Biodivers Conserv (2015) 24:2273–2291
DOI 10.1007/s10531-015-0982-9

ORIGINAL PAPER

Factors influencing early secondary succession and ecosystem carbon stocks in Brazilian Atlantic Forest

Samuel J. B. Robinson[1] · **Eduardo van den Berg**[2] · **Gabriela S. Meirelles**[2] · **Nick Ostle**[1]

Received: 15 February 2015 / Revised: 3 August 2015 / Accepted: 10 August 2015 /

Abstract Ecologically relevant restoration of secondary Atlantic forest on abandoned land offers a potential means to recover biodiversity and improve crucial ecosystem services, including carbon sequestration. Early secondary successional trajectories are determined by a range of environmental factors that influence plant community development. Context-specific understanding of forest vegetation communities, their dynamics, and underlying drivers is needed for future restoration strategies. In this study we examined relationships between soil (chemical and physical) and environmental (landscape and topographical) characteristics, plant community attributes, and carbon stocks during early secondary succession. Data were collected at two sites undergoing early secondary succession in seasonally-dry Atlantic Forest (Rio de Janeiro State, Brazil). Both sites were previously used for pasture and abandoned at similar times, but showed differing vegetation communities. We found tree biomass and diversity and ecosystem carbon storage to be strongly positively related to the amount of surrounding forest, less steep slopes and clay soils, and negatively to the abundance of the shrub *Leandra aurea*. Soil carbon pools significantly increased with aboveground tree biomass. The only factor significantly affecting the metric of overall successional development (combining tree biomass and diversity) was total surrounding forest cover. Our findings suggest recovery of secondary forest and below- and aboveground carbon storage is limited by the amount of adjacent forest, some soil properties and dense shrub establishment down-regulating the succession process. Overall we offer evidence of potential to improve recovery of Atlantic forest with

---

Communicated by Jefferson Prado, Pedro V. Eisenlohr and Ary T. de Oliveira-Filho.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-015-0982-9) contains supplementary material, which is available to authorized users.

✉ Samuel J. B. Robinson
sjbrobinson@hotmail.co.uk

[1] Plant and Soil Ecology Laboratory, Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster LA1 4YQ, UK

[2] Departamento de Biologia, Universidade Federal de Lavras, Lavras, MG CEP37200-000, Brazil

ecologically relevant seeding/planting programmes and selective shrub removal that could benefit ecosystem carbon storage.

Keywords Tropical secondary forest · Abandoned pasture · Soil characteristics · Ecological restoration · Facilitation · Inhibition · Melastomataceae · *Leandra aurea* · Seed dispersal

Introduction

The Atlantic Forest tropical biome is recognised as one of the most important global biodiversity hotspots (Loyola et al. 2013). It is characterised by high endemism and diversity (Carnaval et al. 2009), greater than that of most Amazonian forests (Morellato and Haddad 2000). However, these biologically unique forests are some of the most threatened (Metzger 2009), and have undergone heavy anthropogenically-driven deforestation and degradation over the past five centuries (Tabarelli et al. 2010). Only around 11.7 % of the original extent of 150 million hectares remains, and the majority of the existing forest fragments are isolated, unprotected and small in area (Ribeiro et al. 2009). This has greatly impacted on the provision of important ecosystem functions (Ferraz et al. 2014) that underpin vital services provided by these forests, including the offsetting of global carbon emissions and climate change (DeFries et al. 2002; Zarin 2012). Consequently, the Atlantic Forest is now regarded as a priority biome for global biodiversity conservation (Martini et al. 2007).

Although the preservation of primary forest is crucial for biodiversity conservation and the maintenance of resultant ecosystem functions (Gibson et al. 2011), the natural and managed development of secondary forest on degraded land could have great potential for recovery ecosystem services (Chazdon 2008; Melo et al. 2013) including carbon storage (Pan et al. 2011). This could be achieved through large-scale ecological restoration initiatives (Brancalion et al. 2013) in human-modified landscapes throughout the neotropics where land has been left abandoned as a result of changes in agricultural practices (Wright 2010). Today many restoration programmes deploy strategic seeding (Kettle 2012) and planting programmes (Celis and Jose 2011) to achieve desired vegetation composition and structure. However, there is evidence that past efforts to accelerate recovery of Brazilian Atlantic Forest have been challenged by a lack of context-specific knowledge of these communities and their ecology (Rodrigues et al. 2009). It is clear that improved understanding of the factors governing secondary succession in tropical forest ecosystems, including Atlantic Forest, is vital for restoration and management (Chazdon 2008; Ferraz et al. 2014; Putz and Redford 2010).

Secondary succession in tropical forests is characterised by an increase in tree abundance, biomass, species richness, spatial heterogeneity and floristic similarity with surrounding mature forest over time (Cook et al. 2005; Finegan 1996; Kappelle et al. 1995), although these processes are not necessarily unidirectional or gradual (van Breugel et al. 2006). Increases in soil nutrient status, organic matter and carbon storage are also expected with increasing tree biomass (Amazonas et al. 2011; Deng et al. 2013; Hooker and Compton 2003). Secondary succession of Brazilian Atlantic Forest can result in a wide range of realised vegetation communities that depend on a number of local biotic factors and environmental forces (Rees et al. 2001). These factors act to influence the rate and direction of forest secondary succession by affecting the establishment of pioneer plant species and ecological interactions (Connell and Slatyer 1977).

Early-successional trajectories on tropical abandoned land have been shown to be strongly influenced by the type, duration, frequency and intensity of previous land use (Valdez-Hernández et al. 2014; Holl and Zahawi 2014). This includes the size of the disturbed site and subsequent proximity to seed sources (Holl 1999; Muiz-Castro et al. 2006; Zimmerman et al. 2000), and the amount and distribution of forest within the surrounding landscape matrix as a regulator of seed dispersal vector movements (Uriarte et al. 2011). Soil chemical and physical characteristics can also affect the speed of forest recovery (Chazdon 2003; Johnson et al. 2000; Moran et al. 2000). These may be principle drivers of developmental rates towards a woody-dominated state (Chazdon et al. 2007; Fridley and Wright 2012), as well as influencing plant species distributions (Condit et al. 2013). Soil nutrients are an important regulator of vegetation regrowth (Celentano et al. 2011) and strategies for soil nutrient management may be a prerequisite for forest re-establishment where soils have been degraded (Chazdon 2003; Macedo et al. 2008). The return of nutrients to the soil is in turn dependent on the composition of developing vegetation (Melvin et al. 2011). Topography can also influence succession through a mediation of edaphic conditions. Factors such as gradient of slope are linked with plant species richness and diversity and tree seedling recruitment, by affecting water drainage and the washing-out or accumulation of nutrients (Fu, et al. 2004; Osman and Barakbah 2010; Bentos et al. 2013). Although many studies have investigated interrelationships and feedbacks between soil characteristics and vegetation community attributes during forest regeneration throughout the tropics (e.g. Amazonas et al. 2011; Fonseca et al. 2012; Holl and Zahawi 2014; Li et al. 2013; Yassir et al. 2010), few studies have been undertaken in the context of early secondary succession in Brazilian Atlantic Forest.

The overarching aim of this study was to investigate the relationships between soil and environmental characteristics, plant community attributes, and above- and belowground carbon stocks across differing vegetation communities during tropical secondary succession. Vegetation, soil and environmental metrics were recorded across sites of early secondary succession in Brazilian Atlantic Forest, focussing on two areas previously used for pasture with similar time since abandonment, located between the Serra da Mantiqueira and Serra do Mar mountain ranges. This study contributes to a comparative analysis of succession in the area to provide a basis for future restoration strategies focused on re-establishing a corridor between two important protected areas (Itatiaia National Park to the north and Serra da Bocaina State Park to the south). The key objectives of this work were to investigate (1) underlying drivers of differences in vegetation communities and carbon stocks and (2) mutual influences of vegetation and soil conditions (chemical properties) during early secondary succession. As soil properties and environmental factors can affect rates of development towards mature forest, and soil quality is expected to improve during forest recovery, we hypothesised that (a) variations in vegetation layers (grasses, shrubs and trees) can be explained by environmental and soil characteristics, (b) forest re-establishment (accumulation of aboveground tree biomass and diversity) is limited by low soil nutrient capital, soil texture, slope gradient and amount of adjacent closed-canopy native forest, and that (c) soil properties (i.e. nutrient status and carbon content) and total (above- and belowground) carbon storage recover with increasing tree biomass.

