Journal of Tropical Ecology

www.cambridge.org/tro

Litter production in successional forests of southern Bahia, Brazil

Janaine Isabela da Silva Rocha[1], Luiz Fernando Silva Magnago[2] and Daniel Piotto[2]

[1]Programa de pós-graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz (UESC), Rodovia Ilhéus-Itabuna, Km. 16. Salobrinho, 42662-900, Ilhéus, BA, Brazil and [2]Centro de Formação em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Ilhéus, BA, Brazil

Research Article

Cite this article: Rocha JIS, Magnago LFS, and Piotto D. Litter production in successional forests of southern Bahia, Brazil. *Journal of Tropical Ecology* https://doi.org/10.1017/S0266467422000281

Received: 30 November 2021
Accepted: 29 May 2022

Keywords:
carbon; ecosystem functioning; regeneration; secondary succession; successional; tropical forests

Author for correspondence:
Janaine Isabela da Silva Rocha,
Email: janainerocha@yahoo.com.br

Abstract

Litter production plays an important role in the functioning of the ecosystem, providing several ecosystem services, such as nutrients cycling and carbon storage. We studied litter production patterns and its relationship with forest structure over a chronosequence of secondary forests in southern Bahia, Brazil. In the study area, 15 pairs of mature and secondary forest were used, in a chronological sequence, being 10, 25 and 40-year-old secondary forests and mature forests. Plots were created for the collection of aboveground biomass data, and within these plots, litter collectors were installed and monitored for 1 year. The results showed that litter production was lower in 10-year-old secondary forests when compared with older forests. On the other hand, in the 10-year-old forests, annual litter production represents 47.8% of the stored biomass, while in mature forests annual litter production represents only 4%. We found that structural variables (basal area, number of stems and canopy opening) influence significantly litter production, as well as litter as percentage of forest biomass. The study emphasizes the importance of biomass production through litterfall in regenerating tropical forests, and its importance for carbon storage and for the maintenance of ecosystem services.

Introduction

Tropical forests are responsible for storing around 37% of the terrestrial carbon of the planet in the form of plant biomass (Aguiar et al. 2016, USDOE 2010). Forest biomass is stored in about 80% of the aboveground biomass (AGB) (Cairns et al. 1997) which is related to vegetation structure (Houghton et al. 2009). In tropical forests, more than 50% of primary annual production is returned to the soil in the form of organic debris in litter (Wardle et al. 2004). The Intergovernmental Panel on Climate Change (IPCC) identified litter as one of the five carbon reservoirs in forest ecosystem (Nizami 2012), with 5% of the AGB being stored in litter (Pan et al. 2011).

The return of organic matter to the soil is one of the main processes of ecosystem functioning (Alves et al. 2010); it represents the transfer route of organic matter and mineral elements from the vegetation to the soil (Camargo et al. 2015, Silver et al. 2014, Vitousek & Sanford 1986). This process is essential in tropical forests as those are environments with highly weathered soils (Poggiani 2012) and with low fertility (Vitousek & Sanford 1986). Because of that, the vegetation depends on the cycling of nutrients contained in plant debris for the absorption of nutrients (Kuruvilla et al. 2016, Rawat et al. 2010). In addition, litter production becomes essential for the functioning of the ecosystem, transferring nutrients to the soil (Pandey et al. 2007), maintaining soil fertility in forest ecosystems (Guendehou et al. 2014, Montagnini & Jordan 2002, Tripathi et al. 2006) and for the global carbon cycle (Berg & Mcclaugherty 2014).

Litter production occurs by the elimination of vegetative parts of plants, which can be caused by senescence, abiotic factors, stress and these factors combined, as well as by the death of a plant (Chakravarty et al. 2019, Krishna & Mohan 2017). The pattern of litter production depends on some factors such as climate (Sayer 2006) and vegetation structure and composition (Nickmans et al. 2019, Vidal et al., 2007). There is a significant number of studies designed to understand the effect of climate in litter production patterns. For example, the relationship of seasonality with increased litter production (An et al. 2019), as in the warmer seasons of the year, on increasing light time, plants can prepare for more favourable growth, and thus replace the old leaves with new ones (Devi & Garkoti 2013), higher production in the dry season (Barlow et al. 2007) and decrease the production of litter with increase in elevation (Majila et al. 2005, Zhou et al. 2007).

In addition to climate, vegetation characteristics can modify litter production, such as vegetation structure and composition (Nickmans et al. 2019, Schumacher et al. 2011) and the changes in development strategies of the plants with forest succession (Poorter & Bongers 2006). As the forest develops, there is an increase in the size of large trees, increase in the basal area, and the well-developed forest structure reflects a well-developed canopy, which can favour the production of litter (Kunhamu et al. 2009, Vidal et al. 2007). Changes in plant functional traits can affect litter production with the change of plants dominance from acquisitive to conservative traits during secondary succession (Craven et al. 2015, Facelli & Pickett 1991; Werneck et al. 2001).

In theory, litter production pattern is related to the canopy development that occurs differently, depending on the individual characteristics of the species (Carrera et al. 2008). For example, in young secondary forests, the dominant species have resource acquisition characteristics, with high growth and mortality potential (Rozendaal & Chazdon 2015), fragile tissues (Reich 2014), low-density wood and short-lived leaves (Adler et al. 2013), contributing more to litter production because they have leaves and branches with less lignified materials, in addition to being rich in N and low C/N ratio that can accelerate litter turnover (Zhou et al. 2019). With forest development, dominance gradually changes towards species with conservative resource characteristics, which present the production of denser tissues (as a higher density of wood), high C/N ratio, long-lived leaves and low renewal leaves rates (Adler et al. 2013, Craven et al. 2015, Reich 2014). Thus, areas in the advanced stage of forest development, with higher species diversity and abundance of late-successional species, show the poorest litter in terms of N concentrations, and with a high C/N ratio, which leads to lower litter turnover rates (Parton et al. 2007, Zhou et al. 2019). In this way, changes in species dominance will modify the quantity and quality of the litter and, consequently, the flows of biomass and nutrients with forest development.

Here, we used a chronosequence of secondary and mature forests of the Atlantic Forest biome in Brazil, to assess changes in litter production with forest development. In addition, we studied the relationship between litter production and standing AGB to detect changes in plant characteristics with forest development. We hypothesized that (a) there would be an increase in litter production because of the increase in standing AGB with forest development; (b) there would be a significant shift in the relationship between litter production and standing AGB with forest development because of changes in dominance from plants with acquisitive to conservative strategies and (c) and the increase of litter production is associated with successional changes in forest structure.

