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Linking vegetation and soil functions during secondary forest succession in the Atlantic forest

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ABSTRACT

Secondary forest succession can be an effective and low-cost strategy to increase forest cover and the associated biodiversity and soil functions. However, little is known about how soil functions develop during succession, and how vegetation attributes influence soil functions, especially in highly biodiverse and fragmented landscapes in the tropics. Here we assessed a wide range of indicators of taxonomic (e.g. number of tree species), structural (e.g. basal area, canopy openness) and functional diversity (e.g. community weighted means of functional traits) of tree species, as well as indicators for soil functions related to soil organic matter accumulation, nutrient cycling and soil cover in secondary forest patches ranging from 5 to 80 years. Two recently abandoned agricultural fields were included as the starting point of forest succession and two primary forest patches served as references for the end point of forest succession. Four ecological hypotheses, centred around the role of functional diversity, structural diversity and biomass, were tested to explore mechanisms in which forest vegetation may influence soil functions. Most measures of structural, taxonomic and functional diversity converged to values found in primary forests after 25–50 years of succession, whereas functional composition changed from acquisitive to conservative species. Soil carbon and nutrient cycling showed a quick recovery to the levels of primary forests after 15 years of succession. Although soil cover also increased during succession, levels of primary forests were not reached within 80 years. Variation in tree height and trait dominance were identified as aboveground drivers of carbon and nutrient cycling, while aboveground biomass was the main driver of litter accumulation, and the associated soil cover and water retention. Our results indicate that secondary forest succession can lead to a relative fast recovery of nutrient and carbon cycling functions, but not of soil cover. Our findings highlight the essential role of secondary forests in providing multiple ecosystem services. These results can be used to inform management and reforestation programmes targeted at strengthening soil functions, such as soil cover, nutrient and carbon cycling.

1. Introduction

Processes of ongoing deforestation and forest degradation pose a threat for biodiversity and the provision of ecosystem services (FAO, 2015), but at the same time, there is room for the restoration of 0.9 billion hectares of canopy cover worldwide (Bastin et al., 2019). Forest restoration can potentially revert environmental degradation (Reij and Garrity, 2016) and improve human well-being (de Souza et al., 2016; Sansevero et al., 2016; Shimamoto et al., 2018). In areas where levels of disturbance are not extreme (e.g. after mining) and primary or old secondary forests as a source of seeds are present in the landscape (Sloan et al., 2016), the natural regeneration of the vegetation, also known as secondary succession, can be an effective and low-cost strategy to increase forest cover and the associated biodiversity and soil functions (Chazdon and Guariguata, 2016; Quijas et al., 2019; Shimamoto et al., 2018).

Global findings on secondary succession in the tropics indicate the high capacity of tropical forests to recover aboveground biomass after disturbances, and consequently, contribute to carbon storage and climate change mitigation (Chazdon et al., 2016; Poorter et al., 2016). Secondary forests can also be important biodiversity reservoirs, capable to restore species richness (but not floristic composition) to the level of

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primary forests within decades of succession (Rozendaal et al., 2019). Although global patterns of changes in vegetation composition and structure across secondary succession become more and more evident, the effects of succession on belowground properties and processes are less clear. On the one hand, organic carbon content and biological activity tend to increase with the aging of forest (Deng et al., 2013; Ferreira et al., 2018; Hall et al., 2017; Robinson et al., 2015; Yan et al., 2006). On the other hand, there are also reports that soil properties and processes are hardly influenced by successional stage, as in the case of mycorrhizal fungi species composition in the Brazilian Amazon (Reyes et al., 2019), and organic carbon in the mid-Atlantic US (Yesilonis et al., 2016) and tropical China (Lu et al., 2015). Therefore, beyond focusing on how one or few variables respond to succession, new studies are needed to explore the ecological mechanisms that can explain changes on multiple soil functions, considering a wide variety of above and belowground indicators. For instance, changes in vegetation structure and/or composition during succession can affect the activity of enzymes and microorganisms in the soil that play a role in organic matter accumulation (Acosta-Martinez et al., 2018), which in turn, can limit soil erosion and water run-off (Liu et al., 2018). In addition, it is important to consider appropriate time scales at which forest-mediated functions recover, since belowground responses can rapidly occur in the first months or years of succession (Knelman et al., 2017), but can also take decades or even centuries to fully recover.

The effect of vegetation on the functioning of soils and ecosystems are complex, and therefore, a range of ecological indicators may be useful to capture the environmental responses to land use change and management (Fischer et al., 2019; Liu et al., 2018). Beyond species richness and floristic composition (taxonomical diversity), other vegetation attributes can also be relevant (Díaz et al., 2006). For example, structural diversity, typically assessed as the variance of total height and/or diameter, and functional composition, defined as the range and abundance of species traits, are considered main drivers of changes on ecosystem functions (Ali et al., 2016; Grigulis et al., 2007; Lavorel et al., 2011). Based on the current knowledge on vegetation and ecosystem functioning, four different ecological hypotheses are used to understand ecological mechanisms that can explain the influence of vegetation on soil functions during secondary forest succession. The niche complementarity hypothesis postulates that the greater the variability in species traits, the broader the spectrum of soil microorganisms that will be able to develop and cycle carbon and nutrients (Lange et al., 2015). The biomass ratio hypothesis states that functional traits of the most dominant species in the system, indicated by the community weighed means (CWM), are the most important drivers of soil ecosystem functions (Finegan et al., 2015; Grime, 1998). The structural diversity hypothesis proposes that the variance in height may have consequences for soil functions as it is a measure of the ability of the system to regenerate, efficiently capture light and retain water (Ali et al., 2016). Finally, the green soup hypothesis states that age of the forest, and consequently, the forest biomass, is the most direct driver of soil functions (Lohbeck et al., 2015). Despite the large theoretical background, few studies have shown empirical evidence on the mechanistic effect of different vegetation attributes on ecosystem functions. Besides, the focus of existing studies is often on soil chemical and physical properties, litter and other aboveground functions (Ali et al., 2016; Finegan et al., 2015; Lohbeck et al., 2015; van der Sande et al., 2017), whereas the effects on soil microbiology remain poorly understood, especially in highly biodiverse and fragmented landscapes in the tropics (Mendes et al., 2019; Shimamoto et al., 2018).

In our paper, a combination of above and belowground properties and processes were used as indicators of the soil functions: (i) soil cover, (ii) carbon regulation, and (iii) phosphorus cycling. The study was conducted in Zona da Mata, a mountainous region located in the south eastern area of the state of Minas Gerais, Brazil. The region is a highly fragmented and human modified landscape that is part of the Atlantic forest biome, recognised as the 5th hotspot of biodiversity in the world (Myers et al., 2000). The recovery of secondary forests in Zona da Mata can be an efficient strategy to increase the provision of ecosystem services of local and global importance, such as such as water regulation, soil erosion control, carbon storage and production of forest products. The general aim of this paper is to assess the effect of secondary succession on vegetation and soil functioning. Two specific research questions were addressed:

(i) How do vegetation and soil functions change in response to forest age?
(ii) What ecological mechanisms can explain the influence of vegetation on soil functions during secondary forest succession?