Materials and methods

Study site

This study was conducted at three areas of previously abandoned pasture within seasonally dry semi-deciduous Brazilian Atlantic Forest, located around the Funil Reservoir in the Paraíba do Sul river catchment, near to the town of Itatiaia, Rio de Janeiro (22°28′00.60″S, 44°34′51.65″W) as shown on the map (Online Resource 1). Soils under these forests are characterised primarily as Ultisols and Oxisols (Bernoux et al. 2002). Two areas (Areas 1 and 2) were chosen to represent areas undergoing early secondary succession. Both of these areas comprised shrub dominated communities with intermittent grasses and trees with no established canopy. They were located near a large fragment of closed-canopy native forest, with patchy remnant stands also occupying the surrounding landscape matrix. According to local accounts, both sites were abandoned approximately 30 years ago. They were assumed to have similar land use histories. Area 2 was perceived as demonstrating faster successional rates owing to a markedly greater abundance and diversity of trees (Fig. 1a, b). The shrub *Leandra aurea* exhibited high abundance in both areas, particularly dominant in Area 1 (Fig. 1c). A control area of more mature secondary forest was studied for comparison (Fig. 1d).

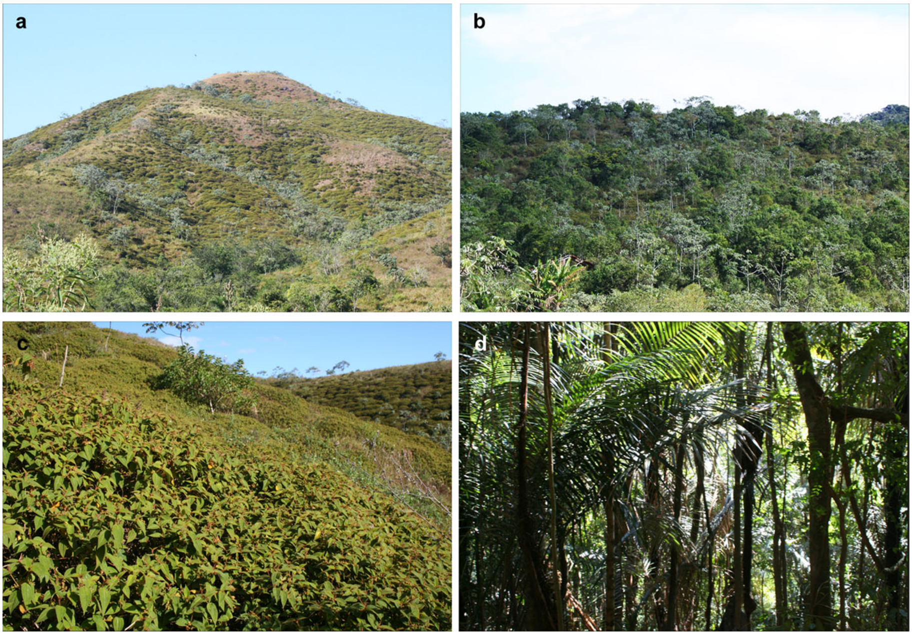

Fig. 1 Images of study sites, Area 1 (**a**) demonstrating a markedly lower abundance of trees in comparison to Area 2 (**b**), indicating slower rates of succession and forest recovery. The pioneer shrub *L. aurea* shrub was also abundant, being particularly dominant in Area 1 (**c**). The control Area (**d**) was chosen to represent an advanced stage of succession for comparison with early successional sites

Sampling and measurements

Edaphic and environmental metrics

Five 20 × 20 m plots were established in each area. This size was chosen for consistency with other plots already established in the region as part of a wider chronosequence study (in which the control area is also included). These were large enough to minimize the overestimation of aboveground biomass associated with smaller plots (Brown et al. 1995; Marín-Spiotta et al. 2007), whilst also allowing for enough replication to account for high variability in soil and environmental metrics, and to maximise heterogeneity in vegetation communities (Garcia et al. 2014). Soil cores were taken at five points within each plot (one in the centre, and one in the centre of each quarter) to a depth of 20 cm with a 5 cm diameter soil auger for chemical and physical analysis. Samples were air dried, sieved (2 mm mesh), homogenised, and then analysed for pH in water, P concentrations (determined by the Mehlich-1 extraction method described in Bortolon et al. (2011)) and particle size. Further subsamples were taken to determine total C and N percentages by dry combustion using an Elementar Vario EL III elemental analyser. Soil bulk density and soil profiles were assessed by digging a soil pit in the centre of each plot. Undisturbed soil cores were taken at six depths of equal intervals with a volumetric ring to 30 cm. Samples were oven dried at 105 °C to constant weight. Bulk density for each depth was determined by dividing the dry weight of each sample by the ring volume, and averaged to provide mean soil bulk density to 30 cm. Soil horizons were delimited from the soil pit wall according to colour and texture. Leaf litter depth was measured at each corner of a 50 × 50 cm quadrat placed at each sampling point. All litter, fine and course woody debris within the quadrat was collected for determining forest floor litter mass. Slope and elevation were recorded with a clinometer and GPS respectively.

Vegetation metrics

As the study is concerned with early successional stages associated with smaller trees, all individuals with a diameter at breast height (dbh, at 1.3 m from the ground) >3 cm were identified in all plots. Species were identified with the help of taxonomists, and samples collected were deposited in the herbarium in the Departamento de Biologia, Universidade Federal de Lavras (UFLA). Methods for estimating aboveground biomass were derived after Berenguer et al. (2014). Total height was visually estimated and circumference at breast height was measured for each tree. Circumference was measured just below stem defects or trunk irregularities if they occurred at 1.3 m from the ground. For trees with bifurcations below 1.3 m, circumferences for all stems were measured. The allometric equation in Chave et al. (2014) (derived from pantropical tree data including from Brazilian Atlantic Forest) was used for all trees excluding *Cecropia* and palms. Aboveground biomass for *Cecropia* and palms was estimated using the specific equations in Nelson et al. (1999) and Saldarriaga et al. (1988) respectively as they have different growth forms (Table 1). Species-specific wood densities were obtained from the Global Wood Density Database dryad data package (Zanne et al. 2009) (see Chave et al. 2009). When species specific data were not available, estimates were calculated by averaging the wood densities of other species within the closest taxonomic level (Flores and Coomes 2011). Only species from tropical South America were used where possible (Berenguer et al. 2014).

Table 1 Allometric equations for determining aboveground biomass for trees (total dry weight expressed in kg)

Parameter	Equation	R^2	N	Source
Trees > 3 cm dbh (excluding *Cecropia* and palms)	$\exp(-2.6986 + 0.976\ln(\rho D^2 H))$	–	4004	Chave et al. 2014
Cecropia > 3 cm dbh	$\exp(-2.5118 + 2.4257\ln(D))$	0.980	27	Nelson et al. 1999
Palms	$\exp(-6.3789–0.877\ln(1/D^2) + 2.151\ln(H))$	0.890	19	Saldarriaga et al. 1988

Where dbh is tree diameter at breast height (1.3 m from the ground), D = dbh (cm), ρ = wood density (gcm-^{3}) and H = tree height (m)

Shrub biomass was estimated as an indicator of shrub abundance. Shrub cover was visually estimated at the plot level in increments of 10 %. 40 random individuals were selected across areas 1 and 2. Trunk diameter above the rootstock and total height was measured, and crown area was calculated using maximum and perpendicular widths. Aboveground biomass was estimated using the same procedure as for trees. Regression analysis revealed crown area to be a statistically significant predictor of shrub biomass ($R^2 = 0.383$, $p < 0.001$, $N = 40$). Number of shrubs per plot was estimated using average crown area, and the following model was used to estimate total shrub biomass:

$$AGB_s = 0.605 + (0.088 \times C_a) \tag{1}$$

where AGB_t is shrub biomass and C_a is shrub crown area. Analysis of covariance showed no significant difference in the prediction of biomass by crown area between areas or plots ($p > 0.05$), therefore the same model was used for all sites.

