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REGULAR ARTICLE

Site and plant community parameters drive the effect of vegetation on litterfall and nutrient inputs in restored tropical forests

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Abstract

Background and aims Restoring healthy ecosystem depends on recovering not only biodiversity, but also ecosystem processes and functionality. We investigated the effects of tree community parameters and site abiotic conditions on nutrient cycling in restored forests.

Methods We assessed litter production and nutrient inputs in five 16-year old restored forests established using different restoration methods and species combinations, i.e. unplanted control (natural regeneration), direct seeding, agroforestry, mixed commercial species plantation (commercial mix), and high-diversity plantation, replicated at two sites that differed in soil fertility. We used adjacent seasonal semideciduous forest remnants as references.

Results Restoration treatments with intermediate and high species richness had higher litter and nutrient inputs and did not differ from the reference forest. In the more fertile site, litter and nutrient inputs increased across different treatments with increasing stand density, whereas in the low fertility site, litter and nutrient inputs in the different treatments increased with increasing tree species richness and the proportion of putative nitrogen-fixing tree species.

Conclusions Restoration treatments, even those with low species richness, but with a relatively high proportion of trees with nitrogen-fixing capability might be effective in restoring nutrient cycles in lower fertility soils, whereas in the more fertile soils it is possible to increase nutrient inputs by establishing restoration treatments at high stem densities. Our results suggest that the magnitude of relationships among plant community parameters and nutrient cycling depends strongly on site conditions.

Keywords Nutrient cycling · Ecological restoration · Tropical seasonal forest · Species richness · Nitrogen-fixing tree · Litterfall · Atlantic forest

Introduction

The effects of biodiversity on ecosystem functioning is a topic of increasing interest over the past three decades,

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mainly due to the negative effects that biodiversity loss can cause to ecosystems services (Hooper et al. 2005), and therefore to human well-being (Cardinale et al. 2012; Tilman et al. 2014). Biodiversity is considered the major determinant of ecosystems productivity (Tilman et al. 2014; Guerrero-Ramírez et al. 2017; Huang et al. 2018a) and their loss within communities can reduce the biomass production, organic matter decomposition and nutrient recycling (Cardinale et al. 2012).

Nutrient cycling is a key aspect of ecosystem functioning that can be regulated by multiple factors, both biotic and abiotic. Litterfall accounts for up to 41% of annual net primary production in old-growth tropical forests (Chave et al. 2010), representing the main pathway for transfer of carbon and mineral elements from vegetation to the soil surface (Vitousek and Sanford 1986; Aragão et al. 2009), thereby recycling nutrients for plant growth. Studies in forest ecosystems have highlighted major effects of soil properties (e.g. soil fertility) on litter production and nutrient inputs (Vitousek 2004; Dent et al. 2006; Fyllas et al. 2009; Chave et al. 2010). Furthermore, litter and nutrient inputs in forests depend on climate, and forest physiognomy, as well as vegetation attributes, such as forest age, species composition and forest structure (Vitousek and Sanford 1986; Facelli and Pickett 1991; Clark et al. 2001; Martinelli et al. 2017). During forest succession, development of stand structural components (e.g. plant height, density and basal area) and species diversity usually increase (Marques et al. 2014), positively affecting litter production (Martinelli et al. 2017). Although the factors that affect nutrient dynamics have been well studied in tropical forests (Clark et al. 2001; Chave et al. 2010), few studies have examined these dynamics, the effects of species richness, or their interactions and relative importance, in mixed plantations commonly used for forest restoration (Celentano et al. 2011; Lanuza et al. 2018; Huang et al. 2018a; Huang et al. 2018b).

Plant functional traits at the community level have been reported to affect ecosystem properties (Lavorel 2013). For instance, positive effects of nitrogen-fixing tree species on litter production and nutrient cycling have been reported in the literature (Santana et al. 2009; Celentano et al. 2011; Hoogmoed et al. 2014), as have the positive effects of nitrogen-fixing tree species on soil carbon and nutrient pools (Macedo et al. 2008; Wang et al. 2010; Hoogmoed et al. 2014; Winbourne et al. 2018). The phenology of tree species also can affect community-level litterfall and nutrient cycling patterns. For example, deciduous species (drought-avoiding) drop all their leaves during the dry season to reduce water loss (Tomlinson et al. 2013), have higher values of specific leaf area (Somavilla et al. 2014) and higher leaf nutrient content (Chen et al. 2013; Somavilla et al. 2014; Rossato et al. 2015). Thus, we expect positive effects of deciduous plants on litterfall nutrient inputs to the forest floor. Knowledge about how diversity (i.e. species and functional diversity) and vegetation structure affect ecosystem functioning (i.e. nutrient cycling) can guide restoration practices. Although studies testing mixture of species have shown positive effects of species richness on nutrient cycling (Peng et al. 2016; Huang et al. 2018a; b), other studies did not find such a relationship (Scherer-Lorenzen et al. 2007; Gazell et al. 2012; Duarte 2018), demonstrating the lack of consensus in the literature regarding the relationships between species richness and litter production.