2. Material and methods

2.1. Study site

The Atlantic forest biome is considered a hotspot of biodiversity (Myers et al., 2000). Currently only around 6% of the original total cover of the Atlantic forest still remains (SOS Mata Atlântica and INPE, 2013), mainly due to illegal logging and expansion of the agricultural frontiers in the last 200 years. The Zona da Mata region is located within the Atlantic forest and its vegetation is classified as seasonal semi-deciduous (SOS Mata Atlântica and INPE, 2013) because the vegetation is conditioned by two well-defined seasons along the year: a dry cold versus rainy warm period and because up to 50% of the tree species can lose (part of) their leaves during the dry period (IBGE, 2012). The average temperature in the region is 19 °C and average precipitation is 1300 mm (De Mello et al., 2007; Golfari, 1975). The landscape is mountainous, leading to heterogeneous bio-physical conditions, predominance of family farmers and limiting mechanization, as heavy machinery is hard to operate in steep areas (Andrade et al., 2012; Valverde, 1958). The main soil type dominating the upper slopes is classified as Oxisol, which is highly weathered, deep, well-drained and acidic (Sarcinelli et al., 2009). The landscape in Zona da Mata can be understood as a dynamic mosaic of land uses (Vandermeer and Perfecto, 2007) predominated by pastures, coffee fields and secondary forest patches. The study was conducted in a community located in the municipality of Divino. The municipality has a strong tradition with coffee and milk production, as in the rest of the region. More than 75% of the farms are considered family farmers (IBGE, 2006) and forest cover is around 30% (Carvalho, in review). The altitude of the study area ranges from 900 to 1305 m.a.s.l. We selected this particular study area because there is an active farmer community that is interested in maintaining and increasing forest cover to improve the provision of ecosystem services, such as soil erosion control and water regulation.

2.2. Selection of forest patches and allocation of plots

A chronosequence approach was used for studying the temporal dynamics of plant communities and soil functions across secondary forest succession after agricultural abandonment. A chronosequence consists of space-for-time substitutions, enabling the assessment of changes across long time-scales (Walker et al., 2010). Our time series included the following areas: two recently abandoned pasture and coffee fields (0.5 and 1 year), eight secondary forest patches with age ranging from 5 to 80 years, and two forest patches of primary forest (> 100 years). The latter plots were used to provide a baseline for “desirable” or optimum indicator values (Rozendaal et al., 2019). Our sample size was restricted because of the limited availability of forest patches in the study area that matched our selection criteria (see below).

The criteria for plot selection were forest age and position in the landscape. The specific age of each patch since abandonment (age) was assessed by interviewing farmers who were knowledgeable about the history of the sites. We interviewed farmers individually, which allowed us to triangulate and validate the information provided by farmers. We chose this method because tropical trees often do not show clear distinction between year rings and because satellite images often fail to provide accurate information (i.e. first years since abandonment cannot be detected). In each of the twelve areas, a 45 × 20 m plot was established. The longest central axis of the plot (45 m) was allocated uphill, in the convex part of the soil landscape to standardize soil type and natural conditions among plots. The starting point of the central axis was randomly defined using the Random Number App. This plot size was small enough to be established in the sometimes small forest patches. Each plot was then divided into three subplots of 15 × 20 m to assess the relationship between vegetation composition and structure and soil functions. In contrast to vegetation composition and structure, variation in soil properties and processes unfolds typically at a much smaller scale than at the size of our plots (900 m^2), and therefore, calculating an average of three soil composite samples for the whole plot would not be appropriate.

2.3. Forest structure and diversity metrics

We assessed three main attributes of tree diversity: taxonomical, structural, and functional diversity in all subplots (Table 1). All individuals with diameter ≥5 cm at 1.3 m height (DBH) were tagged, measured and taxonomically identified. Taxonomical diversity was assessed in terms of the number of tree species (total_species) and Shannon-Weiner index (shannon). Species composition similarity among subplots was assessed using a Jaccard distance based cluster dendrogram (Appendix B). Forest structure was assessed in terms of aboveground biomass, total basal area and variance in basal area and height. DBH was measured with a metric tape and height was measured using a Vertex IV and Transponder T3. Aboveground biomass (above_biomass) of trees was estimated using an allometric equation developed for secondary forests classified as seasonal semi-deciduous Atlantic forest, using height and DBH as explanatory variables ($AGB = 0{,}024530*DBH^{2{,}443356}*Height^{0{,}423602}$; $R^2 = 95.0$) (Amaro, 2010). Canopy images were taken from the forest understorey using a fish-eye lens mounted on a camera at a fixed height of 130 cm. Images were analysed using the Gap Light Analyzer software for calculating canopy openness (canopy_open) (Fraser, 1999). Standard deviations of tree height (sd_height) and basal area (sd_basal_area) were used as proxies for structural diversity. For estimating functional diversity, five leaf traits of 70 tree species that covered on average 92.6% (range 84.3–99.4%) of the total basal area per plot were measured. Four to ten adult and healthy individuals of each tree species were selected for functional traits measurements. When possible, all samples were taken from trees in the established plots, otherwise additional samples were taken from nearby trees in similar growing conditions. The sampling and measurement of leaves followed standardized protocols proposed by Pérez-Harguindeguy et al. (2013). The leaf petiole was included in the measurements. In the case of compound leaves, the leaflet was considered as the unit of analysis. A hand-held chlorophyll meter (SPAD – Soil-Plant Analysis Development) was used to obtain leaf chlorophyll content (Chlo). Leaves were flattened and photographed, and leaf area (LA) calculated with the software ImageJ, based on pixel counting. Leaf thickness (LT) was obtained using a digital micrometer. Leaf fresh mass was measured using a precise scale of five decimal places. Then, leaves were dried in the oven at 65 °C until constant weight to obtain leaf dry mass. Leaf dry matter content (LDMC) was calculated as the ratio between dry mass (mg) and fresh mass (g). Specific Leaf Area (SLA) was calculated as the ratio between leaf area (m^2) and leaf dry mass (kg). The use of species average trait values was chosen for the purpose of the present study because all plots were allocated under very similar climatic and pedogenetic conditions, and therefore low intraspecific trait variation was expected. Functional trait data at species level was scaled to the community level using indices of functional diversity and functional composition. As an indicator of functional diversity, the multi-

Table 1

Overview of all variables used as metrics of vegetation composition and structure and soil functions. Data were collected in plots differing in age since agricultural abandonment (from 0.5 to 80 years) and primary forests, in Zona da Mata, Brazil. All trees > 5 cm in DBH were sampled in the plots.

	Variable	Code	Unit	**Indicator of**
Vegetation composition and structure				
Structural diversity	Aboveground biomass	aboveground_biomass	ton/ha	Aboveground tree biomass
	Total basal area	basal_area	m^2/ha	Tree basal area
	Basal area standard deviation	sd_basal_area	m^2/ha	Variance in tree basal area
	Height standard deviation	sd_height	m	Variance in tree height
	Canopy openness	canopy_open	%	Light incidence in the forest understorey
Taxonomical diversity	Number of tree species	total_species	#	Tree species richness
	Shannon-Weiner index	shannon	–	Tree species richness and evenness
Functional diversity	Leaf Area – CWM	CWM.LA	cm^2	Average leaf size in the community
	Chlorophyll content – CWM	CWM.Clo	SPAD units	Average leaf chlorophyll content in the community
	Leaf dry matter content – CWM	CWM.LDMC	mg/g	Average leaf dry matter content in the community
	Specific Leaf Area – CWM	CWM.SLA	m^2/kg	Average leaf specific leaf area in the community
	Leaf thickness – CWM	CWM.LT	mm	Average leaf thickness in the community
	Functional attribute diversity	MFAD	–	Functional trait diversity
Soil functions				
Carbon cycling	Metabolic quotient	qCO2	μg CO_2./μg C-mic/ h	Ecosystem development and disturbance
	Microbial biomass carbon	MBC	μg/g dry soil	Carbon contained in the living component of the soil
	Soil basal respiration	basal_respiration	μmol CO_2/g/h	Microbiological activity due to mineralisation of organic matter
	Beta glucosidase activity	beta_glucosidase	μg p-nitrophenol/g dry soil/ h	Enzyme activity which results in release of glucose
	Soil organic matter	SOM	dag/kg	Soil organic matter accumulation
	Soil water	water_soil	%	Water retained in the soil
Phosphorus cycling	Alkaline phosphomonoesterase activity	alk_phosphatase	μg p-nitrophenol/g dry soil/ h	Enzyme activity which results in release of phosphate
	Soil phosphorus content	P	mg/ dm^3	Available phosphorus in the soil; soil fertility
Soil cover	Soil leaf litter carbon per area	litter_leaf_carbon	g/m^2	Soil litter cover
	Water in soil leaf litter per area	litter_water	ml/m^2	Water retained in soil litter

trait index Modified Functional Attribute Diversity (MFAD) was calculated based on the dissimilarity between the functional trait values of all selected species in each plot. For functional composition the aggregate value of leaf traits in each plot was measured using Community Weighed Mean (CWM) for each leaf trait. All diversity indices were calculate using the FDiversity software and FD package (Di Rienzo et al., 2008) in R 3.3.3.

