Pierre	-	-	-	-	-	-	-	1	1	-	-	1	-	NA
Micropholis gnaphaloclados (Mart.) Pierre	-	-	-	-	-	-	-	-	-	-	-	-	1	NT
Pouteria bangii (Rusby) T.D.Penn.	-	-	-	-	-	1	-	2	4	-	1	4	2	NA
***Pouteria bullata* (S.Moore) Baehni**	-	-	-	-	-	-	-	-	-	-	-	-	1	EN
***Pouteria coelomatica* Rizzini**	-	-	-	-	-	-	-	-	-	-	-	1	-	VU
Pouteria guianensis Aubl.	-	-	-	-	-	-	-	-	-	1	-	1	1	NA
***Pouteria macahensis* T.D.Penn.**	-	-	-	-	-	-	-	-	-	-	-	-	1	EN
Pouteria macrophylla (Lam.) Eyma	-	-	-	-	-	-	-	-	-	2	-	-	-	NA
***Pouteria pachycalyx* T.D.Penn.**	1	-	-	-	-	-	-	-	-	-	1	-	1	VU
Pouteria venosa subsp. amazonica T.D.Penn.	-	-	-	-	-	-	-	-	-	-	1	-	-	NA
***Pradosia lactescens* (Vell.) Radlk.**	-	-	-	-	-	1	-	1	-	-	1	2	-	LC
SCHOEPFIACEAE														
Schoepfia brasiliensis A.DC.	-	-	-	-	-	-	-	-	-	-	-	7	1	NA
SIMAROUBACEAE														
Simarouba amara Aubl.	-	-	-	-	1	-	-	2	-	-	-	-	1	NA
SIPARUNACEAE														
Siparuna reginae (Tul.) A.DC.	-	-	-	-	-	-	-	1	-	-	-	1	1	LC

SOLANACEAE														
***Solanum pseudoquina* A.St.-Hil.**	-	-	-	-	-	-	-	-	-	-	1	-	-	LC
***Solanum sooretamum* Carvalho**	-	-	-	-	-	-	-	3	-	-	2	-	-	LC
URTICACEAE														
Cecropia pachystachya Trécul.	-	-	2	-	1	-	-	-	-	-	-	-	-	NA
VIOLACEAE														
***Paypayrola blanchetiana* Tul.**	-	-	-	-	-	-	-	-	1	-	-	-	2	NA
***Rinorea bahiensis* (Moric.) Kuntze**	-	-	-	-	-	-	-	1	2	-	1	10	11	NA
VOCHYSIACEAE														
***Vochysia angelica* M.C.Vianna and Fontella**	-	-	-	-	-	-	1	1	-	-	-	-	-	EN
UNKNOWN FAMILY														
Unidentified sp.1 **	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
Unidentified sp.2 **	-	-	-	-	-	-	-	-	-	-	-	1	-	NA
Unidentified sp.3 **	-	-	-	-	-	-	-	-	-	-	-	-	1	NA
Unidentified sp.4 **	-	-	-	-	-	-	-	-	-	-	-	-	1	NA

Table S3: Aboveground and total C stock, soil properties of 13 fragments of Atlantic lowland rain forest sampled in the northern Espírito Santo, Brazil. The number following the letter S refers to the age of the secondary forests.

Second-growth forests	**Aboveground C stock** (Mg ha^{-1})	**Total C stock** (Mg ha^{-1})	**Soil organic C** (Mg ha^{-1})	**Available P** (mg kg^{-1} soil)	**Exchangeable Al^{3+}** (cmol$_c$ kg^{-1} soil)	**Sum of bases** (cmol$_c$ kg^{-1} soil)	**Silt** (%)	**Clay** (%)	**Fine Sand** (%)	**Coarse Sand** (%)
S07	16.58	45.78	29.20	1.22	0.18	2.85	5.4	46.2	9.0	39.4
S14_1	15.02	37.13	22.11	4.67	0.05	2.98	3.2	11.9	18.5	66.4
S14_2	30.86	53.38	22.52	1.50	0.00	2.54	3.6	12.8	16.3	67.3
S19	19.19	54.47	35.28	2.30	0.25	3.17	2.7	35.5	10.1	51.7
S23	68.44	90.90	22.46	1.41	0.48	1.24	3.7	23.8	11.3	61.2
S26	66.85	86.21	19.36	1.90	0.15	1.59	2.1	7.8	10.1	80.0
S28_1	57.19	74.88	17.69	1.30	0.22	1.28	1.5	8.0	18.0	72.5
S28_2	41.45	83.49	42.04	1.54	0.77	1.88	3.0	25.5	11.6	59.9
S28_3	49.54	77.73	28.19	1.35	0.13	2.90	1.8	25.5	10.0	62.7
S28_4	52.61	90.87	38.26	1.74	0.20	3.88	3.6	32.5	10.4	53.5
S29	56.17	77.92	21.75	0.90	0.21	1.66	2.5	10.2	15.7	71.5
Old-growth forests										
M_1	363.21	395.09	31.88	2.09	0.64	1.95	3.0	19.3	12.1	65.6
M_2	205.92	230.28	24.36	2.00	0.16	2.44	3.0	11.6	15.0	70.4