Study site

The study was carried out in the Serra do Conduru State Park - PESC, located in southern Bahia, Brazil, at 14º 30'16" S, and 39º 6'36" W (Figure 1). The Park has an area of approximately 10,000 ha, composed of a forest mosaic in different stages of regeneration, from secondary forests at different ages to well-preserved areas (Piotto et al. 2009). The vegetation is classified as tropical rain forest, in the Atlantic Forest biome, with emergent, canopy, subcanopy and herbaceous layers and extremely high species diversity (Thomas 2003). The average monthly temperature is 24°C, with an average annual rainfall of 2,000 mm evenly distributed throughout the year (Santos et al. 2018). The selected secondary forest areas were established after deforestation and burnings, followed by 1–2 years of cassava cultivation (Piotto et al. 2009).

Methods

Classification of chronosequence

Based on aerial photographs and satellite imagery from 1965 to 2009, it was possible to track changes in forest cover and land use in the study region. A total of 95 secondary forest stands larger than 3 ha and adjacent to a mature forest were found in the study region. Then, maps of forest age classes were derived. Ages of secondary forests ranged from 10 to 43 years. Fifteen pairs of secondary forests adjacent to mature forests were randomly selected to represent three age groups of secondary forests: 10 years (10–12 years), 25 years (22–25 years) and 40 years (37–43 years) (Figure 1). Interviews with local farmers were conducted to validate information on forest age and type and intensity of previous land use.

AGB data

In each pair of mature and secondary forests, five plots of 20 × 10 m (200 m^2) were established in each age class (10, 25 and 40 years) and one plot of 20 × 30 m (600 m^2) in mature forest. A total of 75 plots were installed in secondary forests and 15 plots in mature forests (total of 90 forest inventory plots). All trees with a diameter at breast height (dbh) equal to or greater than 5 cm were identified and measured for dbh and total height. We calculated basal area (m^2/ha) and tree density (number of trees with dbh > 5 cm/ha) for each plot. In addition, we estimated AGB using the following allometric equation for tropical forests (Chave et al. 2014):

$$\mathrm{AGB} = 0.0673\,(\rho \mathrm{D}^2\mathrm{H})^{0.976}$$

based on diameter D (cm), height H (m), and wood-specific gravity ρ ($g.cm^{-3}$). AGB is in kg. Plot biomass represents the estimated biomass of all trees within a plot, which was then extrapolated to estimate the AGB in Mg/ha. Specific wood density data were collected for each species in the world database (Zane et al 2009), when species data were not available, we used genus data, and when this was not available, we used family data.

Litter and canopy data

Litter production was sampled in each forest inventory plot using 90 collectors established in mature and secondary forests. In each pair of mature and secondary forests, six collectors were installed with a distance of 20 m between each collector, located at the central point of the forest inventory plots. The collectors consisted of a cone of a fine mesh fabric (2 mm) attached to a circular wire of 1 m^2, installed at 50 cm aboveground. The collections of material deposited in the collectors were carried out monthly from February 2008 to January 2009. The collected litter was dried in a lab oven at 50º for 48 hours. After drying, each monthly sample was weighted to obtain the monthly dry mass per collector. For the calculations, results from each collector for all months were added and then transformed into hectares, thus obtaining the values of litter in total weight in tons per hectare per year. At every collector, canopy opening was estimated using hemispherical photographs.

Besides AGB and structural variables, we also used as a response variable the ratio between litter biomass and AGB (here considered as a proportion of litter related to AGB), where we consider the percentage of biomass that is stored in litter in relation to AGB. For the calculation of the ratio, litter production values were divided by the AGB values, both in Mg/ha, and were multiplied by 100, to be represented in %.

Statistical analysis

To assess the relation between litter production with age and the relation of AGB and litter biomass with age, we adjusted a linear