Alpha diversity (within-plot diversity) for trees was assessed using the Shannon-Wiener diversity index, H'. The measure of equitability, J', was also calculated (Rodrigues et al. 2004). Beta diversity (similarity in species composition between the areas) was determined using the Sørensen community coefficient, CC, to compare sites of early secondary succession with more mature forest as an indication of floristic recovery or species turnover (Kappelle et al. 1995).

Importance values for each tree species were calculated for each area as the sum of the relative density (proportion of each species accounting for total number of individuals), the relative dominance (proportion of each species accounting for total basal area) and relative frequency (number of plots in which each species occurs as a proportion of total frequency) and divided by the maximum total (Holl 1999; Kuers 2005).

Evaluation of forest recovery

The metrics chosen to indicate successional development were aboveground tree biomass and diversity, taken from the five main community attributes described in Chazdon et al. (2007), as they incorporate aspects of other measures (stem density, basal area,[1] species density and richness). We derived an overall value indicative of forest recovery status, where diversity was weighted by aboveground biomass:

---

[1] Aboveground biomass was chosen as a more direct measurement of abundance compared to basal area alone (Chazdon et al. 2007).

$$ISS = AGB_t \left(\frac{H'}{H'_h} + 1 \right) \tag{2}$$

where ISS is the overall index of successional status, AGB_t is total aboveground tree biomass in a plot, H' is plot diversity and H'_h is the maximum plot diversity found across all areas including the control (in this way diversity values were standardised to give values between 0 and 1. 1 was added to each value to account for plots where only one species was present, $H' = 0$).

Carbon stocks

Carbon stocks for aboveground, forest floor and carbon pools in each plot (MgCha^{-1}) were estimated following Berenguer et al. (2014). Carbon was assumed to account for 50 % of the total biomass in aboveground living biomass, litter and dead wood (IPCC 2006). Therefore, aboveground carbon stocks were estimated as half of the sum of aboveground tree and shrub biomass. For the forest floor carbon pool (i.e. carbon stored in leaf litter and woody debris), litter samples were transferred into paper bags and dried at 65 °C to constant weight to determine biomass (Godinho et al. 2014), multiplied by 0.5 to estimate carbon mass, and divided by the quadrat area. Soil carbon stocks were estimated by multiplying soil carbon content by soil bulk density by layer thickness using average bulk density to the depth that soil cores were taken (20 cm).

Influence of adjacent closed-canopy native forest

To evaluate the potential influence of the amount of adjacent closed-canopy native forest, hereafter referred to simply as forest (i.e. proximity and size of nearby forest fragments), on plant community attributes and carbon stocks, 5 m resolution RapidEye aerial imagery was acquired[2] for the study site and analysed using ArcMap, ver. 10.1. Forest was distinguished from other land cover using supervised classification through the maximum likelihood technique. A buffer of 200 m was demarcated around each plot (to account for both shorter-range and the major effects of long-range seed dispersal, defined by Cain et al. (2000) as over 100 m). Forest cover was estimated from the relative number of pixels identified as accounting for forest within each buffer.

Statistical analyses

Statistical analyses were conducted using IBM SPSS Statistics for Windows, ver. 21.0. The data were assessed for normality, and means for measured variables were calculated for each area and plot and compared for difference through one-way analysis of variance. Post-hoc Tukey tests were applied where necessary to distinguish homogenous groups. The two areas undergoing early succession were also compared for all metrics using a t test. Significant relationships between vegetation and soil/environmental metrics across the early successional sites were identified using a General Linear Model (GLM). Relationships were considered to be significant at the 5 % critical level ($p < 0.05$). Highly correlated variables were linearly combined into single components through Principle Components Analysis where it made conceptual sense. Potential main drivers of forest recovery and

---

[2] Images were obtained from the Departamento de Ciências Florestais, Universidade Federal de Lavras (UFLA).

carbon storage were then identified by backward elimination using a generalized linear mixed model (GLMM) to accommodate for non-normal distributions and correlations between predictor variables.

Results

Comparison of secondary succession systems

Environmental parameters, pasture grass and shrub characteristics, and soil properties

Plots in Area 1 generally had steeper slopes at slightly higher elevations, and were shown to have consistently less amounts of forest in the surrounding landscape matrix compared to Area 2. Significantly higher mean values for biomass of the *L. aurea* shrub were found in Area 1 where it was found to be strongly dominant (ranging from 80 to 90 % cover across all plots compared to minimum and maximum values of 30 and 90 % respectively in Area 2). Pasture grass cover was generally higher in Area 2, with *Andropogon bicornis* and *Melinis minutiflora* being the dominant species. The only soil physical parameter that was not significantly different between areas 1 and 2 was proportion of silt. Soil clay content (Online Resource 2 a), leaf litter, organic and mixed layer depths were all higher in Area 2 (the latter two variables greater still in the control) whereas proportion of sand was lower (Online Resource 2 b). Areas 1 and 2 displayed significantly different means for all soil chemical properties (see Online Resource 3 for means of all measured variables and statistics). Lower concentrations of C, N and P were found in Area 1 (Online Resource 2c,d,e) although much variability was found. When all sites were considered, the control did not significantly differ from Area 2 for mean N or C percentages, although P concentrations were significantly higher in the control. Soils in Area 2 were consistently more acidic than in Area 1, and pH values were significantly lower in the control compared to early successional sites (Online Resource 2 f).

Tree community metrics

We measured a total of 736 trees in all studied areas, of which 715 were identified to the level of species. A full species list can be found in the online supplementary material (Online Resource 4). Tree biomass, diversity, evenness, and overall successional indices were all shown to be significantly higher in Area 2 compared to Area 1 when compared without the control, although a high degree of within-site variability was found among all of these parameters (Online Resource 3). However, when the control area was included in the comparison, tree abundance was not shown to significantly differ between areas 1 and 2, owing to a substantially greater tree biomass values in the control (Fig. 2a). The other measures of tree community structure, tree height and DBH, showed trees to be significantly taller in Area 1 than Area 2 (and taller still in the control), whereas mean DBH was statistically similar in both areas of early succession (although values were significantly smaller than in control forest). Tree diversity (Fig. 2b) and equitability were larger in Area 2 compared to Area 1, and significantly greater in the control area. Sørensen community coefficients for beta diversity gave values of 0.05 between Area 1 and the control forest, 0.10 between Area 2 and the control forest and 0.80 between areas 1 and 2. Tree communities in the control area were therefore shown to be generally more floristically similar to those in Area 2 than Area 1. Tree communities in areas 1 and 2 were, however, comparatively more similar to each other than to the control forest. The most important tree species were *Cecropia pachystachia* in Area 1 (accounting for 88.1 % of individuals), and *Myrcia splendens* in Area 2 (65.0 %).

Carbon stocks

Total carbon stocks were significantly higher in Area 2 than in Area 1, and higher still in the control forest (Fig. 2c). Soil carbon stocks were significantly lower in Area 1 than in Area 2, although soil carbon pools in Area 2 were statistically similar to the control. Differences in forest floor (leaf litter and woody debris) carbon stocks were not found between areas 1 and 2, although values were significantly greater in the control. We found aboveground carbon stocks (displaying the greatest amount of within-site variability) in areas 1 and 2 to be statistically similar between themselves, but significantly lower compared to the control. A comparison of the relative proportions of each carbon pool to total carbon stocks demonstrates a larger proportion of carbon stored in the aboveground pool in Area 2 than Area 1, and much more in the control. Conversely, the proportion of total carbon stored in the soil is lower in Area 2 than Area 1, and to a considerably lesser extent in the control (Fig. 2d,e).