2.4. Soil-related functions and properties

Leaf litter samples were taken in a 1-m^2 quadrant in the centre of each 15 × 20 m subplot. The woody material (diameter $>$ 2 cm) was separated from the leaves. The litter fresh and dry weights were measured, before and after drying at 65 °C until constant mass. The water content in the litter per area (litter_water) was calculated as the difference between the fresh and dry mass. As carbon content within plant dried material is rather constant, the amount of litter carbon per area was calculated by using the formula litter_leaf_carbon = dry mass (g) × 0.475/1 m^2 (the area of the quadrant) (Magnussen and Reed, 2004).

In each subplot, five soil sub-samples were collected from the 0–10 cm depth layer. The five soil sub-samples were placed in a bucket and thoroughly mixed to create one single composite soil sample per subplot. The sample was divided in two parts, one half was immediately stored for the microbiological analysis in a cooler box with ice packs and stored at 4 °C until processing in the laboratory. The other half was stored at room temperature for the chemical analysis. The microbial analyses were performed within one week of storage at the laboratory of Biotechnology and Biodiversity for the Environment at the Universidade Federal de Viçosa (UFV), Brazil. The chemical analyses were performed at the laboratory of Soil Fertility, also at UFV. All litter and soil samples were collected on the same day, in the beginning of the rainy season (September 2018), six days after a rain fall ($>$ 10 mm) in the study site.

Microbial biomass carbon (MBC) in the soil was determined using the fumigation and extraction method (Vance et al., 1987). Soil basal respiration (basal_respiration) was estimated from the respiration values obtained after incubation of the samples in flasks coupled to a respirometer (Sable Systems – Mod. TR-RM8 Respirometer Multiplexer), equipped with an infrared CO_2 detector (Alef and Nannipieri, 1995; Heinemeyer et al., 1989). The enzyme activities were determined by colorimetry. Paranitrophenylphosphate was used as the substrate in the enzymatic reaction to determine Alkaline phosphomonoesterase activity (alk_phosphatase) (Margenot et al., 2018; Tabatabai, 1994), while p-nitrophenyl-beta-D-glucoside was used as the substrate to measure the activity of beta-glucosidase (beta_glucosidase) from the concentration of p-nitrophenol resulting from the enzyme activity after incubation of the soil samples in modified universal buffer (Eivazi and Tabatabai, 1988). The microbial metabolic quotient (qCO_2) was calculated as soil basal respiration divided by microbial biomass carbon. The gravimetric method was used to calculate soil water content (water_soil), expressed as percentage of soil water to dry soil weight (Dobriyal et al., 2012). Soil phosphorus (P) was determined using a spectophotometer and Melich-1 as extractor (Mylavarapu et al., 2002). The determination of soil organic matter (SOM) was based on the Walkley-Black chromic acid wet oxidation method (Walkley and Black, 1933).

2.5. Data analysis

To assess how vegetation, soil properties and soil processes change during secondary forest succession (Fig. 1) mixed effect linear models were used. Each vegetation and soil variable was included in the model as the response variable, age was included as the explanatory variable and plot was included as random factor to take into account for the lack of independence between subplots. A separate model was constructed for each response variable (Table 1). The statistical significance was assessed according to the p-values for F-tests computed using the Satterthwaite approximation. The marginal and conditional coefficients of determination (R^2m and R^2c) were used to estimate the explained variance of each model (Nakagawa and Schielzeth, 2013). We tested both linear and log-linear responses of each variable to forest age. The model with best fit, based on p-values and coefficients of determination, was selected. Primary forest plots were not included in the regression analysis as it was not possible to determine their exact age. Instead, these data were used as reference values for the end point of secondary forest succession. The analysis was performed using the packages lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017) and MuMIn (Barton, 2019) of R 3.5.3.

For the plots without trees (recently abandoned pasture and coffee fields), it was not possible to obtain values for the leaf traits CWM. For allowing the inclusion of these plots without trees in the sub-sequent analysis, two alternative mixed linear models were tested for each trait. In the first model, the plots with missing data on CWM were excluded of the analysis. In the second model, projected values for the plots with missing data based on the estimates from the first model were included. As there was no meaningful change in the estimates, we here report the second model because this allows incorporation of early succession data in the structural equation models (see below). Hence, CWM values for the first year of succession are based on extrapolation and should be interpreted with care.

To assess which diversity attributes are driving key soil functions we developed structural equation models because these models can be used to make inferences about causal relationships between multiple variables. Four alternative ecological hypotheses were used to explain changes in soil functioning in response to vegetation composition and structure: niche complementarity, biomass ratio, structural diversity and greensoup (Fig. 1). As there are more than one variable that can be used as indicator for each ecological hypothesis (e.g. CWM of specific leaf area and CWM of leaf dry matter content for the biomass ratio hypothesis), one representative variable was selected based on ecological knowledge and the correlation between variables (Appendix A). Functional diversity was selected for the niche complementarity hypothesis because of the high correlation with indices of species diversity (R $>$ 0.9) (Appendix A, Fig. 4) and because functional diversity is suggested to play a larger role on ecosystem functions than taxonomical diversity (Díaz et al., 2006). For the biomass ratio hypothesis CWM of specific leaf area (CWM.SLA) was selected because of the high correlation with the other traits (R $>$ 0.7) and because SLA is obtained by combining two of the other traits (leaf area and leaf dry matter content) (Fig. 4, Appendix A). Variation in height (sd_height) was selected for the structural diversity hypothesis because the other candidate variable, variance in basal area, was highly correlated with aboveground biomass (R = 0.9) and also very sensitive to the presence of trees with very large DBH in the mature forest plots. Finally, for the greensoup hypothesis, aboveground biomass was included because it is the most direct and logical indicator of plant biomass and it was highly correlated with total basal area (R = 0.9, Fig. 4, Appendix A). The soil functions: (i) carbon cycling, (ii) phosphorus cycling and (iii) soil cover were assessed using different measurements of soil properties and processes (Schulte et al., 2015). Metabolic quotient (qCO2), basal respiration (basal_respiration), microbial biomass carbon (MBC) and beta-glucosidase activity (beta_glucosidase) were considered as intermediate soil processes related to soil organic matter accumulation; phosphomonoesterase activity (alk_phosphatase) as an intermediate processes related to soil available phosphorus; and litter carbon per area (litter_carbon) as an intermediate soil processes related to water retention in the litter. Structural equation models were developed for each of the six intermediate soil processes. All the six models had the four selected diversity indicators as explanatory variables and one soil process as response variable. According to the intermediate soil process, one specific soil property was selected in each model as the final response variable (SOM, P,