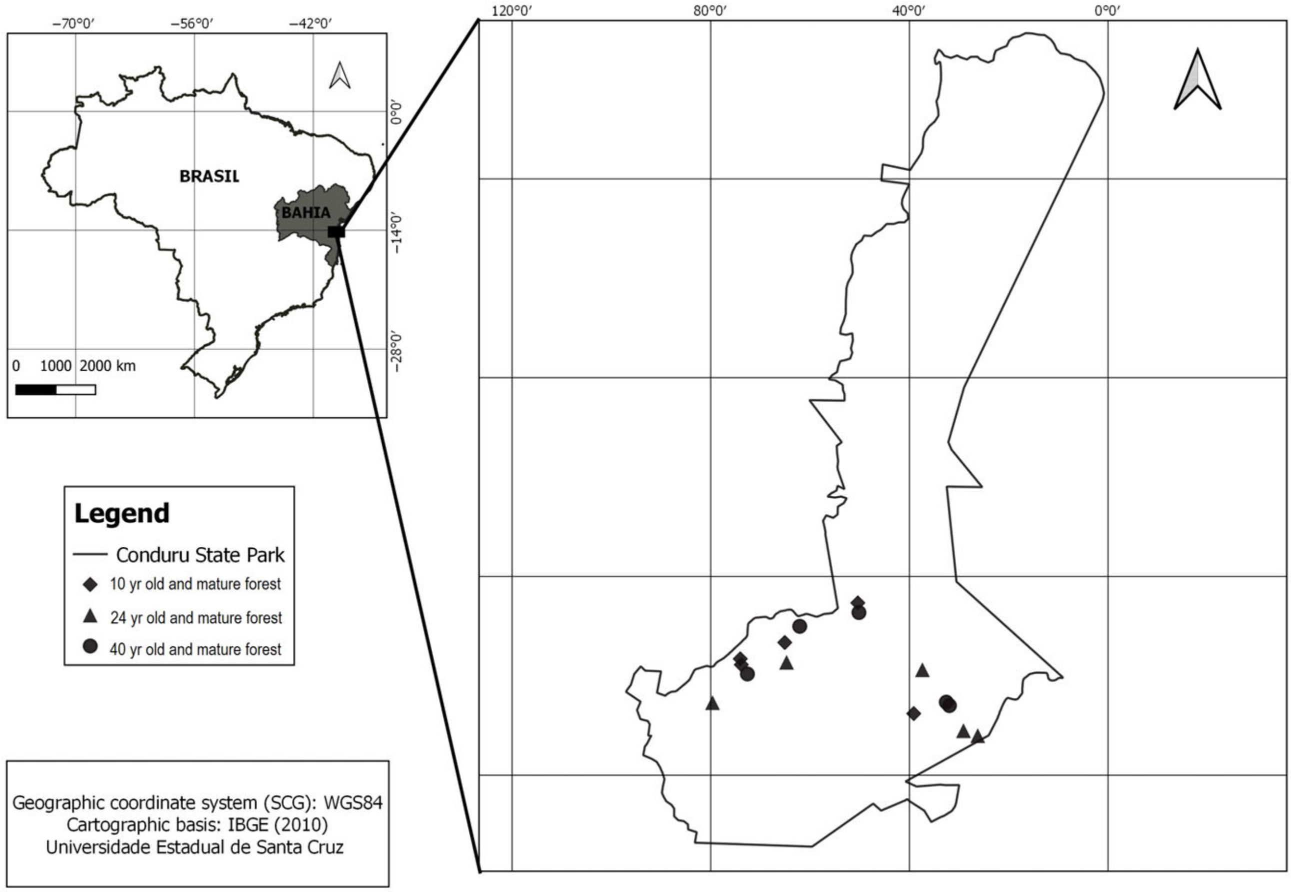

Figure 1. Location map of the Serra do Conduru State Park, with the location of the study plots, Bahia, Brazil.

mixed model (LMM), including the site as a random factor. We used LMM approach to control temporal pseudoreplication (Zuur et al. 2009). Thus, for each response variable (litter production and relation of aboveground and litter biomass), we use one model with age as an explanatory variable. For the validation of the model, we tested the normality of the residues, using the Shapiro–wilk test and plot of the residues.

Then, we investigated how the density of the stem (number/ha), canopy openness (%) and basal area (m^2/ha), can influence litter production and how these variables influence the aboveground and litter biomass ratio. As the forest structure data was considered non-normal, we used generalized linear models (GLM). For each response variable (annual litter production and aboveground and litter biomass ratio), we fit four models for each explanatory variable (stems density (number/ha), canopy openness (%) and basal area (m^2/ha)): 1) a model with annual litter production as the response variable in relation to an explanatory variable (stems density or canopy openness or basal area), 2) a model with annual litter production in relation to the log of the explanatory variable (stems density or canopy openness or basal area), 3) model with a log of annual litter production and log of the explanatory variable (stems density or canopy openness or basal area) and finally 4) a model with log annual litter production in relation to an explanatory variable (stems density or canopy openness or basal area). The same was done with the other response variable (aboveground and litter biomass ratio). We considered the best model when its AICc was at least two units lower than the subsequent best model. The relationships were considered significant with $P < 0.05$. The models were validated using the relationship between standardized residuals and standardized normal quantiles and, the residuals were tested for deviation from the normal distribution using the Shapiro–Wilk test. All analyzes were performed using the free software R 4.0 (R Development Core Team 2020), using the packages "lme4" and "lmerTest" (Bates et al. 2015, Kuznetsova et al. 2017).

Results

In total, the annual average production of litter was 7.89 Mg/ha^1/y −1. The annual average production of 10-year-old secondary forests differed significantly from the other age classes (6.58 ± 2.28 Mg/ha^1/y−1; $P < 0.05$, Figure 2), showing the lowest values of annual litter production. Whereas 25-year-old secondary forests (7.96 ± 1.93 Mg/ha^1/y−1), 40-year-old (8.86 ± 2.38 Mg/ha^1/y−1, Figure 2) and mature forest (8.31 ± 1.02 Mg/ha^1/y−1) presented similar annual litter production. The results showed that annual litter production had a strong positive relation with forest age, with a rapid increase in annual litter production early in succession.

Annual litter production represented 20.36% (from 6,63 to 47,8%) of the total standing AGB in 10-year-old plots. These values decreased significantly with forest development ($P < 0.05$), with average of 13.16% (3.92 to 37.28%) in 25-year-old plots, 7.14% (2.77 to 34.17%) in 40-year-old plots and 2,33% in mature forests

https://doi.org/10.1017/S0266467422000281 Published online by Cambridge University Press

Table 1. Structural features of vegetation present at sites of different ages along the succession, at the ages of 10, 25 and 40 years and mature forests, in the Serra do Conduru State Park, Bahia, Brazil. Mean ± SD

	Ages along succession			
Parameters	10 years old	25 years old	40 years old	Mature forest
Aboveground biomass (Mg/ha)	41.13 ± 22.55	80.77 ± 48.75	159.67 ± 70.93	391.65 ± 138.7
Basal area (m^2/ha)	10.91 ± 4.52	18.15 ± 8.14	28.32 ± 8.76	42.1 ± 11.96
Density (number/ha)	1810 ± 728.16	2096 ± 681.29	2990 ± 755.53	3040 ± 394.36
Canopy openness (%)	20.28 ± 8.6	16.57 ± 3.25	13.61 ± 3.21	13 ± 1.86