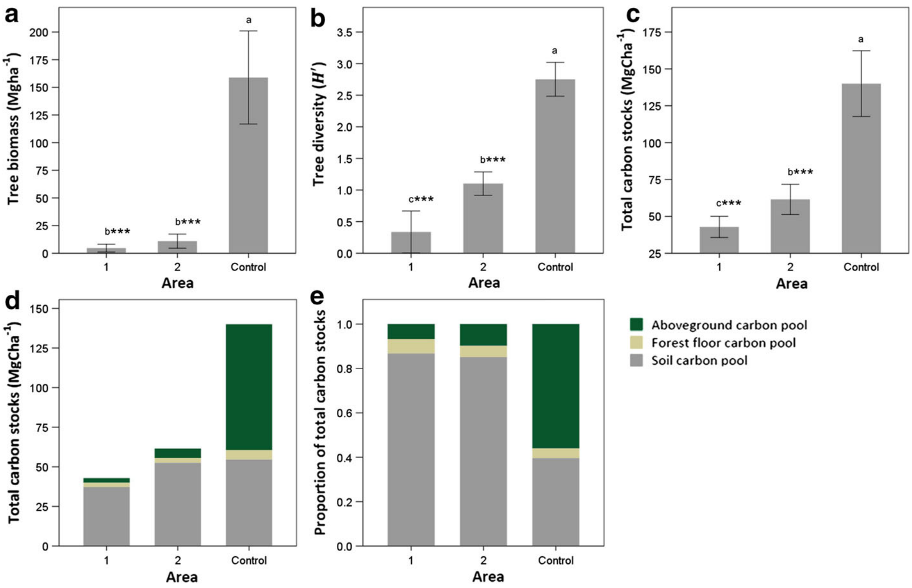

Fig. 2 Mean values for vegetation and carbon metrics for each area for **a** tree biomass and **b** diversity, and **c** total carbon stocks (± 1 *SD*, $N = 5$), **d** total carbon stocks divided into each carbon pool, and **e** relative proportions of each carbon pool contributing to overall carbon storage. Similar superscript letters indicate statistically homogenous groups for each parameter identified by the Tukey test at $p < 0.05$, with letters a to c representing highest to lowest group means. Early successional areas 1 and 2 were also compared separately without the control area using a *t* test. *** indicates significant differences between metrics of the two early successional sites at the $p < 0.001$ level, ** $p < 0.01$, and *$p < 0.05$

Relationships across early successional sites

A strong positive relationship was found between tree biomass and diversity and amount of adjacent forest ($R^2 = 0.305$, $p < 0.001$ and $R^2 = 0.674$, $p < 0.001$ respectively) (Online Resource 5a,b), whereas both of these parameters decreased with greater shrub abundance ($R^2 = 0.447$, $p < 0.001$ and $R^2 = 0.129$, $p = 0.01$ respectively) (Online Resource 5c,d). Higher tree biomass values were weakly associated with less steep slopes ($R^2 = 0.085$, $p = 0.040$). There was no significant correlation between tree biomass and concentration of N or P ($p > 0.05$), although it was positively correlated with soil clay content ($R^2 = 0.231$, $p < 0.001$) (Online Resource 5 e) and negatively with the proportion of sand ($R^2 = 0.164$, $p = 0.004$). Tree diversity was also strongly positively affected by soil clay content ($R^2 = 0.599$, $p < 0.001$) (Online Resource 5f). Leaf litter, organic and mixed layer thickness all increased with tree biomass, as did Soil C content (although weakly) ($R^2 = 0.154$, $p = 0.005$, $R^2 = 0.524$, $p < 0.001$, $R^2 = 0.238$, $p < 0.001$ and $R^2 = 0.107$, $p = 0.020$ respectively) whilst the opposite trend was observed with pH levels ($R^2 = 0.229$, $p < 0.001$) and soil bulk density ($R^2 = 0.229$, $p < 0.001$). Shrub biomass was positively related to soils of lower N and P concentrations ($R^2 = 0.317$, $p < 0.001$ and $R^2 = 0.228$, $p < 0.001$ respectively) and steeper slopes ($R^2 = 0.392$, $p < 0.001$). Tree diversity increased with higher concentrations of N ($R^2 = 0.546$, $p < 0.001$) and P ($R^2 = 0.129$, $p = 0.010$) as well as overall tree abundance ($R^2 = 0.230$, $p < 0.001$). Less diverse tree communities were more likely to be found on soils with a greater proportion of sand ($R^2 = 0.578$, $p < 0.001$) at higher elevations ($R^2 = 0.270$, $p < 0.001$). There was also a positive correlation between soil clay and N content ($R^2 = 0.308$, $p < 0.001$).

Total carbon stocks were strongly positively correlated with aboveground tree biomass ($R^2 = 0.275$, $p < 0.001$) through a direct association with aboveground carbon stocks ($R^2 = 0.998$, $p < 0.001$), as well as forest floor ($R^2 = 0.151$, $p = 0.005$) and soil ($R^2 = 0.086$, $p = 0.038$) carbon stocks. Soil carbon stocks were positively related to leaf litter depth ($R^2 = 0.104$, $p = 0.022$). There were also positive relationships between soil carbon stocks and N and P concentrations ($R^2 = 0.753$, $p < 0.001$ and $R^2 = 0.489$, $p < 0.001$ respectively).

When these relationships were tested across all sites including the control, pH was shown to decline with greater tree biomass ($R^2 = 0.739$, $p < 0.001$), while soil C increased ($R^2 = 0.158$, $p < 0.001$). P concentrations increased with tree biomass ($R^2 = 0.335$, $p < 0.001$) as did soil and forest floor carbon pools ($R^2 = 0.141$, $p = 0.01$ and $R^2 = 0.443$, $p < 0.001$ respectively). There was a positive relationship between tree diversity and soil N across all sites ($R^2 = 0.142$, $p = 0.001$).

As the two soil textural parameters of clay and sand content were highly correlated ($R^2 = 0.889$, $p < 0.001$), a new variable representing clayey soils was created as a linear combination of the two through for analysis of main drivers of successional development though Principle Components Analysis where the extracted component explained 97.1 % of the variance. The same procedure was taken for the correlated variables shrub biomass and pasture grass cover ($R^2 = 0.978$, $p < 0.001$), to represent shrub dominance, where the extracted component explained 99.4 % of variance. The GLMM showed the two predictors having the largest effect on tree biomass to be amount of adjacent forest and slope ($F = 9.835$, $p = 0.003$ and $F = 4.537$, $p = 0.038$ respectively). The parameters having the largest effect on tree diversity were found to be the proportion of clay in the soil ($F = 26.208$, $p = < 0.001$), the proportion of shrub in relation to pasture grass cover ($F = 15.844$, $p = < 0.001$), and soil N content ($F = 8.655$, $p = 0.005$). The only significant parameter found to be most strongly affecting the overall measure of early forest recovery status, *ISS* was the amount of forest in the surrounding area ($F = 7.648$, $p = 0.008$).

Discussion

Drivers of early successional trajectories

Our results show that variation in vegetation community attributes (i.e. tree biomass and diversity, and relative abundance of shrub species) can, in part, be explained by landscape and topography parameters (amount of adjacent forest and slope) and soil characteristics (proportion of clay in the soil) in these early successional sites, although we recognise the limitations due to errors associated with estimating tree height for calculating tree biomass. The hypothesis that forest recovery may be influenced by the amount of nearby closed-canopy native forest was supported through its strong positive effect on the index of overall forest recovery status. The proportion of clay in the soil was shown to be an important significant predictor of tree abundance and diversity, allowing the rejection of the null hypothesis that soil texture does not limit successional development. However, the lack of a significant relationship between soil nutrient parameters and tree biomass suggests woody biomass accumulation is not limited by soil N or P status at these early successional sites. Tree biomass and diversity were also negatively associated with the dominance of the abundant shrub species *L. aurea* and slope steepness.

Overall, more developed forest communities were found on soils richer in clay at sites with greater amounts of adjacent forest located on less steep slopes, where shrubs were less abundant. As the amount of surrounding forest was shown to be the strongest predictor of overall forest recovery, faster recovery rates would be expected in areas with higher connectivity irrespective of other soil or environmental parameters. Shrub abundance was the second most important factor strongly affecting tree biomass (the parameter most closely linked to total carbon stocks), therefore we suppose that areas independent of the amount of surrounding forest cover could experience slowed overall growth and recuperation of carbon storage when shrub cover is high.