Table S4: List of ant species found in the 13 fragments of Atlantic lowland rain forest sampled in the northern Espírito Santo, Brazil. The number following the letter S refers to the age of the secondary forests. The species exclusive to mature forests are in bold.

SUBFAMILY	**Second-growth forests**											**Old-growth forests**	
Species	**S07**	**S14_1**	**S14_2**	**S19**	**S23**	**S26**	**S28_1**	**S28_2**	**S28_3**	**S28_4**	**S29**	**M_1**	**M_2**
AMBLYOPONINAE													
Fulakora fae01	-	-	-	-	-	-	1	-	-	1	-	-	-
DOLICHODERINAE													
Dolichoderus imitator	-	-	-	-	-	1	-	-	-	-	-	-	1
Linepithema pulex	-	-	-	-	-	-	-	1	-	-	-	-	-
DORYLINAE													
Neivamyrmex sp.1	-	-	-	-	1	-	-	-	-	-	-	-	-
Neocerapachys ufv-02	-	-	-	-	-	-	-	1	-	-	-	-	-
ECTATOMMINAE													
Ectatomma brunneum	1	-	-	-	-	-	-	-	-	-	-	-	-
Ectatomma edentatum	-	-	-	-	-	-	-	-	-	-	-	-	1
Ectatomma permagnum	1	-	-	-	-	-	-	-	-	-	-	-	-
Ectatomma planidens	-	1	-	-	1	-	-	-	-	-	-	-	-
Typhlomyrmex sp.1	-	1	-	-	-	-	-	-	-	-	-	-	-
FORMICINAE													
Acropyga sp.2	-	-	-	-	-	-	1	-	-	-	-	-	-
Brachymyrmex sp.1	2	2	2	5	1	4	1	-	2	-	-	-	-
Brachymyrmex sp.2	1	2	-	-	-	-	-	-	-	-	-	-	-
Brachymyrmex sp.3	-	-	-	1	-	2	-	-	4	2	2	-	1
Brachymyrmex sp.4	-	3	4	-	-	-	-	-	-	1	-	-	-

Nylanderia sp.1	-	-	-	1	1	-	-	-	-	-	-	-	1
Nylanderia sp.2	-	1	-	-	-	-	2	-	1	1	-	1	2
MYRMICINAE													
Apterostigma sp.1	-	-	-	-	-	-	-	-	-	1	-	-	-
Atta sp.1	-	-	-	1	-	-	1	-	-	-	-	-	-
Basiceros scambognathus	-	-	-	-	-	1	-	-	-	-	-	-	-
Carebara brasiliana	-	-	-	-	-	-	-	1	2	-	-	1	-
***Carebara* sp.1**	-	-	-	-	-	-	-	-	-	-	-	-	1
Carebara ufv-03	-	-	1	-	-	1	-	-	-	-	-	1	-
Carebara urichi	-	-	-	-	-	-	-	-	-	-	2	-	-
Cephalotes maculatus	-	-	-	1	-	-	-	-	-	-	-	-	-
Crematogaster indet	-	-	-	-	-	1	-	-	-	-	-	-	-
Crematogaster sp.1	-	-	-	-	-	-	1	-	-	-	1	-	-
Crematogaster sp.2	1	2	-	-	-	-	-	-	-	-	-	-	-
Cryptomyrmex longinodus	-	-	-	-	-	-	-	-	-	-	-	-	1
Cyphomyrmex sp.1	-	-	-	-	-	1	-	-	-	-	1	1	1
Cyphomyrmex sp.2	1	2	-	-	-	-	-	-	-	-	-	-	2
Eurhopalothrix bruchi	-	-	-	-	-	1	-	-	-	-	-	-	-
Hylomyrma balzani	-	-	-	-	-	3	-	-	1	-	3	3	1
Megalomyrmex sp.1	-	-	2	-	-	-	-	-	-	-	-	-	-
Megalomyrmex sp.2	-	-	-	-	1	-	-	-	-	-	-	-	-
Megalomyrmex sp.3	-	-	-	-	-	-	-	-	1	-	-	-	-
Mycetophylax sp.1	-	-	-	-	-	-	-	-	-	-	1	1	1
Mycocepurus goeldii	-	-	-	1	1	-	-	-	-	-	-	-	1
Octostruma iheringi	-	-	-	-	-	1	-	-	1	-	-	-	-
Octostruma petiolata	-	-	-	1	-	-	-	-	-	-	-	-	-