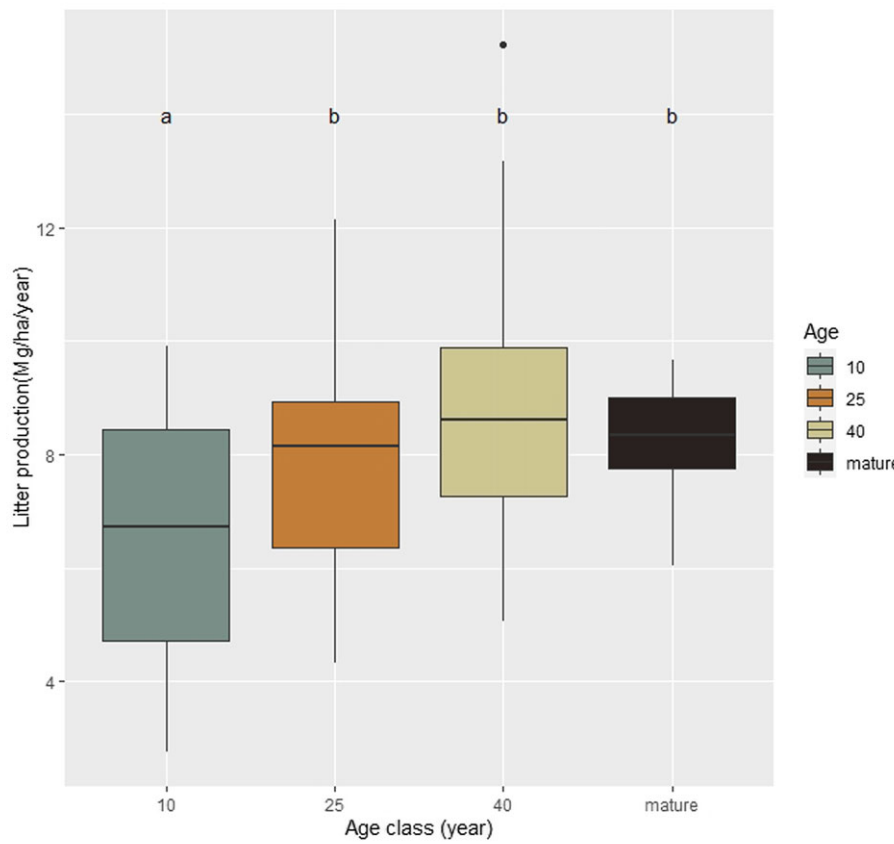

Figure 2. Annual litter biomass production in Mg/ha[1]/y −1along succession, at the ages of 10, 25 and 40 years and mature forests, in the Serra do Conduru State Park, Bahia, Brazil.

(1.02 to 4.22%) (Figure 3). The results showed a negative and significant effect of age in relation to annual litter production and total standing biomass ($P < 0.05$) (Figure 3).

In general, our GLMs showed a significant influence of vegetation structure on annual litter production (Figure 4). The basal area and stem density significantly and positively influenced annual litter production ($P < 0.01$), whereas canopy opening had a negative influence on annual litter production ($P < 0.01$; Figure 4).

The ratio of annual litter production in relation to total standing AGB showed a significant association with all forest structure variables. Basal area and stem density significantly and negatively influenced the ratio of annual litter production and total standing AGB ($P < 0.001$), while canopy opening had a positive influence ($P < 0.001$; Figure 5).

Discussion

Our results reflect the gradual recovery in aboveground primary productivity during tropical forest succession, which tends to stabilise at around 20 years (Ewel, 1976; Brown & Lugo, 1990). The recovery and stability in litter production between secondary and mature forests were also reported in other studies carried out in tropical forests (Barlow et al. 2007; Ostertag et al 2008). This stability of litter production early in succession (20 and 40 years old) can be effective in restoring ecosystem processes such as litter production and decomposition, which can represent one of the major pathways of nutrient cycling (Camargo et al. 2015), essential for maintaining soil fertility in forest ecosystems (Li & Ye 2014, Montagnini & Jordan 2002, Tripathi et al. 2006).

In young secondary forests, there is a dominance of pioneer species (Rozendaal & Chazdon 2015; van Breugel et al. 2006). These early successional species generally have the characteristics of being resource acquisitive, presenting less lignified materials with rich N constitution and low C/N ratio (Reich 2014; Hantsch et al., 2014). N concentration can have a positive effect on litter mass loss (Cornwell et al. 2008; Patoine et al, 2017), because the consumption of N-rich plant material is necessary for detritivores (Eisenhauer et al, 2009; Schwarz et al, 2015). The content of

https://doi.org/10.1017/S0266467422000281 Published online by Cambridge University Press

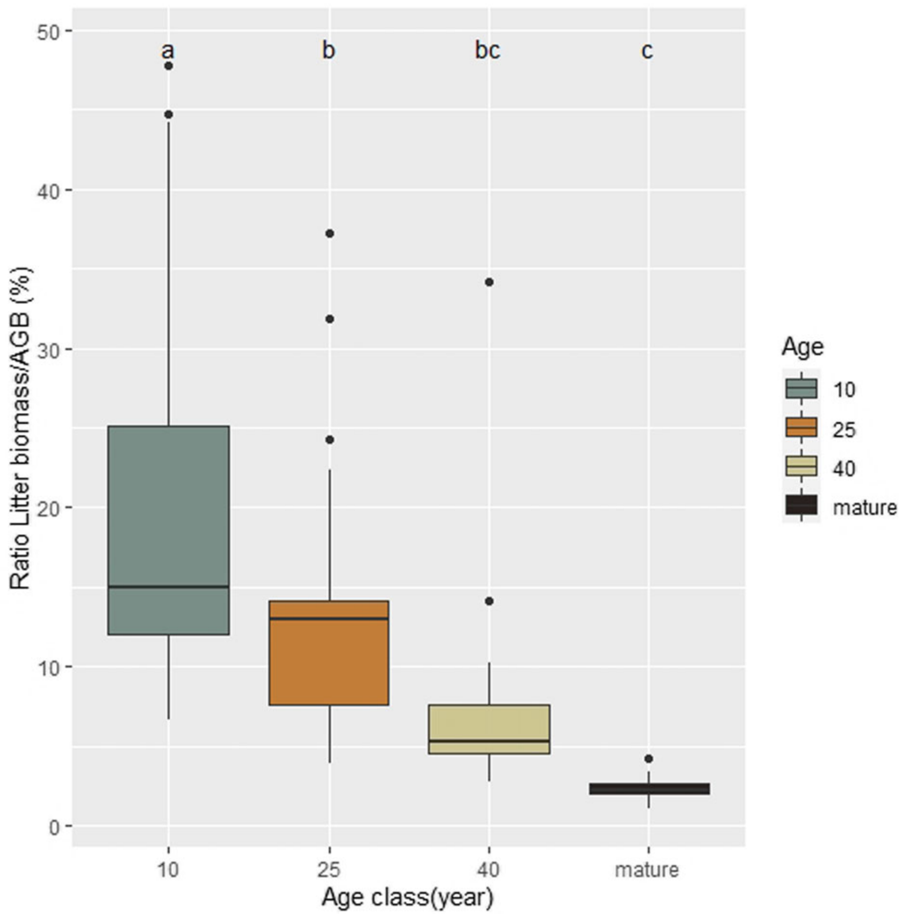

Figure 3. Relation between annual litter production and the total aboveground biomass at the ages of 10, 25 and 40 years and mature forest, in the Serra do Conduru State Park, Bahia, Brazil.

nitrogen and carbon are also commonly used as predictors of decomposition rate (Cornwell et al. 2008; Eichenberg et al. 2014). Pioneer species also have low content of secondary compounds (phenolics and tannins), which can accelerate the decomposition process (Parton et al, 2007). What happens in the opposite way to late successional species, with high leaf carbon content, high leaf toughness (Garnier et al. 2004, Cortez et al. 2007). Thus, litter quality is expected to change over the course of succession, with high decomposition rates in early successional forests (Garnier et al. 2004).