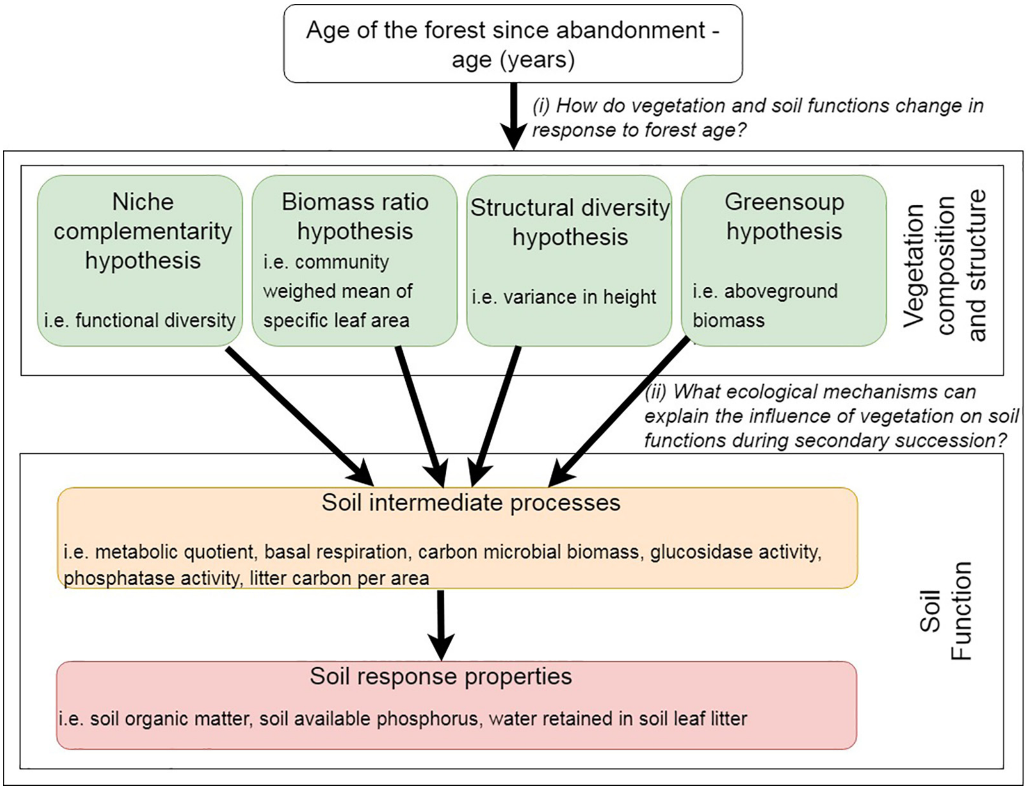

Fig. 1. Schematic representation of the outline of the study. In the first research question, we assess the response of each above and belowground variable to forest age. In the second research question, we evaluate four hypotheses to explain how aboveground vegetation attributes influence soil functions.

litter_water) (Fig. 1). The direct influence of diversity indicators on the final response variables was not tested in the model because we targeted the indirect effect of vegetation on soil properties through soil processes. In addition, we built relatively simple models (only five tested associations per model) to avoid biased estimation of path coefficients due to our relatively small sample size. We also only accepted models with a high fit (CFI $>$ 0.95; SRMR $<$ 0.08; chi-square p-value $>$ 0.8; Appendix D) and we confirmed the significance of associations identified in the structural equation models in separate linear models.

To account for the lack of independence among subplots, adjustments to point and variance estimator were calculated using the package lavaan.survey in R (Oberski, 2014). The strength of causal relationships between variables was assessed using standardized parameter values. Relationships were considered significant when the p-value was $\leq$0.05. The residuals of the correlational units obtained by subtracting the observed and model-implied matrices were further assessed to confirm that the model is not over or under-predicting (res $>$ 0.1) the association between variables. Calculations were made using the packages lavaan (Rosseel, 2012) and lavaan.survey (Oberski, 2014) in R 3.5.3. Correlations between the variables were calculated based on Pearson‘s method (Appendix A).

3. Results

3.1. Changes in tree diversity, tree composition, soil functions and properties during secondary succession

In total, 1639 trees (diameter $\geq$5 cm) were measured, 94% of all individuals were identified at species level, 4% at genus level, 0.5% at family level and 1.5% were not identified. A total of 46 taxonomical families and 159 species were identified.

All vegetation attributes were significantly associated with age (Table 2). Aboveground biomass (above_biomass) and total basal area (basal_area) showed linear responses to age (Fig. 2 A, B). Standard deviation of basal area (sd_basal_area) and height (sd_height) increased, and canopy openness (canopy_open) decreased in the first 30 years of secondary forest succession, and showed less prominent changes in later succession (log-linear response; Fig. 2 C, D, E). Yet, sd_height and canopy_open reached values similar to primary forests after 40 years of succession, whereas this was not the case for sd_basal_area, which values found in primary forests remain higher than values found in secondary forests. The indices of taxonomic (total_species and shannon) and functional diversity (MFAD) showed similar responses to age, increasing through succession, and reached values similar or higher than primary forests (Fig. 2 F, G, H). Regarding functional composition, CWM of leaf area (CWM.LA), leaf chlorophyll (CWM.Clo), leaf dry matter content (CWM.LDMC) and leaf thickness (CWM.LT) increased with age, whilst specific leaf area (CWM.SLA) decreased (Fig. 2 I, J, K L, M). All functional composition variables reached in late successional stages similar values than primary forests.

Changes in species composition also showed a clear pattern across secondary succession as evidenced by the change in species dominance (Appendix B – Dissimilarity cluster dendrogram). In the first years of succession, *Piptadenia gonacantha* is the species with greatest proportion of basal area. Across the years, the relative dominance of *P. gonacantha* drops sharply until the species is no longer present in the systems after 60 years of secondary succession. In contrast, the species *Euterpe edulis* appears after 25 years of succession and becomes a more dominant species in primary forests (Appendix C).

The response of soil functions and properties to age were not always linear (Table 2). In the case of soil basal respiration (basal_respiration), enzymatic activity of beta-glucosidase (beta_glucosidase), alkaline-phosphatase (alkaline-phosphatase) and soil water (water_soil) a log linear response was observed, with a sharp increase in the first 15–20 years of succession (Fig. 3 B, C, D, E, H). Litter carbon per area (litter_carbon) had a marginally significant log linear response to age and litter water (litter_water) had a positive and linear response to age.

Table 2

. Results of mixed effect linear models of vegetation and soil attributes in response to forest age (years). Age of the forest in years is the fixed effect explanatory variable, vegetation and soil attributes are response variables and plot was added as random effect variable. The marginal R^2m and conditional R^2c coefficients of determination indicate the explained variance of the fixed factor (age) and of the fixed and random effect (plot) of each model, respectively. p-values were obtained using Satterthwaite approximation. p-values < 0.05 are marked in bold.