The differences we found between Area 1 and 2 are consistent with recent studies on abandoned land where distance from more mature forest has been negatively related to tree basal area, abundance and diversity (Muiz-Castro et al. 2006). In light of other studies linking proximity and distribution of nearby forest fragments to low numbers of wind- and animal-dispersed seeds (Holl 1999; Uriarte et al. 2011; Zimmerman et al. 2000), these results suggest lack of dispersal may be a main barrier to succession. Selective seeding in addition to planting may therefore be necessary to improve tree recruitment (Kettle 2012) where little or no forest is present in the nearby landscape. In terms of forest structure, our results also show trees were generally taller in Area 1 with less surrounding forest. Greater mean values for tree biomass in Area 2 were therefore driven by overall number of individual trees rather than tree height or DBH. Not only were there fewer trees in Area 1, but individuals were almost exclusively *Cecropia pachystachia*, which have relatively lower biomass for their height as the stems of this genus are hollow (Berenguer et al. 2014).

The colonisation of grasslands by pioneer shrubs has been shown in some tropical ecosystems to improve tree seedling establishment by acting as ‘succession facilitators’, i.e. promoting dispersal, improving soil nutrient status through litter production (for example in Amazonian forests (Vieira et al. 1994)) and providing favourable microclimatic conditions to overcome competition from aggressive grasses in open pasture (Celis and Jose 2011; Klanderud et al. 2010). Conversely, other studies of shrub-tree relationships have shown that establishment of tree seedlings may be impeded where shrubby species have become dense (Styger et al. 2007) through root and shoot competition for nutrients and light (Putz and Canham 1992). As such, well-developed shrub communities can have a high resistance to tree invasion, especially on poor soils (Hill et al. 1995). Our findings suggest abundant presence of the shrub *L. aurea* may be inhibiting the recuperation of secondary forest and carbon storage capacity in this region of Atlantic Forest. As the identified trees were pioneers species, which are typically highly light-demanding (Guariguata and Ostertag 2001), we suggest that intensified photosynthetic competition in areas where shrub canopies are dense may be preventing recruitment of later pioneer species. The family *Melastomataceae*, to which this species belongs, are often apomictic and not reliant on cross-pollination, a characteristic that can offer a competitive advantage for colonisation (dos Santos et al. 2012). We found that high shrub abundance was also most likely to occur on less nutrient rich and sandy soils, suggesting a higher adaptability to poorer conditions. The resistance of later successional colonists may continue as this dominant shrub species persists as per the model of inhibition (Connell and Slatyer 1977). Whereas the active introduction of native shrubs into tropical grassland ecosystems has been advocated in recent studies (Yassir et al. 2010), these findings suggest the selective removal of *L. aurea* may also be beneficial in promoting natural forest recovery. Other studies in Brazilian forests have found this species to be an important constituent of early successional systems (Rondon Neto et al. 2000). Indeed, as these Melastomes are fruit bearing, they may be beneficial in forest recovery through offering a food supply for frugivores and other dispersal vectors, promoting the development of other zoochoric species. For this reason, and for their potential for creating stepping-stones between forested areas in highly fragmented landscapes, plants of the Melastomataceae have been recommended for ecological restoration programmes particularly in Atlantic forest (Silveira et al. 2013). However, this dominance of one species may be limiting as diversity of phenological patterns amongst growth-forms is required for catalysing forest regeneration due to differences in seasonal resource availability for fauna (Garcia et al. 2014). The degree of shrub control needed to facilitate further succession remains unclear, and further research is required to quantify the effect of and selective removal of *L. aurea* where it is dense.

We found the proportion of clay in the soil positively influenced metrics of successional status, corresponding with other studies of transition of grassland towards mature forest in young secondary succession systems where higher sand content impeded the development of shrubs and trees (Yassir et al. 2010). This may be interpreted as an effect of soil water availability, as soils with finer particles have a greater potential and water retention (Wall and Heiskanen 2003), a major determinant of plant growth and survival in seasonally dry secondary tropical forests (Cooper et al. 2012; Hasselquist et al. 2010). Lower capacity for free-drainage with more moderate gradients may further contribute to soil moisture holding capacity. Impedance of forest recovery by lack of water availability is a problematic barrier to remove and even irrigation does not necessarily provide beneficial results in terms of pioneer species growth (e.g. Fortini et al. 2010). The establishment of tree canopies can positively affect local humidity (Holl 1999), and a focus on seeding/planting of hardy native pioneer tree species may offer potential under poor conditions (Zimmerman et al. 2000). Recovering ecosystems in these regions may come under increasing pressure from drier conditions and greater extremes between wet and dry seasons associated with future climate scenarios (Collins et al. 2013; Wright 2010).

The lack of a significant relationship between soil nutrient parameters and tree abundance contrasts with some studies in secondary tropical forest on abandoned land, where soil N and P have been shown to limit accrual of aboveground biomass (Davidson 2004; Davidson et al. 2007; Amazonas et al. 2011), but are congruent with others where neither N nor P explained much of the variation in aboveground tree biomass in young Costa Rican secondary forest and plantations (Holl and Zahawi 2014). However, the positive relationship we found between soil N content and tree diversity is consistent with the notion that accrual of mature tree species during forest recovery can depend on the amount of N available in the soil (Chazdon 2008; Martinez-Garza and Howe 2003). Other recent studies in tropical secondary forest ecosystems have linked soil N to reductions in species evenness and diversity (Lu et al. 2011; Siddique et al. 2010) in the context of soil N enrichment. In the present study, we suggest tree density is not sufficiently high enough to lead to competitive exclusion between these early pioneer trees, which may mutually benefit from higher nutrient concentrations through being particularly adapted (Ellsworth and Reich 1996; Lawrence 2003). Soil N concentrations were moderately linked to the metric of overall forest recovery status when considered alone through this positive relationship with tree diversity, but no soil nutrients were shown to have a significant effect in comparison with other model parameters, i.e. amount of adjacent forest, slope, shrub abundance and soil clay content. Implications for restoration are to focus efforts on these other barriers to succession, being seed dispersal limitation and processes of tree-shrub competition.

Vegetation and edaphic trends across differing communities

We found tree communities in Area 2 to be more similar in composition to the control, also predicted by other studies (Kappelle et al. 1995), possibly indicating that successional processes here are occurring at a faster rate. *M. splendens* and *Siparuna guinanesis* both present in Area 2 (the former an important species) are in some studies considered to be later-successional tree species, (de Meira Junior et al. 2015; de Souza et al. 2007), as opposed to *C. pachystachya*, belonging to a genus regarded as representing early pioneer species (Zalamea et al. 2012), which accounted for the vast majority of individuals identified in Area 1. *Guapira opposita*, regarded as a very late successional species (Alves and Metzger 2006), was found in Area 2 but was absent from Area 1. We suggest the presence of these more successionaly mature species may be linked to greater amounts of adjacent forest, soil clay content, and lower abundance of shrub that we have shown to influence tree biomass and overall diversity. A quantification of the composition of adjacent forest could improve understanding of directions of community recovery (Nascimento et al. 2006).

Our results show a significant positive relationship between tree biomass, leaf litter and P concentrations, suggesting increases in P cycling through organic inputs from secondary vegetation, also found by Hughes et al. (1999). However, this contrasts with studies in tropical China which demonstrated lower levels of soil P in a more advanced successional stage of a chronosequence (Li et al. 2013). The lack of a significant relationship between tree biomass and soil N concentration suggest N pools may remain fairly constant during succession in these areas. This is consistent with some other comparisons between recovering and mature tropical forest (Reiners et al. 1994) and chronosequence studies in Amazonia (Hughes et al. 1999), and may be suggestive of increasing cycling rates observed with recovery in young Atlantic Forest (Amazonas et al. 2011). Lu et al. (2002)

showed plant-facilitated recuperation of soil fertility on Ultisols and Oxisols in secondary Amazonian forest may be much slower compared to other types. We suggest nutrient accumulation to be limited on these highly weathered soils, and that nutrients do not remain long in the soil due to increasing cycling rates with tree biomass, typical of tropical forest ecosystems (Davidson 2004; Davidson et al. 2007). The hypothesis that nutrient stocks improve with forest age cannot be corroborated for all nutrients as N levels did not demonstrate increases with tree biomass. The implications therefore remain unclear and further research through a broader chronosequence analysis may aid understanding of soil nutrient dynamics during secondary succession in Brazilian Atlantic Forest.