In our study, we found litter production as an important biomass reservoir. In recently modified forests, annual litter production represents more than 47% of the total standing biomass, demonstrating its importance as a biomass reservoir early in succession. Our data showed that in these forests (10 years old), the vegetation has a more simplified structure, such as areas with lower average DBH, lower basal area and lower density of individuals. In addition, litter has greater representation when compared to total standing AGB, as well as areas with the largest canopy opening (Figure 5). These areas have a dominance of pioneer species, which have high growth rates, but short longevity (Reich et al. 2008, Rees 2001), making their litter biomass more representative at this stage of succession. Thus, when compared to forests in more advanced stages, younger areas depend much more on litter biomass to maintain various ecosystem services, such as those related to soils, a favorable soil environment, such as maintaining the microclimate, regulating temperature and humidity of soil (Amatangelo et al.2008, Bond-Lamberty & Thomson 2010, Sayer 2006) and ecosystem services related to climate regulation, as an important carbon reservoir (Sayer et al. 2007), since the vegetation structure is less developed.

In the final stages of the succession, we found a greater basal area and greater density of individuals, as well as greater canopy closure. Forests in the final stages of succession are more complex ecosystems, with a better-developed canopy structure (Werneck et al. 2001), in addition to having a greater surface area of branches and foliage (Lowman & Schowalter 2012). This more complex vegetation structure is generally associated with the majority of species that have a longer life span (Rees et al. 2001), high density of wood, slow growth and thus greater survival (Chave et al. 2009, Rees et al. 2001). In this way, even having a more developed structure, these mature forests produce similar amounts of litter when compared to secondary forests (20 and 40 years old), as their dominant species tend to retain plant parts longer than dominant species present in secondary forests (Rees et al. 2001). Therefore, the litter contributes less to the storage of biomass, which represents less than 4% of the total biomass, while most of the AGB is stored in tree trunks, in resource-conservative species (Reich 2014, Adler et al. 2013). This relation explains that vascular plants change from rapid acquisition of resources to the conservation of resources with successional age (Jackson et al. 2013, Poorter & Bongers 2006).

Conclusion

Implications for forest management and climate mitigation

High rates of litter production in secondary forests can represent major contributions to organic matter and nutrients for

https://doi.org/10.1017/S0266467422000281 Published online by Cambridge University Press

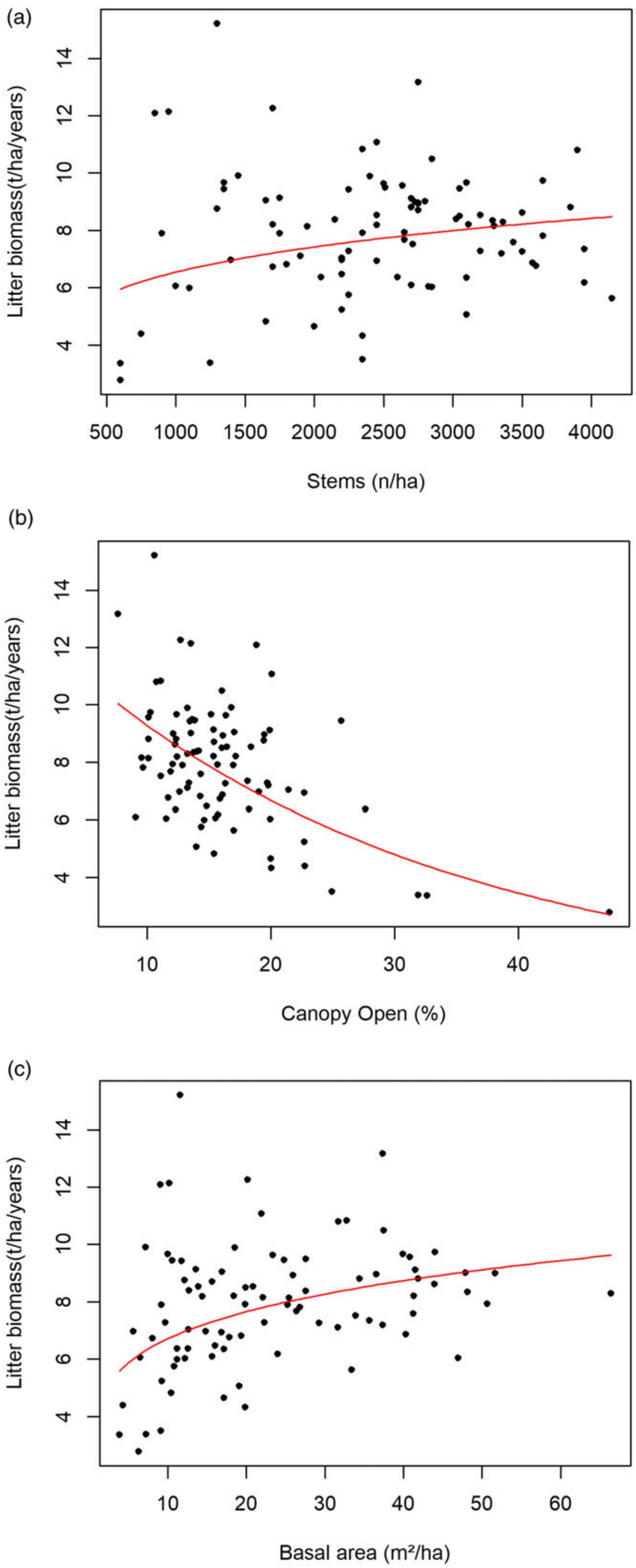

Figure 4. Relations between annual litter production and structural variables: (a) stems (number/ha), (b) basal area (m^2/ha) and (c) percentage of canopy opening.