Models	Type of model	fixed effects			R^2m	R^2c	overall model p-value	significance
		x estimate	intercept estimate					
Vegetation composition and structure	above_biomass ~ age + (1|plot)	linear	2.003	9.268	0.72	0.73	< **0.0001**	***
	basal_area ~ age + (1|plot)	linear	0.1465	0.9536	0.80	0.90	< **0.0001**	***
	sd_basal_area ~ log(age) + (1|plot)	log	0.0003	0.0065	0.37	0.53	**0.0106**	*
	sd_height ~ log(age) + (1|plot)	log	1.23	0.4599	0.86	0.86	< **0.0001**	***
	canopy_openness ~ log(age) + (1|plot)	log	−19.42	88.94	0.94	0.99	< **0.0001**	***
	total_species ~ age + (1|plot)	linear	0.4066	0.2164	0.93	0.93	< **0.0001**	***
	shannon ~ age + (1|plot)	linear	0.6121	−0.0554	0.81	0.90	< **0.0001**	***
	CWM.LA ~ age + (1|plot)	linear	0.3046	36.33	0.11	0.11	0.0688	.
	CWM.Clo ~ age + (1|plot)	linear	0.2069	37.28	0.84	0.85	< **0.0001**	***
	CWM.LDMC ~ age + (1|plot)	linear	1.58	213	0.56	0.73	**0.002**	**
	CWM.SLA ~ age + (1|plot)	linear	−0.2803	37.02	0.66	0.75	**0.0003**	***
	CWM.LT ~ age + (1|plot)	linear	0.0017	0.1456	0.47	0.73	**0.0066**	**
	MFAD ~ age + (1|plot)	linear	0.0518	0.0785	0.89	0.89	< **0.0001**	***
Soil properties and processes	qCO2 ~ log(age) + (1|plot)	log	0.0046	0.0329	0.06	0.19	0.2843	NS
	CMB ~ log(age) + (1|plot)	log	7.01	79.07	0.11	0.40	0.1775	NS
	basal_respiration ~ log(age) + (1|plot)	log	0.0106	0.0561	0.45	0.54	**0.0027**	**
	beta_glucosidase ~ log(age) + (1|plot)	log	77.84	161	0.49	0.72	**0.0052**	**
	alkaline_phosphatase ~ log(age) + (1|plot)	log	10.19	10.01	0.42	0.59	**0.0066**	**
	litter_leaf_carbon ~ log(age) + (1|plot)	log	73.61	109	0.26	0.91	0.0896	.
	SOM ~ log(age) + (1|plot)	log	0.7864	6.44	0.12	0.94	0.2791	NS
	water_soil ~ log(age) + (1|plot)	log	3.02	17.07	0.46	0.94	**0.01751**	*
	P ~ age + (1|plot)	linear	−0.0097	1.67	0.02	0.74	0.6032	NS
	litter_leaf_water ~ age + (1|plot)	linear	7.35	57.26	0.65	0.69	< **0.0001**	***

For both variables, values found in primary forests were not reached even after 80 years of succession (Fig. 3 F, J). In contrast, soil metabolic quotient (qCO_2), microbial biomass carbon (MBC), organic matter (SOM) and phosphorus (P) were not significantly associated with age (Fig. 3 A, G, I). Yet, soil organic matter was highly correlated with soil water ($R = 0.8$).

3.2. *Drivers of soil functions across secondary succession*

Six different structural equation models were developed to assess the effects of vegetation composition and structure on each soil function (Fig. 4). CWM.SLA was the only diversity indicator that significantly explained variations in basal_respiration (−0.615) and alk_phosphatase (−0.522). Variance in height was the only diversity indicator that explained MBC (+0.793) and beta_glucosidase (+0.660), which are metrics related to carbon cycling. MBC, beta_glucosidase and basal_respiration had positive effects on SOM (+0.449; +0.472; +0.432), while qCO_2 did not. No significant effects of alk_phosphatase on soil P was detected. Above_biomass was the only significant driver of soil cover, positively influencing litter_leaf_carbon (+0.542), which in turn had a strong effect (+0.884) on litter_water.

4. Discussion

In the present paper, a wide variety of above and belowground metrics were assessed to inform how biodiversity and soil functions change and interact during forest secondary succession. Patterns of aboveground change showed the decrease in canopy openness and an increase on biomass and biodiversity in response to forest age. Furthermore, we observed a sharp increase of soil microbiological processes associated with carbon and nutrient cycling in the first years of succession, suggesting that soils are resilient and can rapidly respond to changes in vegetation and land use. Soil litter cover and litter water also increased during succession, but values found in primary forest were not reached even eight decades after agricultural abandonment. In general, although vegetation indexes were highly correlated and presented clear patterns of change across secondary succession, only trait dominance (i.e. CWM.SLA) and structural heterogeneity of the forest (i.e. sd_height) explained changes in carbon and nutrient cycling (Fig. 4). In the case of soil cover, the only significant driver was aboveground biomass (Fig. 4).

4.1. *Changes in different measures of diversity during forest succession*

Changes through secondary succession in structural, taxonomical and functional diversity converged towards values found in primary forests, supporting the equilibrium model of successional dynamics and reinforcing the importance of secondary forests for biodiversity conservation (Norden et al., 2009; Rozendaal et al., 2019). Structural diversity in terms of the standard deviation in tree height showed a sharp increase in the first 25 years of succession and then, slowly increased towards values found in primary forests (Fig. 2 D). This finding reflects the establishment of multi-layer strata already at early stages of forest vegetation development, which allow the forest system to efficiently capture nutrients, light, water and other resources (Danescu et al., 2016; Potzelsberger and Hasenauer, 2015). Although basal area, variance in basal area and aboveground biomass also increased during succession, they did not reach the same values found in primary forests. The higher variance in basal area in primary forests compared to old secondary forests can be explained by the presence of very large, and probably centenary trees only found in primary forests (Lucas-borja et al., 2016), which is also reflected in higher basal area and aboveground biomass (Fig. 2A, B, C). These results contrast with results obtained elsewhere (Lohbeck et al., 2012; Lu et al., 2015; Poorter et al., 2016). The slower recovery rates of basal area and aboveground biomass in Zona da Mata than in other tropical regions may be due to higher landscape fragmentation and relatively low rainfall (1300 mm/year). In addition, the small size of subplots may have overestimated basal area, variation in basal area and aboveground biomass in primary forests.