Octostruma sp.1	-	-	-	-	-	-	1	-	-	-	2	1	-
Pheidole fracticeps	1	1	5	1	5	6	2	2	-	-	4	-	2
Pheidole midas	-	-	1	-	-	-	-	-	1	-	-	1	-
Pheidole mosenopsis	-	-	-	-	-	-	2	-	3	1	1	3	4
Pheidole radoszkowskii	-	-	-	3	-	2	-	-	1	2	1	4	-
Pheidole rufipilis	-	-	-	1	2	-	-	1	1	-	1	-	-
Pheidole sensitiva	-	-	-	-	-	1	-	-	-	-	-	-	-
Pheidole sp.4	-	-	-	-	-	1	-	-	-	-	-	-	1
Pheidole sp.5	-	1	-	-	-	-	1	1	1	1	1	2	1
Pheidole sp.7	1	-	-	-	-	-	-	-	-	-	-	-	-
Pheidole sp.9	-	-	-	2	-	-	-	-	-	-	-	-	-
Pheidole sp.11	-	1	-	1	-	-	1	-	-	-	-	-	-
Pheidole sp.13	-	-	-	-	-	-	-	-	1	-	2	-	-
Pheidole sp.14	-	1	-	-	-	-	-	-	-	-	-	-	-
Pheidole sp.15	-	-	1	-	-	-	-	-	-	-	-	-	-
Rhopalothrix ufv sp1	-	-	-	-	-	-	-	-	2	-	1	1	1
***Rhopalothrix* ufv-04**	-	-	-	-	-	-	-	-	-	-	-	-	1
Rogeria sp.1	1	-	-	-	5	1	-	-	-	-	-	-	-
Rogeria sp.2	2	1	2	-	-	-	-	-	-	-	-	-	-
Rogeria sp.3	-	1	1	-	-	-	-	-	-	-	-	-	1
***Rogeria* sp.4**	-	-	-	-	-	-	-	-	-	-	-	2	-
Sericomyrmex bondari	-	-	-	1	-	2	-	-	1	-	1	-	-
Sericomyrmex sp.1	-	-	-	-	-	-	1	-	-	-	1	2	-
Solenopsis indet	-	-	-	1	-	-	1	-	-	-	-	-	-
Solenopsis saevissima cf	-	-	-	-	-	-	-	-	-	1	1	-	-
Solenopsis sp.1	1	3	2	1	5	3	5	3	5	7	2	4	10

Solenopsis sp.2	2	5	4	6	8	6	3	8	5	4	2	2	4
Solenopsis sp.3	-	-	-	-	-	-	1	-	-	-	-	-	1
Solenopsis sp.4	-	-	-	-	-	-	-	1	1	1	3	1	1
***Solenopsis* sp.5**	-	-	-	-	-	-	-	-	-	-	-	2	-
Solenopsis sp.6	1	2	3	-	-	1	4	2	-	2	4	6	1
Solenopsis sp.7	-	-	-	1	1	-	2	-	-	-	1	2	-
Solenopsis sp.8	-	-	-	-	5	-	2	1	1	2	1	1	1
Solenopsis sp.9	-	-	-	-	-	-	2	1	1	-	1	-	1
Solenopsis sp.11	1	4	5	2	2	1	-	-	-	-	-	-	-
Solenopsis sp.12	-	-	-	-	-	-	-	-	-	-	1	-	-
Solenopsis sp.15	-	-	-	-	-	-	1	-	-	-	-	-	-
Solenopsis ufv-17	-	-	-	-	-	-	-	-	-	1	-	-	-
***Solenopsis* ufv-32**	-	-	-	-	-	-	-	-	-	-	-	1	-
Solenopsis ufv-33	-	-	-	1	-	-	-	1	-	-	-	-	-
Strumigenys carinithorax	-	-	-	-	-	1	-	-	-	-	-	-	-
Strumigenys denticulata	-	-	-	-	1	1	1	1	-	-	1	4	3
Strumigenys eggersi	1	2	5	1	4	3	3	2	1	-	3	-	-
Strumigenys elongata	-	-	-	-	1	1	1	-	-	-	1	-	2
Strumigenys emmae	-	1	-	-	-	-	-	-	-	-	-	-	-
Strumigenys epelys	-	-	-	-	-	1	-	-	-	-	-	-	-
Strumigenys grytava	-	-	2	1	-	-	-	-	-	-	-	-	-
Strumigenys subedentata	-	-	-	-	1	-	-	-	-	-	-	-	-
Strumigenys ufv-04	-	1	-	-	-	-	1	-	6	1	1	-	1
Strumigenys ufv-31	-	-	-	2	-	-	-	-	-	-	-	-	-
Trachymyrmex sp.1	-	-	-	-	-	-	-	2	-	-	-	-	-
Wasmannia auropunctata	8	6	-	4	8	1	8	6	6	2	5	2	8