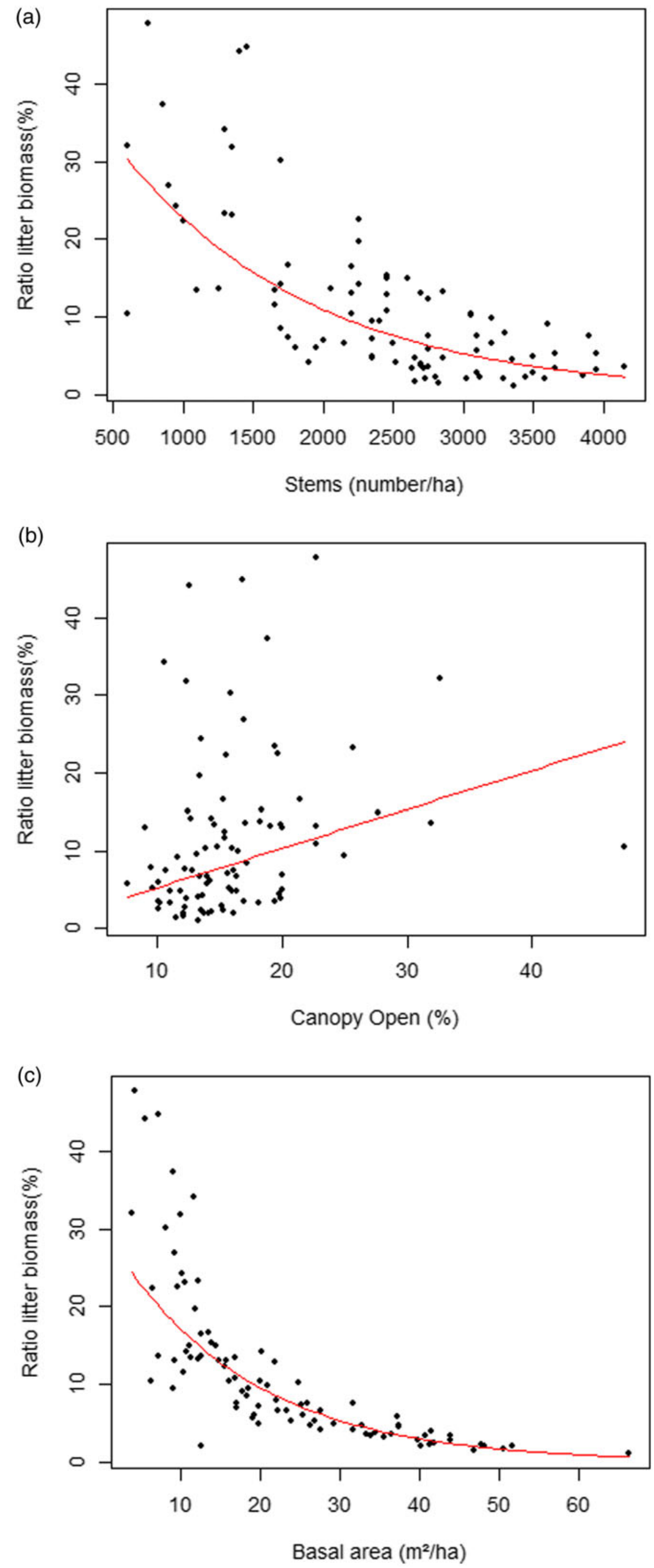

Figure 5. Relations between the ratio of annual litter production and total standing aboveground biomass and structural variables: (a) stems (number/ha), (b) basal area (m^2/ha) and (c) percentage of canopy open.

biogeochemical cycles, in addition to representing an improvement of chemical, physical and biological properties of the soil (León & Osorio 2014, Sánchez-Silva et al.2018). Our results highlight the fundamental role of another ecosystem service provided by litter production, as a carbon reservoir in tropical forests, especially in young secondary forests, just as it has been reported for woody debris by Yang et al (2021), who demonstrated that these woody debris store carbon and delay the release of CO_2 to the

https://doi.org/10.1017/S0266467422000281 Published online by Cambridge University Press

atmosphere after tree mortality in Amazon and African forests. In general, our results showed that litter production increases with the development of the forest structure, stabilizing at age 40 and that annual litter production represents an important biomass reservoir in the early stages of succession, reaching 47% of the AGB.

Our results demonstrated the importance of conserving secondary forests, mainly by the storage of carbon in litter maintaining some ecosystem services. These services can contribute to the regeneration of modified environments, such as the maintenance of soil microclimate and nutrient cycling that are essential for areas in the initial stage of succession (Guendehou et al. 2014). This highlights the importance of understanding how litter affects the carbon balance of tropical ecosystems. The flows of these carbon storage components should be considered in future work, further improving our forecasts of regional carbon dynamics in future climate scenarios. The results should also be used in conservation strategies with the quantification of litter as a place for carbon storage, contributing as an ecosystem service and mitigating climate change and REDD +.

Acknowledgements. JISR received a doctoral scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. And I thank the discipline Data Analysis and Writing of Scientific Manuscripts and Dr. Larissa Rocha for the collaboration in the manuscript.

Financial support. This work was supported by the Fundo Brasileiro para a Biodiversidade (Funbio) and Humanize Institute (grant number: 111/2019)

Competing interests. The authors declare none.

Ethical statement. None.

References

Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C and Franco M (2013) Functional traits explain variation in plant life history strategies. *PNAS* **111**, 740–745.

Aguiar APD, Vieira ICG, Assis TO, Dalla-Nora EL, Toledo PM, Santos-Junior RAO, Batistella M, Coelho AS, Savaget EK, Aragão REOC, Nobre CA and Ometto JPH (2016) Land use change emission scenarios: anticipating a forest transition process in the Brazilian Amazon. *Global Change Biology* **22**, 1821–1840.

Alves LF, Vieira SA, Scaranello MA, Camargo PB, Santos FAMC, Joly A and Martinelli LA (2010) Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecological Management* **260**, 679–691.

Amatangelo KL, Dukes JS and Field CB (2008) Responses of a California annual grassland to litter manipulation. *Journal of Vegetation Science* **19**, 605–612.

An JY, Han SH, Youn WB, Lee SI, Rahman A, Dao HTT, Seo JM, Aung A, Choi H, Hyun HJ and Park BB (2019) Comparison of litterfall production in three forest types in Jeju Island, South Korea. *Journal of Forestry Research* **31**, 945–952.

Barlow J, Gardner TA, Ferreira LV and Peres CA (2007) Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. *Forest Ecological Management* **247**, 91–97.

Bates D, Maechler M, Bolker B and Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48.

Berg B and Mcclaugherty C (2014) *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*. Berlin Heidelberg: Springer Verlag.

Bond-Lamberty B and Thomson A (2010) Temperature-associated increases in the global soil respiration record. *Nature* **464**, 579–582. doi: 10.1038/nature08930

Brown S and Lugo AE (1990) Tropical secondary forests. *Journal of Tropical Ecology* **6**, 1–32.

Cairns MA, Brown S, Helmer EH and Baumgardner GA (1997) Root biomass allocation in the world's upland forests, *Oecologia*, **111**, 1–11.