Our study showed that soil acidity increases with greater tree biomass. This is consistent with other chronosequence-based and temporal studies of natural forest regeneration (Li et al. 2013) and in plantations (Sang et al. 2013) in the tropics. The positive relationship between leaf litter depth and pH suggests a release of humic acids into the soil through accumulation of litter produced by these communities, as has been found in other tropical forest ecosystems (Melvin et al. 2011), including mature Atlantic Forest (Montagnini et al. 1995). Greater soil acidity, sometimes indicative of poorer soil fertility status (Guariguata and Ostertag 2001), may therefore be representative of ecosystem recovery in these early succession systems.

We found total carbon stocks (the sum of aboveground, soil and forest floor pools) to be strongly positively related to tree biomass, primarily through a well-established direct relationship between tree abundance and aboveground carbon storage (Hughes et al. 1999). As tree biomass was mostly affected by the amount of surrounding forest, this study suggests that connectivity can have a large influence on the recuperation of carbon stocks. Soil carbon stocks have been noted to rise with plantation ages in Costa Rica as trees increase in size (Fonseca et al. 2012), as well as during tropical forest succession in China, which suggested carbon accumulation resulted from increased mixing through greater root biomass, and microbial activity and biogeochemical cycling through decomposition of greater amounts of organic material produced by woody species (Deng et al. 2013; Xiong et al. 2014). Our results showed that estimated soil carbon stocks in the control were not significantly different from Area 2, where tree biomass values were highest for the early successional sites. This may indicate that belowground carbon pools become relatively stable during secondary forest development, a trend observed previously in tropical forests (Hughes et al. 1999). These findings also suggest soil carbon stocks may increase faster than aboveground carbon pools, and recover quickly to levels comparable to those of more mature with relatively small increases in tree abundance even where trees remain sparse, implying great potential for improving ecosystem services through restoration actions. However, clay soils shown here to be related to greater aboveground biomass, may facilitate soil carbon build-up (Knoepp et al. 2000), which clouds direct conclusions. Disentangling the relative drivers of soil carbon storage remains a challenge and further research across broader scales comparing carbon storage across different soil types would help to address this.

In this study we investigated the relationships between vegetation, soil and environmental characteristics during early secondary succession in Brazilian Atlantic Forest. Our approach focussed on two sites of differing vegetation on previous pastureland that were abandoned at similar times. We evaluated underlying drivers of forest recovery and recuperation of ecosystem carbon stocks. Our results show that vegetation community attributes can in part be explained by edaphic and landscape/topographic factors, in addition to internal interactions between plant growth forms. The overall metric of successional development (tree biomass weighted by diversity) was most strongly affected by the amount of adjacent forest, soil clay content, abundance of the shrub *L. aurea* and slope steepness. These findings suggest that forest recovery and recuperation of carbon storage may be limited by lack of seed sources, soil water availability, and inhibition of tree species establishment through competition with pioneer shrubs. There remain significant challenges to restoration programmes and conservation work in these areas of recovering forest. However, (i) strategic seeding and planting programmes in areas distant from existing forest fragments and (ii) selective shrub removal may aid tree recruitment and the recovery of biodiversity and crucial ecosystem functions on abandoned land within this unique and valuable biome. Further research into the precise outcomes of different degrees of shrub clearance is required to evaluate the effects on tree seedling establishment and the facilitative potential of *L. aurea* on soil and microclimate conditions in grassland environments. Broader spatial and chronosequence analyses may offer a more robust understanding of influences of different soil types on complex coupled vegetation and soil nutrient dynamics, and subsequent feedbacks that underpin the development of the exceptionally diverse communities of the Brazilian Atlantic Forest.

Acknowledgments This study was carried out as part of the project "Comparative analysis of fragments and restored areas surrounding the Funil reservoir to readjust Eletrobrás-Furnas restoration projects" ("Análise comparativa dos fragmentos e reflorestamentos no entorno do reservatório, visando à readequação de projetos de restauração na Eletrobrás Furnas", funded by Furnas-Aneel). We thank the Centro de Recuperação de Itatiaia for granting access to study areas. We acknowledge and thank Professors Rubens Manoel dos Santos and Mariana Esteves Mansanares, Universidade Federal de Lavras (UFLA), for plant species identification, and the Departamento de Ciências Florestais for providing aerial imagery. We express our thanks to those who assisted in the fieldwork and analyses, including William dos Santos Ribeiro, Luan Fereira, Danilo Almeida, Leonardo Tavares, Flávia Freire de Siqueira and Guilherme Ramos Demetrio. We are sincerely grateful to Professor Carlos Alberto Silva, Departamento de Ciência do Solo, Universidade Federal de Lavras (UFLA), for valuable advice and the use of equipment.

References

Alves LF, Metzger JP (2006) Forest regeneration in secondary forest areas at Morro Grande Forest Reserve, Cotia, SP (A regeneração florestal em áreas de floresta secundária na Reserva Florestal do Morro Grande, Cotia, SP). Biota Neotropica 6(2). http://www.biotaneotropica.org.br/v6n2/pt/abstract?article+bn00406022006. Accessed 15 Feb 2015

Amazonas NT, Martinelli LA, Piccolo MD, Rodrigues RR (2011) Nitrogen dynamics during ecosystem development in tropical forest restoration. For Ecol Manag 262(8):1551–1557. doi:10.1016/j.foreco.2011.07.003

Bentos TV, Nascimento HEM, Williamson GB (2013) Tree seedling recruitment in Amazon secondary forest: importance of topography and gap micro-site conditions. For Ecol Manag 287:140–146. doi:10.1016/j.foreco.2012.09.016

Berenguer E et al (2014) A large- scale field assessment of carbon stocks in human- modified tropical forests. Glob Change Biol 20(12):3713–3726. doi:10.1111/gcb.12627

Bernoux M, Carvalho MDS, Volkoff B, Cerri CC (2002) Brazil's soil carbon stocks. Soil Sci Soc Am J 66(3):888–896

Bortolon L, Gianello C, Welter S, Almeida RGO, Giasson E (2011) Simultaneous extraction of phosphorus, potassium, calcium and magnesium from soils and potassium recommendations for crops in southern brazil. Pedosphere 21(3):365–372. doi:10.1016/S1002-0160(11)60137-9

Brancalion PH, Viani RA, Calmon M, Carrascosa H, Rodrigues RR (2013) How to organize a large-scale ecological restoration program? The framework developed by the Atlantic Forest Restoration Pact in Brazil. J Sustain For 32(7):728–744

Brown IF, Martinelli LA, Thomas WW, Moreira MZ, Cid Ferreira CA, Victoria RA (1995) Uncertainty in the biomass of Amazonian forests: an example from Rondônia, Brazil. For Ecol Manag 75(1):175–189. doi:10.1016/0378-1127(94)03512-U

Cain ML, Milligan BG, Strand AE (2000) Long- distance seed dispersal in plant populations. Am J Bot 87(9):1217–1227

Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. Science (New York, NY) 323(5915):785. doi:10.1126/science.1166955

Celentano D, Zahawi RA, Finegan B, Casanoves F, Ostertag R, Cole RJ, Holl KD (2011) Tropical forest restoration in Costa Rica: the effect of several strategies on litter production, accumulation and decomposition. Rev Biol Trop 59(3):1323–1336

Celis G, Jose S (2011) Restoring abandoned pasture land with native tree species in Costa Rica: effects of exotic grass competition and light. For Ecol Manag 261(10):1598–1604. doi:10.1016/j.foreco.2010.10.005

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum vol 12. Oxford, UK. doi:10.1111/j.1461-0248.2009.01285.x

Chave J et al (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. Glob Change Biol 20(10):3177–3190. doi:10.1111/gcb.12629

Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. Perspect Plant Ecol, Evol Syst 6(1):51–71. doi:10.1078/1433-8319-00042

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320(5882):1458–1460

Chazdon RL, Letcher SG, van Breugel M, Martínez-Ramos M, Bongers F, Finegan B (2007) Rates of change in tree communities of secondary neotropical forests following major disturbances. Philos Trans 362(1478):273–289

Collins M et al. (2013) Long-term climate change: projections, commitments and irreversibility

Condit R, Engelbrecht BMJ, Pino D, Perez R, Turner BL (2013) Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. Proc Natl Acad Sci U S A 110(13):5064–5068. doi:10.1073/pnas.1218042110