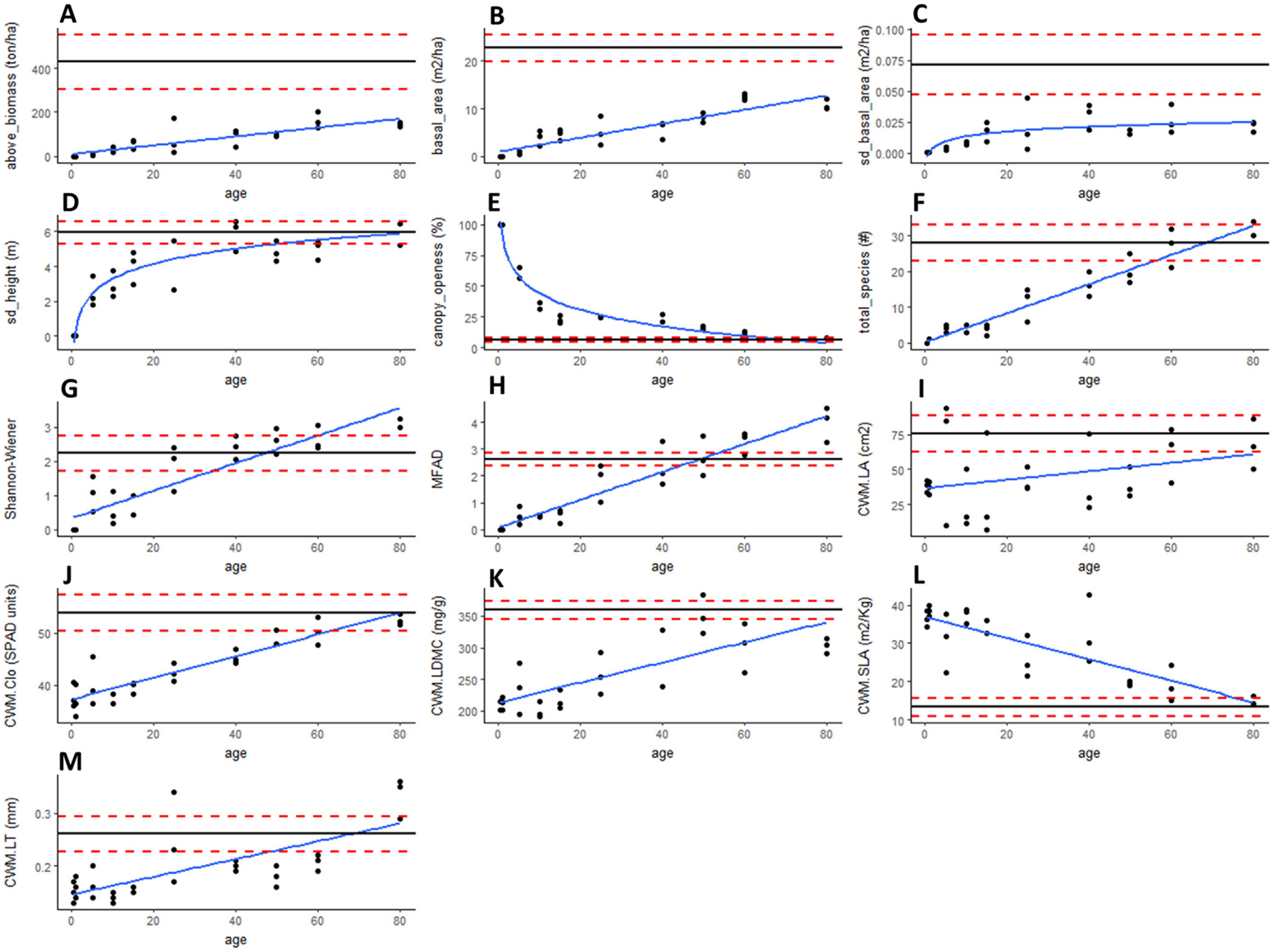

Fig. 2. Changes in vegetation attributes in response to forest age (years). Vegetation attributes are response variables, age of the forest is the fixed effect explanatory variable, and plot is added as random effect variable. Average and standard deviation of values found in primary forests are displayed as reference values with the horizontal black (average) and dotted (standard deviation) red lines. Each dot represents one subplot. CWM leaf area had a marginally significant association with age ($p < 0.07$), while all other variables had a significant response ($p < 0.05$). For more information on statistical results see Table 2, and for full name of vegetation parameters see Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Taxonomical diversity attributes (shannon and total_species) took longer to recover than structural diversity (i.e. sd_height), reaching values found in primary forests after 40–50 years of succession (Fig. 2 F, G). Although the identical sampling design for all plots was necessary to enable a fair comparison, the inclusion criteria of trees with DBH ≥5 cm may have underestimated species diversity of very young stands. Nevertheless, the recovery of taxonomical diversity in secondary forests in Zona da Mata is in line with other studies (Guariguata and Ostertag, 2001; Martin et al., 2013; Rozendaal et al., 2019) probably due to proximity between secondary forest plots and propagule sources (e.g. primary forests), and because land use before abandonment is characterized by low intensity management (e.g. permanent fields and no use of heavy machinery). In addition, the slightly higher species richness observed in older secondary forest plots compared to primary forests can possibly be explained due to the co-existence of pioneer and late successional species in secondary forests (Bongers et al., 2009; Huston and Smith, 1987). When soils are too degraded and there are no sources of seeds in the landscape, the recovery of secondary forests can be much slower, as new species are not able to arrive and/or establish (Chazdon, 2008a,b; Sloan et al., 2016). Therefore, the conservation of key stone species (e.g. *Euterpe edulis*) both in primary and old secondary forest remnants and in the agricultural matrix, can be crucial to support seed dispersal and the successful development of secondary forests in highly fragmented landscapes (Bechara et al., 2016; Norden et al., 2009; Perfecto and Vandermeer, 2010).

Functional diversity (i.e. MFAD) had a similar response to age than taxonomic attributes (Fig. 2 H), suggesting that niche overlap among species was low (Díaz and Cabido, 2001). In terms of functional composition, pioneers species dominating early stage forests had a more acquisitive strategy, associated with higher leaf turn-over and relatively high growth rate (Boukili and Chazdon, 2017; Craven et al., 2015). Later succession species had a more conservative strategy, displaying tougher leaves (higher LDMC and LT and lower SLA), with lower turnover and higher capacity to resist herbivory and absorb light (higher Chlo) (Fig. 2 I, J, K L, M) (Lu et al., 2015; Poorter and Bongers, 2006; Rijkers et al., 2000). Dynamics in functional composition across succession are probably due to increased competition for resources among tree individuals (Boukili and Chazdon, 2017; Chazdon, 2008a,b). For instance, canopy openness decreased during succession (Fig. 2E), which indicates lower light availability for trees and, therefore, increased competition.

4.2. Changes in soil properties and processes during forest succession

Our results indicate that soil microbiological processes related to carbon and nutrient cycling show a sharp recovery in the first 15 years of secondary succession and then tend to stabilize to the levels of primary forests (Fig. 3 B, C, D, E). Soil functions linked to microbial