Camargo M, Giarrizzo T and Jesus AJS (2015) Effect of seasonal flooding cycle on litterfall production in alluvial rainforest on the middle Xingu River (Amazon basin, Brazil). *Brazilian Journal Biology* **75**, 250–256.

Carrera AL, Bertilier MB and Larreguy C (2008) Leaf litter fall, fine root production, and decomposition in shrub lands with different canopy structure induced by grazing in the Pantagonian Monte, Argentina. *Plant and Soil* **311**, 39–50. doi: 10.100711104-008-9655-8

Chakravarty S, Rai P, Vineeta V, Pala NA and Shukla G (2019) *Litter Production and Decomposition in Tropical Forest*. In Bhadouria R, Tripathi S, Srivastava P, Singh P (eds), *Handbook of research on the conservation and restoration of tropical dry forests*, India: IGI Global Publisher. https://doi.org/10.4018/978-1-7998-0014-9-ch010

Chave J, David C, Steven J, Simon LL, Nathan GS and Amy EZ (2009) Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman MHRC, Martínez-Yrízar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Pélissier R, Ploton P, Ryan CM, Saldarriaga JG and Vieilledent G (2014) Improved pantropical allometric models to estimate the aboveground biomass of tropical forests. *Global Change Biology* **72**, 763–768. doi: 10.1111/gcb.12629

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N, Quested HM, Santiago LS, Wardle DA, Wright IJ, Aerts R, Allison SD, Van Bodegom P, Brovkin V, Chatain A, Callaghan TV, Díaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J, Reich PB, Soudzilovskaia NA, Vaieretti MV and Westoby M (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**, 1065–1071. http://dxdoi.org/10.1111/j.1461-0248.2008.01219.x

Cortez J, Garnier, E, Pérez-Harguindeguy N, Debussche M and Gillon D (2007) Plant traits, litter quality and decomposition in a Mediterranean old-field succession. *Plant Soil* **296**, 19–34.

Craven D, Hall JS, Berlyn GP, Ashton MS and van Breugel M (2015) Changing gears during succession: shifting functional strategies in young tropical secondary forests. *Oecologia* **179**, 293–305.

Devi AF and Garkoti SC (2013) Variation in evergreen and deciduous species leaf phenology in Assam, India. *Trees* **27**, 985–997. https://doi.org/10.1007/s00468-013-0850-8

Eichenberg D, Trogisch S, Huang Y, He JS and Bruelheide H (2014) Shifts in community leaf functional traits are related to litter decomposition along a secondary forest succession series in subtropical China. *Journal Plant Ecology* **8**, 401–410.

Eisenhauer N, Milcu A, Sabais ACW, Bessler H, Weigelt A, Engels C and Scheu S (2009) Plant community impacts on the structure of earthworm communities depend on season and change with time. *Soil Biology and Biochemistry* **41**, 2430–2443. https://doi.org/10.1016/j.soilbio.2009.09.001

Ewel JJ (1976) Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *Journal of Ecology* **64**, 293–308.

Facelli JM and Pickett STA (1991) Plant litter: its dynamics and effects on plant community structure. *The Botanical Review* **57**, 1–32.

Garnier E, Cortez J, Billes G, Navas M, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C and Toussaint J (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**, 2630–2637.

Guendehou GHS, Liski J, Tuomi M, Moudachirou M, Sinsin B and Makipaa, R (2014) Decomposition and changes in chemical composition of leaf litter of five dominant tree species in a West African tropical forest. *Tropical Ecology* **55**, 207–220.

Houghton RA, Hall F and Goetz, SJ (2009) Importance of biomass in the global carbon cycle. *Journal of Geophysical Research* **114**, 203–216.

Jackson BG, Peltzer DA and Wardle DA (2013) Are functional traits and litter decomposability coordinated across leaves, twigs and wood? A test using temperate rainforest tree species. *Oikos* **122**, 1131–1142.

Krishna MP and Mohan H (2017) Litter decomposition in forest ecosystems: a review. *Energy. Ecology & Environment* **2**, 236–249.

Kunhamu TK, Kumar BM and Viswanath S (2009) Does thinning affect litterfall, litterdecomposition, and associated nutrient release in *Acacia mangium*-*stands* of Kerala inpeninsular India? *Canadian Journal Forest Research* **39**, 792–801.

Kuruvilla T, Jijeesh CM and Seethalakshm KK (2016) Litter production and decomposition dynamics of a rare and endemic bamboo species Munrochloa ritcheyi of Western Ghats, India. *Tropical Ecology* **57**, 601–606.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017). "lmer test package: tests in linear mixed effects models. *Journal of Statistical Software* **82**, 1–26.

León JD and Osorio NW (2014) Role of litter turnover in soil quality in tropical degraded lands of Colombia. *The Scientific World Journal*, **2014**: 11 pages. https://doi.org/10.1155/2014/693981

Li Y and Ye Y (2014) Dynamics of decomposition and nutrient release of leaf litter in *Kandelia obovata* mangrove forests with different ages in Jiulongjiang Estuary, China. *Ecological Engineering* **73**, 454–460. doi: 10.1016/j.ecoleng.2014.09.102

Lowman MD and Schowalter TD (2012) Plant science in forest canopies – the first 30 years of advances and challenges (1980–2010). *New Phytologist* **194**, 12–27. doi: 10.1111/j.1469-8137.2012.04076.x

Majila BS, Joshi GC and Kala CP (2005) Patterns in litter fall and litter decomposition along an altitudinal gradient in the Binsar Wildlife Sanctuary, Central Himalaya. *The International Journal of Sustainable Development & World Ecology* **12**, 205–212.

Montagnini F and Jordan CF (2002) Nutrient recycling. In Guariguata MR and Kattan GH (eds), *Ecology and conservation of neotropical forests*. Cartago: Libro Universitario Regional, pp. 167–191.

Nickmans H, Jonarda M, Verheyen J and Ponette Q (2019) Modelling leaf dispersal and nutrient return in tree species mixtures. *Forest Ecology and Management* **436**, 68–78.

Ostertag R, Marın-Spiotta E, Silver WL and Schulten J (2008) Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. *Ecosystems* **11**, 701–714.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, Mcguire AD, Piao S, Rautiainen A, Sitch S and Hayes D (2011) A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993.

Pandey RR, Sharma G, Tripathi SK and Singh AK (2007) Litterfall, litter decomposition and nutrient dynamics in a subtropical natural oak forest and managed plantation in northeastern India. *Forest Ecology Management* **240**, 96–104.