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111(982):1119–1144

Cook WM, Yao J, Foster BL, Holt RD, Patrick LB (2005) Secondary succession in an experimentally fragmented landscape: community patterns across space and time. Ecology 86(5):1267–1279

Cooper M, Dalla Rosa J, Medeiros JC, de Oliveira TC, Toma RS, Juhasz CEP (2012) Hydro-physical characterization of soils under tropical semi-deciduous forest. Sci Agric 69(2):152–159

Davidson EA (2004) Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecol Appl 14(4):S150–S163

Davidson EA et al (2007) Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. Nature 447(7147):995. doi:10.1038/nature05900

de Meira Junior MS, Pereira IM, Machado ELM, Mota SdLL, Otoni TJO (2015) Potential species for recovery of areas of semideciduous forest with iron exploration in the Serra Espinhaço (Especies potenciais para recuperação de áreas de floresta estacional semidecidual com exploração de minério de ferro na Serra do Espinhaço). Biosci J 31(1):283–295

de Souza PB, Martins SV, Costalonga SR, de Oliveira Costa G (2007) Floristics and structure of tree-shrub vegetation in the understory of *Eucalyptus grandis W. Hill ex Maiden* stands in Viçosa, MG, Brazil (Florística e estrutura da vegetação arbustivo-arbórea so sub-bosque de um povoamento de Eucalyptus grandis W. Hill ex Maiden em Viçosa, MG, Brasil). Revista Árvore 31(3):533–543

DeFries RS, Houghton RA, Hansen MC, Field CB, Skole D, Townshend J (2002) Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. Proc Natl Acad Sci USA 99(22):14256–14261. doi:10.1073/pnas.182560099

Deng L, Wang KB, Chen ML, Shangguan ZP, Sweeney S (2013) Soil organic carbon storage capacity positively related to forest succession on the Loess Plateau China. Catena. doi:10.1016/j.catena.2013.06.016

dos Santos APM, Fracasso CM, Luciene dos Santos M, Romero R, Sazima M, Oliveira PE (2012) Reproductive biology and species geographical distribution in the Melastomataceae: a survey based on New World taxa. Ann Bot 110(3):667–679. doi:10.1093/aob/mcs125

Ellsworth DS, Reich PB (1996) Photosynthesis and leaf nitrogen in five amazonian tree species during early secondary succession. Ecology 77(2):581–594. doi:10.2307/2265632

Ferraz S et al (2014) How good are tropical forest patches for ecosystem services provisioning? Landsc Ecol 29(2):187–200. doi:10.1007/s10980-014-9988-z

Finegan B (1996) Pattern and process in neotropical secondary rain forests: the first 100 years of succession. Trends Ecol Evol 11(3):119–124. doi:10.1016/0169-5347(96)81090-1

Flores O, Coomes DA (2011) Estimating the wood density of species for carbon stock assessments. Methods Ecol Evol 2(2):214–220. doi:10.1111/j.2041-210X.2010.00068.x

Fonseca W, Alice F, Rey-Benayas J (2012) Carbon accumulation in aboveground and belowground biomass and soil of different age native forest plantations in the humid tropical lowlands of Costa Rica. Int J Biol Biotechnol Manag Afforestation Refor 43(2):197–211. doi:10.1007/s11056-011-9273-9

Fortini L, Bruna E, Zarin D, Vasconcelos S, Miranda I (2010) Altered resource availability and the population dynamics of tree species in Amazonian secondary forests. Oecologia 162(4):923–934. doi:10.1007/s00442-009-1524-5

Fridley J, Wright J (2012) Drivers of secondary succession rates across temperate latitudes of the Eastern USA: climate, soils, and species pools. Oecologia 168(4):1069–1077. doi:10.1007/s00442-011-2152-4

Fu BJ, Liu SL, Ma KM, Zhu YG (2004) Relationships between soil characteristics, topography and plant diversity in a heterogeneous deciduous broad- leaved forest near Beijing, China. An Int J Plant-Soil Relat 261(1):47–54. doi:10.1023/B:PLSO.0000035567.97093.48

Garcia LC, Hobbs RJ, dos Santos FAM, Rodrigues RR (2014) Flower and fruit availability along a forest restoration gradient. Biotropica 46(1):114–123. doi:10.1111/btp.12080

Gibson L et al (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478(7369):378. doi:10.1038/nature10425

Godinho TD, Caldeira MVW, Rocha JHT, Caliman JP, Trazzi PA (2014) Quantification of biomass and nutrients in the accumulated litter in a section of submontane seasonal semideciduous forest. ES. CERNE 20(1):11–20

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manag 148(1):185–206. doi:10.1016/S0378-1127(00)00535-1

Hasselquist NJ, Allen MF, Santiago LS (2010) Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. Oecologia 164(4):881–890. doi:10.1007/s00442-010-1725-y

Hill JD, Canham CD, Wood DM (1995) Patterns and causes of resistance to tree invasion in rights-of-way. Ecol Appl 5(2):459–470. doi:10.2307/1942036

Holl KD (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31(2):229–242

Holl KD, Zahawi RA (2014) Factors explaining variability in woody above-ground biomass accumulation in restored tropical forest. For Ecol Manag. doi:10.1016/j.foreco.2014.01.024

Hooker TD, Compton JE (2003) Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecol Appl 13(2):299–313

Hughes RF, Kauffman JB, Jaramillo VJ (1999) Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. Ecology 80(6):1892–1907

IPCC (2006) IPCC guidelines for national greenhouse gas inventories. Chapter 4: forest lands. http://www.ipcc-nggip.iges.or.jp/public/2006gl/pdf/4_Volume4/V4_04_Ch4_Forest_Land.pdf. Accessed 15 Feb 2015

Johnson CM, Zarin DJ, Johnson AH (2000) Post- disturbance aboveground biomass accumulation in global secondary forests. Ecology 81(5):1395–1401

Kappelle M, Kennis P, Vries R (1995) Changes in diversity along a successional gradient in a Costa Rican upper montane Quercus forest. Biodivers Conserv 4(1):10–34. doi:10.1007/BF00115312

Kettle CJ (2012) Seeding ecological restoration of tropical forests: Priority setting under REDD +. Biol Conserv. doi:10.1016/j.biocon.2012.03.016

Klanderud K, Mbolatiana H, Vololomboahangy M, Radimbison M, Roger E, Totland Ø, Rajeriarison C (2010) Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar. Biodivers Conserv 19(1):187–204. doi:10.1007/s10531-009-9714-3

Knoepp JD, Coleman DC, Crossley DA, Clark JS (2000) Biological indices of soil quality: an ecosystem case study of their use. For Ecol Manag 138(1):357–368. doi:10.1016/S0378-1127(00)00424-2

Kuers K (2005) Ranking species contribution to forest community composition: calculation of importance values. http://static.sewanee.edu/Forestry_Geology/watershed_web/Emanuel/ImportanceValues/ImpVal_SET.html Accessed 15 Feb 2015

Lawrence D (2003) The response of tropical tree seedlings to nutrient supply: meta-analysis for understanding a changing tropical landscape. J Trop Ecol. doi:10.1017/S0266467403003274

Li YL et al (2013) Changes in forest soil properties in different successional stages in lower tropical China. Plos One. doi:10.1371/journal.pone.0081359

Loyola R, Lemes P, Nabout J, Trindade-Filho J, Sagnori M, Dobrovolski R, Diniz-Filho J (2013) A straightforward conceptual approach for evaluating spatial conservation priorities under climate change. Biodivers Conserv 22(2):483–495. doi:10.1007/s10531-012-0424-x

Lu D, Moran E, Mausel P (2002) Linking amazonian secondary succession forest growth to soil properties. Land Degrad Dev 13(4):331–343. doi:10.1002/ldr.516

Lu X, Mo J, Gilliam FS, Yu G, Zhang W, Fang Y, Huang J (2011) Effects of experimental nitrogen additions on plant diversity in tropical forests of contrasting disturbance regimes in southern China. Environ Pollut 159(10):2228–2235. doi:10.1016/j.envpol.2010.10.037