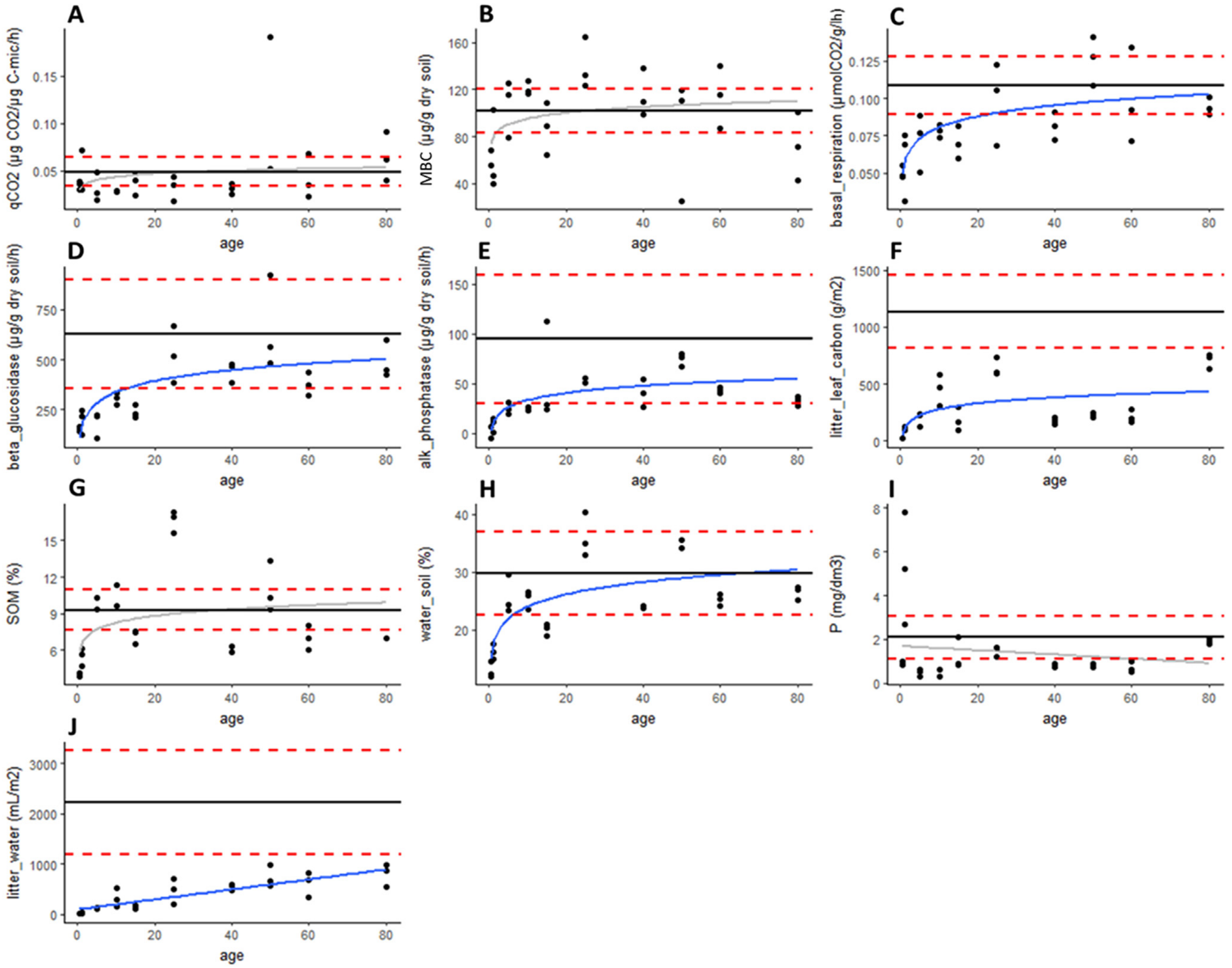

Fig. 3. Changes in soil properties and processes in response to forest age (years). Soil properties and processes are response variables, age of the forest is the fixed effect explanatory variable, and plot is added as random effect variable. Primary forest plots were not included in the regressions. Average and standard deviation of values found in primary forests are displayed as reference values with the horizontal black (average) and dotted red (standard deviation) lines. Each dot represents one subplot. Carbon litter per area (litter_carbon) had a marginally significant association with age ($p < 0.09$). Soil metabolic quotient (qCO2), microbial biomass carbon (MBC), organic matter (SOM) and phosphorus (P) and were not significantly associated with age and indicated by grey regression lines ($p > 0.1$). All other variables had a significant response ($p < 0.05$). For more information on statistical results see Table 2, and for full name of soil parameters see Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

activity tend to recover faster than above-ground vegetation diversity (Winbourne et al., 2018), suggesting that soils are more resilient than the vegetation. Besides, feedback loops between vegetation and soil functions may be crucial for the success of secondary succession as the fast recovery of soil functions in the beginning of succession can play a role in improving edaphic conditions (e.g. water content, nutrient availability and organic matter) to enable the germination and growth of new species (i.e. typical of primary forests) (Chua and Potts, 2018; Qiu et al., 2018). Furthermore, knowledge about soil conditions prior reforestation can assist the selection of adequate interventions, while monitoring soil conditions during reforestation can help to assess the recovery of soil-related ecosystem services as well as the identification of soil processes that may be limiting the development of the vegetation. Therefore, to maximize the success of restoration efforts, soil indicators of environmental quality must also be addressed, which is rarely done, especially for soil microorganisms (Mendes et al., 2019).

Soil carbon or organic matter is considered a key indicator of soil quality (Minasny et al., 2017), and is associated with provision of a range of ecosystem services, such as carbon sequestration, water retention, soil fertility, erosion control, amongst others (Adhikari and Hartemink, 2016). Most studies reported a general increase of soil organic matter (SOM) and soil carbon during succession (Deng et al., 2013; Hall et al., 2017; Lu et al., 2015; Robinson et al., 2015; Yan et al., 2006; Yesilonis et al., 2016). In our study, SOM was not significantly associated to forest age, although SOM was apparently lower in recently abandoned agricultural fields than in forested areas (Fig. 3G). Considering all plots, SOM was highly correlated to water_soil (Appendix A), evidencing the role of organic matter for enhancing water retention and lowering water run-off, one of the main causes of soil, water and nutrient losses in hilly landscapes (Liu et al., 2018).

Our results suggest a quick recovery of alk_phosphatase activity after agricultural abonnement, with a sharp increase in the first years, and then, tending to stabilize. Phosphorus is one of the main limiting nutrients in tropical highly weathered landscapes (Cleveland et al., 2002) and thus, understanding the processes regulating phosphorus cycling can be an important step to promote vegetation health and recovery (Qiu et al., 2018). Although phosphorus cycling across secondary succession is poorly understood, changes in litter and soil nutrient content during succession may drive the response of phosphatase activity to forest age (Zhang et al., 2015). Our results support similar

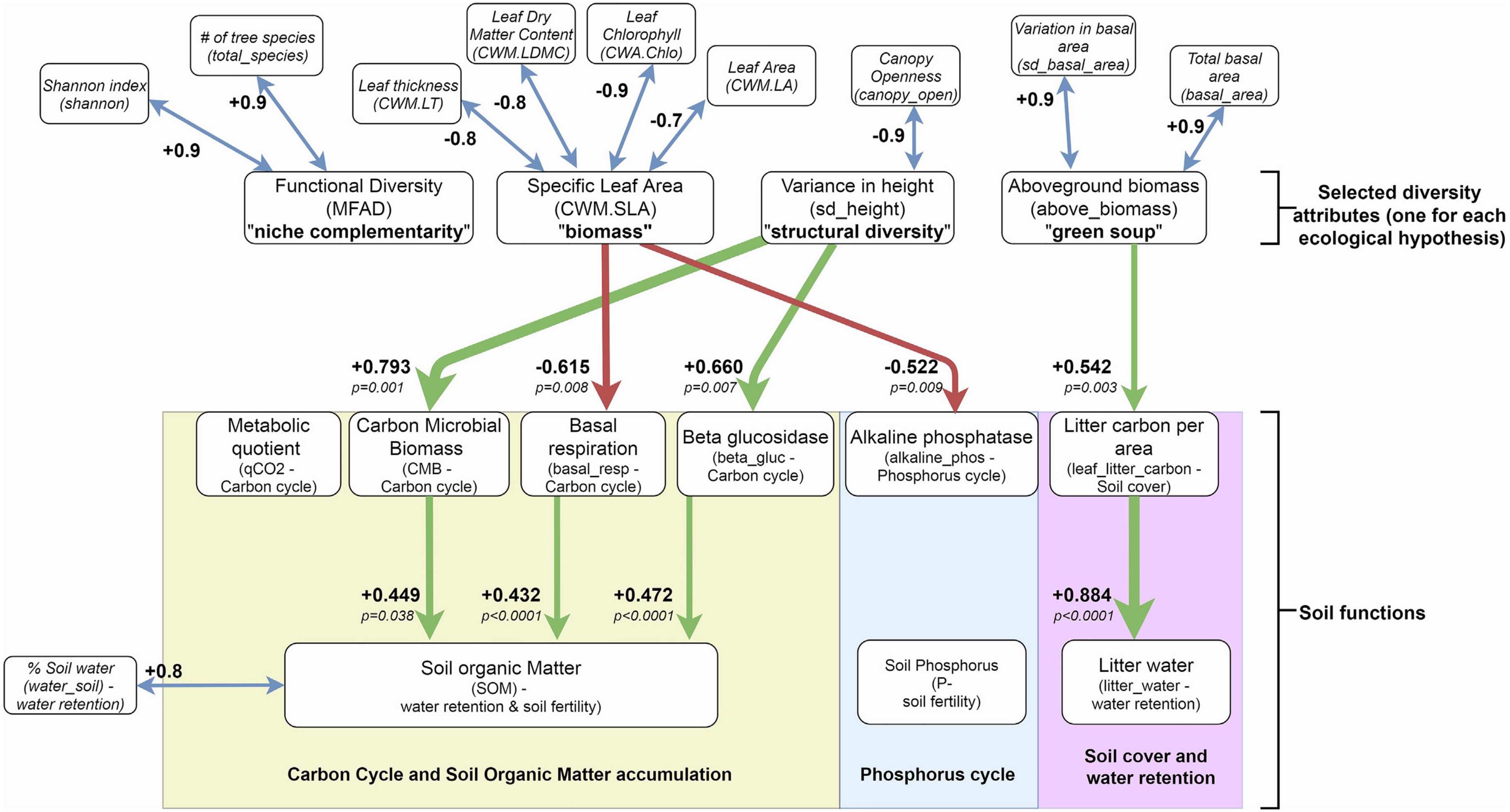

Fig. 4. Overview of the outcomes from structural equation models and Pearson correlations to explain the influence of diversity attributes on soil functions across forest succession. A separate structural equation model was developed for each of the six intermediate soil processes/properties. All initial models had the four selected diversity attributes as explanatory variables, one intermediate soil process, and one specific soil property, which was considered as the final response variable in each model. The coefficients from the structural equation models are displayed next to the green and red arrows. Pearson correlation coefficients with variables not included in the model are shown in the blue arrows and Appendix A. Non-significant relationships were not included in the diagram. See Appendices D, E and F for results of separate models and correlation coefficients. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

studies conducted in tropical forests, showing a general increase of phosphatase activity in response to forest age (Huang et al., 2011; Zhang et al., 2015). In contrast, completely different patterns were observed in pine forests in Spain (Lucas-borja et al., 2016), where alk_phosphatase activity decreased in response to secondary succession, suggesting that phosphorus dynamics can differ in temperate and tropical secondary succession.