Patoine G, Thakur MP, Friese J, Nock C, Hönig L, Haase J, Scherer-Lorenzen M and Eisenhauer N (2017) Plant litter functional diversity effects on litter mass loss depend on the macro-detritivore Community. *Pedobiologia – Journal of Soil Ecology* **65**, 29–42.

Parton W, Silver WL, Burke IC, Grassens L, Harmom ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC and Fasth B (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* **315**, 361–364.

Piotto D, Montagnini F, Thomas W, Ashton M and Oliver C (2009) Forest recovery after Swidden cultivation across a 40-year chronosequence in the Atlantic forest of southern Bahia, Brazil. *Plant Ecology* **205**, 261–272.

Poggiani F (2012) Nutrient cycling in Brazilian forestsl. In Martins SV (ed), *Ecologia de Florestas Tropicais do Brasil*. Viçosa: Editora UFV, pp. 175–251.

Poorter L and Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**, 1733–1743.

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rawat N, Nautiyal BP and Nautiyal MC (2010) Litter decomposition rate and nutrient release from different litter forms in a Himalayan alpine ecosystem. *The Environmentalist* **30**, 279–288. doi: 10.100710669-010-9275-8

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

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275–301.

Reich PB, Tjoelker MG, Pregitzer KS, Wright IJ, Oleksyn J and Machado JL (2008) Scaling of respiration to nitrogen in leaves, stems, and roots of higher land plants. *Ecology Letters* **11**, 793–801.

Rozendaal DMA and Chazdon RL (2015) Demographic drivers of tree biomass change during secondary succession in northeastern Costa Rica. *Ecological Society of America* **25**, 506–516.

Sánchez-Silva S, De Jong BHJ, Aryal DR, Huerta-Lwanga E and Mendoza-Vega J (2018) Trends in leaf traits, litter dynamics and associated nutrient cycling along a secondary successional chronosequence of semi-evergreen tropical forest in South-Eastern Mexico. *Journal of Tropical Ecology* **34**, 364–377. doi: 10.1017/S0266467418000366

Santos FM, Terra G, Chaer GM, Monte MA (2018) Modeling the height–diameter relationship and volume of young African mahoganies established in successional agroforestry systems in northeastern Brazil. *New For*. doi: 10.1007/s11056-018-9665-1

Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems, *Biology Review* **81**, 1–31.

Sayer EJ, Powers JS and Tanner EVJ (2007) Increased litterfall in tropical forests boosts the transfer of soil CO2 to the atmosphere. *PLoS ONE* **2**, 10.

Schumacher MV, Truby P, Marafiga JM, Viera M and Szymczak DA (2011) Predominant species in litter deposition in a seasonal deciduous forest fragment in Rio Grande do Sul. *Ciência Florestal* **21**, 479–486.

Schwarz B, Dietrich C, Cesarz S, Scherer-Lorenzen M, Auge H, Schulz E and Eisenhauer N (2015) Non-significant tree diversity but significant identity effects on earthworm communities in three tree diversity experiments. *European Journal of Soil Biology* **67**, 17–26. doi: 10.1016/j.ejsobi.2015.01.001

Silver WL, Hall SJ and González G (2014) Differential effects of canopy trimming and litter deposition on litterfall and nutrient dynamics in a wet subtropical forest. *Forest Ecology Management* **332**, 47–55.

Thomas WW (2003) *Natural vegetation types in southern Bahia*. In Prado PI, Landau EC, Moura RT, Pinto LPS, Fonseca GAB and Alger K (orgs), *Biodiversity Corridor of the Atlantic Forest of Southern Bahia*. Ilhéus: Publicação em CD-ROM, IESB/CI/CABS/UFMG/UNICAMP.

Tripathi SK, Sumida A, Shibata H, Ono K, Uemura S, Kodama Y and Hara T (2006) Leaf litterfall and decomposition of different above- and belowground parts of birch (Betula ermanii) trees and dwarf bamboo (Sasa kurilensis) shrubs in a young secondary forest in Northern Japan. *Biology and Fertility of Soils* **43**, 237–246.

USDOE (2010) *Climate Research Roadmap Workshop: Summary Report*. U.S. Department of Energy Office of Science.

van Breugel M, Martınez-Ramos M and Bongers F (2006) Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology* **22**, 663–674.

Vidal MM, Pivello VR, Meirelles ST and Metzger JP (2007) Litter production in secondary Atlantic forest in a fragmented landscape (Ibiúna, SP): importance of the edge and size of the fragments. *Revista Brasileira de Botânica* **30**, 521–532.

Vitousek P and Sanford RL (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* **17**, 137–167.

Wardle DA, Bardgett RD, Klironomos JN, Setalã H, van der Putten WH and Wall DH (2004) Ecological linkages between aboveground and belowground biota. *Science* **304**, 1629–1633.

Werneck MS, Pedralli G and Gieseke LF (2001) Litter production in three stretches of a semideciduous forest with different degrees of disturbance in the Ecological Station of Tripuí, Ouro Preto, MG. *Revista Brasileira de Botânica* **24**, 195–198.

Zanne AE, Lopez-Gonzalez G, Coomes DA, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC and Chave J (2009) *Global Wood Density Database*. Dryad Identifier. http://hdl.handle.net/10255/dryad.235

Zhou G, Guan L, Wei X, Zhang D, Zhang Q, Yan J, Wen D, Liu D, Liu S, Huang Z, Kong G, Mo J and Yu Q (2007) Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China. *Plant Ecology* **188**, 77–89.

Zhou G, Shan Xu, Ciais P, Manzoni S, Fang J, Yu G, Tang X, Zhou P, Wang W, Yan J, Wang G, Ma K, Li S, Du S, Han S, Ma Y, Zhang D, Liu J, Liu S, Chu G, Zhang Q, Li Y, Huang W, Ren H, Lu X and Chen X (2019) Climate and litter C/N ratio constrain soil organic carbon accumulation. *National Science Review* **6**, 746–757.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. New York: Statistics for Biology and Health.

Yang H, Ciais P, Chave J, Huang Y, Ballantyne AP, Yu K, Berzaghi F and Wigneron JP (2021) Coarse woody debris are buffering mortality-induced carbon losses to the atmosphere in tropical forests. *Environmental Research Letters* **16**, 011006.

https://doi.org/10.1017/S0266467422000281 Published online by Cambridge University Press