Macedo MO et al (2008) Changes in soil C and N stocks and nutrient dynamics 13 years after recovery of degraded land using leguminous nitrogen- fixing trees. For Ecol Manag 255(5):1516–1524. doi:10.1016/j.foreco.2007.11.007

Marín-Spiotta E, Ostertag R, Silver WL (2007) Long-term patterns in tropical reforestation: plant community composition and aboveground biomass accumulation. Ecol Appl 17(3):828

Martinez-Garza C, Howe H (2003) Restoring tropical diversity: beating the time tax on species loss. J Appl Ecol 40(3):423–429

Martini A, Fiaschi P, Amorim A, Paixão J (2007) A hot- point within a hot- spot: a high diversity site in Brazil's Atlantic Forest. Biodivers Conserv 16(11):3111–3128. doi:10.1007/s10531-007-9166-6

Melo FPL, Arroyo-Rodríguez V, Fahrig L, Martínez-Ramos M, Tabarelli M (2013) On the hope for biodiversity-friendly tropical landscapes. Trends Ecol Evol 28(8):462–468. doi:10.1016/j.tree.2013.01.001

Melvin KKK, Japar SB, Osumanu HA, Nik MAM, Roland KJH, Silvester J (2011) Comparison of carbon and selected macronutrients in forest-floor litter of rehabilitated and secondary forests. Am J Appl Sci 8(10):967

Metzger JP (2009) Conservation issues in the Brazilian Atlantic. Forest. doi:10.1016/j.biocon.2008.10.012

Montagnini F, Fanzeres A, DaVinha SG (1995) The potentials of 20 indigenous tree species for soil rehabilitation in the Atlantic forest region of Bahia, Brazil. J Appl Ecol 32(4):841–856

Moran EF, Brondizio ES, Tucker JM, da Silva-Forsberg MC, McCracken S, Falesi I (2000) Effects of soil fertility and land- use on forest succession in Amazônia. For Ecol Manag 139(1):93–108. doi:10.1016/S0378-1127(99)00337-0

Morellato LPC, Haddad CFB (2000) Introduction: the Brazilian Atlantic Forest. Biotropica 32(4B):786–792

Muiz-Castro MA, Williams-Linera G, Benayas JMR (2006) Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico. J Trop Ecol 22(4):431–440. doi:10.1017/S0266467406003221

Nascimento HEM, Andrade ACS, Camargo JLC, Laurance WE, Laurance SG, Ribeiro JEL (2006) Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. Conserv Biol 20(3):853

Nelson B, Mesquita R, Pereira J, de Souza S, Batista G, Couto L (1999) Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. For Ecol Manag 117(1–3):149–167. doi:10.1016/S0378-1127(98)00475-7

Osman N, Barakbah SS (2010) The effect of plant succession on slope stability. Ecol Eng 37(2):139–147. doi:10.1016/j.ecoleng.2010.08.002

Pan Y et al (2011) A large and persistent carbon sink in the world's forests. Science 333(6045):988–993

Putz FE, Canham CD (1992) Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. For Ecol Manag 49(3):267–275. doi:10.1016/0378-1127(92)90140-5

Putz FE, Redford KH (2010) The importance of defining 'forest': tropical forest degradation, deforestation, long-term phase shifts, and further transitions. Biotropica 42(1):10–20. doi:10.1111/j.1744-7429.2009.00567.x

Rees M, Condit R, Crawley M, Pacala S, Tilman D (2001) Long- term studies of vegetation dynamics. Science 293(5530):650–655

Reiners WA, Bouwman AF, Parsons WFJ, Keller M (1994) Tropical rain forest conversion to pasture: changes in vegetation and soil properties. Ecol Appl 4(2):363–377. doi:10.2307/1941940

Ribeiro M, Metzger J, Martensen A, Ponzoni F, Hirota M (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implic Conserv Biol Conserv 142(6):1141–1153. doi:10.1016/j.biocon.2009.02.021

Rodrigues RR, Martins SV, de Barros LC (2004) Tropical Rain Forest regeneration in an area degraded by mining in Mato Grosso State, Brazil. For Ecol Manag 190(2):323–333. doi:10.1016/j.foreco.2003.10.023

Rodrigues R, Lima R, Gandolfi S, Nave A (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. Biol Conserv 142(6):1242–1251. doi:10.1016/j.biocon.2008.12.008

Rondon Neto RM, Botelho SA, Fontes MAL, Davide AC, Faria JMR (2000) Structure and floristic composition of the tree and shrub community of a forest gap of anthropogenic origin, in a montane semideciduous seasonal forest, Lavras-MG, Brazil (Estrutura e composição florística da comunidade arbustivo-arbórea de uma clareira de origem antrópica, em uma floresta estacional semidecídua montana, Lavras-MG, Brasil). CERNE 6(2):79–94

Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long- term chronosequence of forest succession in the Upper Rio Negro of Colombia and Venezuela. J Ecol 76(4):938–958

Sang PM, Lamb D, Bonner M, Schmidt S (2013) Carbon sequestration and soil fertility of tropical tree plantations and secondary forest established on degraded land. Plant Soil 362(1–2):187–200. doi:10.1007/s11104-012-1281-9

Siddique I et al (2010) Nitrogen and phosphorus additions negatively affect tree species diversity in tropical forest regrowth trajectories. Ecology 91(7):2121–2131

Silveira FAO, Fernandes GW, Lemos-Filho JP (2013) Seed and seedling ecophysiology of neotropical Melastomataceae: implications for conservation and restoration of savannas and rainforests. Ann Mo Bot Gard 99(1):82–99. doi:10.3417/2011054

Styger E, Rakotondramasy HM, Pfeffer MJ, Fernandes ECM, Bates DM (2007) Influence of slash-and- burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. Agric Ecosyst Environ 119(3):257–269. doi:10.1016/j.agee.2006.07.012

Tabarelli M, Aguiar AV, Ribeiro MC, Metzger JP, Peres CA (2010) Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. Biol Conserv 143(10):2328–2340. doi:10.1016/j.biocon.2010.02.005

Uriarte M, Anciaes M, da Silva MTB, Rubim P, Johnson E, Bruna EM (2011) Disentangling the drivers of reduced long- distance seed dispersal by birds in an experimentally fragmented landscape. Ecology 92(4):924–937

Valdez-Hernández M, Sánchez O, Islebe GA, Snook LK, Negreros-Castillo P (2014) Recovery and early succession after experimental disturbance in a seasonally dry tropical forest in Mexico. For Ecol Manag. doi:10.1016/j.foreco.2014.09.018

van Breugel M, Martinez-Ramos M, Bongers F (2006) Community dynamics during early secondary succession in Mexican tropical rain forests. J Trop Ecol. doi:10.1017/S0266467406003452

Vieira I, Uhl C, Nepstad D (1994) The role of the shrub Cordia multispicata Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazônia. Vegetatio 115(2):91–99. doi:10.1007/BF00044863

Wall A, Heiskanen J (2003) Water- retention characteristics and related physical properties of soil on afforested agricultural land in Finland. For Ecol Manag 186(1):21–32. doi:10.1016/S0378-1127(03)00239-1

Wright SJ (2010) The future of tropical forests. Ann NY Acad Sci 11951(1):1–27. doi:10.1111/j.1749-6632.2010.05455.x

Xiong YM, Zeng H, Xia HP, Guo DL (2014) Interactions between leaf litter and soil organic matter on carbon and nitrogen mineralization in six forest litter- soil systems. Plant Soil 379(1–2):217–229. doi:10.1007/s11104-014-2033-9

Yassir I, van der Kamp J, Buurman P (2010) Secondary succession after fire in Imperata grasslands of East Kalimantan, Indonesia. Agric Ecosyst Environ 137(1–2):172–182. doi:10.1016/j.agee.2010.02.001

Zalamea PC et al (2012) The genus cecropia: a biological clock to estimate the age of recently disturbed areas in the neotropics. PLoS One. doi:10.1371/journal.pone.0042643

Zanne AE et al (2009) Global wood density database. Dryad data package. http://hdl.handle.net/10255/dryad.235. Accessed 15 Feb 2015

Zarin DJ (2012) Carbon from tropical deforestation. Science 336(6088):1518–1519. doi:10.1126/science.1223251

Zimmerman JK, Pascarella JB, Aide TM (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restor Ecol 8(4):350–360