4.3. Linking biodiversity to soil functions

Our study is the first to our knowledge to test the effect of different vegetation attributes on key soil processes during secondary succession (Fig. 4). Our findings indicate that variance in height is the only vegetation attribute driving beta_glucosidase and MBC (Fig. 4), highlighting the role of multi-layered strata vegetation to capture and efficiently use carbon, water and light (Danescu et al., 2016; Potzelsberger and Hasenauer, 2015), creating favourable conditions for microbiological activity. The recovery of structural heterogeneity is rather fast in the first years of secondary succession tending to stabilize afterwards (Fig. 2D), which means that levels of MBC and beta_glucosidase can also recover quickly after agricultural abandonment (Fig. 3B, D). Both MBC and beta_glucosidase had a significant positive effect on SOM (Fig. 4). Additionally, trait dominance (i.e. CWM.SLA) was the main aboveground driver of basal respiration (Fig. 4), which also had a positive significant effect on SOM (Fig. 4). These results indicate that tougher leaves with lower SLA are harder to decompose, demanding more energy from soil microorganisms (i.e., higher basal respiration). Although respiration and consequently the emission rate of CO_2 increases across succession, apparently this is compensated by the amount of carbon incorporated in the soil, as basal_respiration had a positive effect on SOM (Fig. 4) (Yan et al., 2006). Yet, our results show strong evidence that the structural diversity and biomass ratio hypotheses can better explain changes in carbon cycling than the other tested hypotheses. In contrast to our findings, experiments using manipulated plant communities with low number of species, supported the niche complementarity hypothesis to explain soil microbiological responses such as increased MBC and basal_respiration (Lange et al., 2015; Zak et al., 2003). Possibly, a low number of species can mask the role of different vegetation attributes, because it tends to result in a more uniform occupation of niche space than in species rich communities, resulting in lower functional redundancy and higher correlation between species richness and other diversity metrics (Díaz and Cabido, 2001). Besides, studies often do not test for different vegetation attributes as possible drivers of ecosystem functions, processes and/or properties, which may lead to biased results (Nadrowski et al., 2010). Therefore, we highlight the need to disentangle different indicators of vegetation composition and structure to better understand the ecological mechanisms that can explain changes in ecosystem functioning.

Our results show that leaf trait dominance (i.e. CWM.SLA) is the main vegetation attribute driving alk_phosphatase activity (Fig. 4). According to the worldwide leaf economics spectrum, tougher leaves with lower SLA tend to have lower P concentrations (Boukili and Chazdon, 2017; Wright et al., 2004). In that case, the lower availability of P in the leaves could induce microorganisms to increase P cycling, as ecological theories indicate that organisms invest energy to cycle and/or capture most limiting resources (Bloom and Mooney, 1985; Fujii et al., 2018). However, soil P was not significantly influenced by alk_phosphatase and did not show a clear pattern across succession (Fig. 3). These findings highlight the complexity of P dynamics in the soil due to uptake and fixation processes (Fujii et al., 2018) and need further studies to assess which plant traits are related to P cycling as well as better soil indicators of P availability.

Litter_leaf_carbon was only influenced by aboveground_biomass (Fig. 4), showing that forest age and biomass are important drivers of litter accumulation (Lohbeck et al., 2015). Thus, litter accumulation can be explained by decades and even centuries of input from the tree canopies, showing the importance of primary forests to provide high levels of soil cover, that cannot be attained by secondary forests even after decades of succession. The strong effect of leaf_litter_carbon on litter_water (Fig. 4), underline the role of carbon to retain water and avoid losses by superficial run-off.

Although in our models we postulated soil functions were driven by vegetation characteristics, in reality there could be feedback mechanisms, in which soil respond to vegetation and vice-versa across time (Duncan et al., 2015). The high dominance of *Piptadenia gonoachanta* in the first years of succession (Domingos et al., 2015; Marangon et al., 2008) indicate the potential role of this leguminous species to colonize degraded landscapes and improve soil conditions for other species to establish. During secondary succession in our study area, *P. gonoachanta* is gradually replaced by other species, such as *Euterpe edulis*, which become more dominant later in succession (Appendix C). *E. edulis* can be considered as a keystone species for the conservation of the Atlantic forest (dos Reis et al., 2000), since its fruits are very much appreciated by birds and other animals that bring seeds from other species to the system, increasing local biodiversity (da Silva and dos Reis, 2018).

4.4. Implications for management

The fast recovery of biodiversity and soil functions indicates the potential of secondary succession as an strategy that farmers can use to convert new areas into forest for increasing the provision of ecosystem services valued by society, such as water and climate regulation, erosion control, forest products and aesthetics (Chazdon, 2008a,b; Ninan and Inoue, 2013; Yuliani et al., 2015). In Brazil, the conservation of forest areas in agricultural land has a major role for increasing national forest cover and is supported by the current Forest Law, which requires farmers to maintain or restore native vegetation in certain areas of their properties (i.e. hilltops, steep slopes, around water springs and along the riparian buffer) (Calmon et al., 2011; Taniwaki et al., 2018). Yet, for the successful restoration of new forest areas, farmers need support from programs, legislation and public policies. It is necessary not only to raise awareness on the importance of forests for the provision of ecosystem services, but also to provide technical guidance and financial subsidies, such as adequate extension services and payments for ecosystem services (Díaz et al., 2019). Despite the high potential to increase forest cover and the associated ecosystem services through secondary succession, primary forests should be conserved and maintained, especially in fragmented landscapes. This is important not only due to the historical and cultural value of primary forests (Garnett et al., 2018), but also because they can serve as propagule source (Robinson et al., 2015; Sloan et al., 2016) and provide ecosystem services that cannot be attained even after decades of succession (Watson et al., 2018). Finally, our results found strong support in the role of multi-layered strata for increasing carbon cycling. Therefore, analogously to forests, the incorporation of trees and shrubs in agricultural fields can increase structural heterogeneity of the systems and consequently, enhance soil processes responsible for soil organic matter accumulation and soil fertility (Altieri, 1999).

5. Conclusions

Our results demonstrated the potential role of secondary forests to relatively quickly restore tree diversity and soil functions to the level of primary forests. Therefore, conservation efforts in highly fragmented and human modified landscapes should consider secondary forest succession as a viable and efficient strategy to increase forest cover and enhance biodiversity conservation and the associated ecosystem services. In Brazil, farmers and land owners can play a key role for successfully increasing forest cover via secondary succession since a great part of the forest areas are located (or must be regenerated) on private properties. Metrics of biodiversity had distinct recovery patterns, showing the importance to disentangle and measure several vegetation attributes. By measuring several soil properties and processes we can gain new insights on the effects of tree diversity on soil functioning. These relationships should be further explored in future studies to get a better understanding on how ecosystem services are recovered through forest succession along climatic and edaphic gradients as well as in different landscape conditions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117696.

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