Wasmannia sp.1	-	-	-	-	-	3	-	-	-	-	-	-	-
Wasmannia sp.2	-	-	-	-	1	1	-	-	1	-	1	1	-
Wasmannia sp.3	-	-	-	-	-	-	-	1	-	-	-	-	-
PONERINAE													
Anochetus neglectus	2	2	-	-	-	-	-	-	-	-	-	-	-
Anochetus oriens	-	1	-	-	-	-	-	-	-	-	-	-	-
Hypoponera foreli	-	-	-	-	-	1	-	-	-	-	-	-	-
***Hypoponera* alw06**	-	-	-	-	-	-	-	-	-	-	-	-	2
Hypoponera sp.1	1	-	-	-	2	1	2	-	-	-	1	2	1
Hypoponera sp.2	-	1	-	-	-	-	6	1	-	1	1	-	1
Hypoponera sp.3	3	2	2	-	1	-	-	2	1	-	-	2	5
Hypoponera sp.4	-	-	-	-	-	2	-	-	-	-	-	-	-
Hypoponera sp.5	-	-	-	-	-	-	-	-	1	-	-	-	3
Hypoponera sp.6	-	-	-	-	1	2	1	-	-	-	1	-	-
Mayaponera constricta	-	-	-	-	-	-	-	-	-	-	-	1	-
Odontomachus meinerti	-	-	-	-	-	-	-	-	-	-	1	1	2
***Odontomachus* sp.1**	-	-	-	-	-	-	-	-	-	-	-	-	1
Pachycondyla harpax	-	-	-	1	1	1	-	1	-	-	-	-	-
Pseudoponera gilberti	-	-	-	-	-	-	1	-	-	-	-	-	-
Rasopone arhuaca	-	-	-	-	1	-	2	1	-	-	1	1	2
Thaumatomyrmex fraxini	-	-	-	-	-	-	-	-	-	1	-	-	-
PROCERATIINAE													
Discothyrea neotropica	-	-	-	-	-	-	-	-	-	-	-	1	-
Discothyrea ufv-01	-	-	-	2	5	3	2	-	2	-	-	-	-
PSEUDOMYRMECINAE													
Pseudomyrmex sp.1	-	-	-	-	-	1	-	-	-	-	-	-	-

V. CONCLUSÕES GERAIS

A partir dos resultados dos dois capítulos podemos concluir que:

(i) Corte raso de uma floresta de tabuleiro madura em solos pobres em nutrientes, seguido de remoção completa do material lenhoso, não causou efeitos drásticos aparentes nas propriedades químicas do solo, o que foi evidenciado pela baixa mobilização de nutrientes após 36 anos de sucessão secundária;

(ii) Distúrbios ambientais afetam os componentes florestais, porém alguns deles se mostraram resilientes, ou seja, apresentaram uma tendência a retornar ao longo da sucessão aos níveis e à composição encontrados em florestas maduras: riqueza e composição florística arbórea, o estoque de carbono total e acima do solo e a composição da fauna de formigas de serapilheira. Por outro lado, a recuperação da riqueza de formigas e das propriedades do solo não foram afetadas pela idade do fragmento. Isso sugere que a riqueza de formigas e o solo de florestas de tabuleiro exibem uma resistência marcante a distúrbios induzidos pelo homem.

As florestas maduras são extremamente importantes para a conservação da biodiversidade e para o funcionamento dos ecossistemas, uma vez que abrigam uma grande riqueza de espécies e espécies com status de conservação, e estocam grandes quantidades de carbono em sua biomassa. Além disso, essas florestas atuam como fontes de recrutas e propágulos de espécies de diferentes grupos, para áreas perturbadas, contribuindo para sua regeneração natural. Contudo, ressaltamos a importância das florestas em regeneração para conservação da biodiversidade e das funções e serviços ecossistêmicos, devido ao seu grande potencial em sequestrar carbono e em abrigar espécies típicas de área de sucessão (i.e., pioneiras) e espécies tolerantes a distúrbios, proporcionando nichos para outros grupos, que geralmente não são encontrados em áreas preservadas.