In the restoration of tropical forests, although high-diversity plantings have been advocated (Naeem 2006; Rodrigues et al. 2009; Lamb 2012), some studies have demonstrated that a smaller number of planted species (e.g. the framework species method; Lamb et al. 1997) can also be used to kick off natural succession and speed up the natural regeneration, assuming there is a potential for natural increase of species over time (Lamb et al. 2005; Durigan et al. 2010; Durigan and Engel 2012). In this case, the combination of functional traits of planted species should be such as to drive positive feedbacks on the ecosystem dynamics, in a way to recover its functioning (Lamb et al. 2005; Celentano et al. 2011; Pontes et al. 2019). As a result, we can hypothesize that some minimum vegetation diversity and structure (e.g. species richness, composition, individual's density and basal area) is needed to ensure the functioning of healthy ecosystems (Naeem 2006; Wright et al. 2009). Considering the need of producing a high number of native tree species in nurseries (Silva et al. 2014), the possibility of using a minimum set of species which will guarantee optimum ecosystem functioning, instead of restoring the whole set of species of a reference ecosystem (Naeem 2006; van Andel and Grootjans 2006; Celentano et al. 2011), would be of relevant interest for forest restoration practice (Engel 2011). However, this hypothesis is still open to debate, due to the lack of enough experimental evidence in forest ecosystems, since most studies examining this question have been carried out in herbaceous communities (Isbell et al. 2015).

To understand how site characteristics and restoration strategies affect aspects of nutrient cycling, we studied a long-term ecological restoration experiment established in 1997 at two sites with contrasting soil conditions and using different forest restoration systems designed for the Atlantic Forest region in Brazil. Our aim was to examine how site and vegetation attributes interact in affecting selected ecosystem functions, namely litter production and nutrient inputs. Specifically, we tested whether: 1) litter production and nutrient content will be higher in restored forests on the more fertile soil; 2) litter and nutrient inputs will increase with tree species richness, the proportion of putative nitrogen-fixing trees and the proportion of deciduous species (% individuals); and 3) litter production and nutrient inputs of 16-year-old restored forests will be similar to reference forest and higher than unplanted (passive restoration system) plots.

Materials and methods

Study area

The study area is located in Botucatu, in the south-central region of São Paulo state, Brazil (22°52′32” S; 48°26′46” W) (Supplementary Material). The climate is classified as subtropical, wet, and hot (Alvares et al. 2013). Annual rainfall average is 1428.4 mm, 75% of which concentrated between the months of October to March (Cunha and Martins 2009). Annual mean temperature is 20.5 °C, and the minimum average occurring in July (17.1 °C) and maximum in February (23.1 °C) (Cunha and Martins 2009). The original natural vegetation cover is classified as tropical seasonal semideciduous forest within the Atlantic Forest biome range (IBGE 2012). According to the “Technical Manual of Brazilian Vegetation” (IBGE 2012), the tropical seasonal semideciduous forest is conditioned by the climatic seasonality, where around 20–50% of the canopy trees shed their leaves during the drier winter.

Experimental design, treatments description and implementation

The design included two experimental sites with contrasting soil properties (Table 1) and landscape context. In Site 1, the soil is a fertile loamy Ultisol (Soil Survey Staff 2014), with an elevation of 700 m (22°49′38” S; 48°25′55” W). It is surrounded by pastures, scattered forest fragments and is around 10 m away from a disturbed riparian forest. Site 2 is characterized by relatively low fertility and sandy Alfisol (Soil Survey Staff 2014), with an elevation of 547 m (22°48′54” S; 48°24′56” W). It is located 50 m away from a late-successional, relatively undisturbed forest remnant.

At each site, a complete randomized block design with three replicates (blocks) and five restoration systems (treatments) was set up in 1997/1998, with 50 × 50 m plots: 1) Control (CON): passive restoration, with no planting nor maintenance interventions; 2) Direct seeding (DSE): direct sowing of five fast growth early-successional tree species); 3) Modified “Taungya” agroforestry system (AGR): included mixed species tree plantings established in triple rows (spacing 1.5 m × 2 m) interspaced by 5 m width alleys, where annual crops were cultivated until canopy closure (at 4–5 years). Within the triple rows, the two outer rows consisted of 10 leguminous multipurpose fast-growing tree species. In the inner rows, 10 slow-growing commercially valuable timber species were planted; 4) Commercial mix (MIX): consisted of a mixture of commercial timber and firewood tree species grown in alternating rows with 10 fast-growing firewood species and 15 slow-growing timber species. This system was similar to the AGR system, but without the 5 m crop alleys; 5) High-diversity system (DIV): a mixture of 40 semideciduous tropical forest native species belonging from different ecological groups. A list of the planted species in each treatment is provided in the Supplementary Material.

Before the establishment of the experiment, both sites were abandoned pasture and crop lands, and were covered with exotic invaders grasses, mainly 2 m-tall *Pennisetum purpureum* in Site 1 and 0.5 m-tall *Urochloa decumbens* in Site 2. They were mechanically roto-tilled (Site 1) and mowed (Site 2) and sprayed with post-emergence herbicide (glyphosate) after grass resprouting. For the direct seeding treatment, site preparation involved minimal tillage, using a soil ripper attracted to a tractor to mark the planting lines. Sowing was made during the summer (in February) of 1997; seeding was done manually at 1 × 1 m spacing and 5 cm depth, using 2–4 seeds per planting spot. Each species was planted in separate rows. Maintenance operations (chemical and manual weeding, and leaf-cutting ant control using bait traps) were undertaken at 30, and 90 days after sowing, and afterwards two to three-

Table 1 Soil properties (mean values) in Site 1 (Ultisol) and Site 2 (Alfisol) for the restoration treatments (DSE: direct seeding; AGR: agroforestry; MIX: commercial mix; DIV: high-diversity), unplanted control (CON) and reference forest (REF), 16 years after the experiment establishment, Botucatu, São Paulo, Brazil

	pH	P_{resin}	TN	TC	S.B.	CEC	BS	Sand	Clay	Silt
	($CaCl_2$)	(g cm^{-3})	(g kg^{-1})	(g kg^{-1})	----($cmol_c$ dm^{-3})----		(V %)	-------------(%)-------------		
Site 1										
DSE	5.14	8.55	2.06	22.93	91.19	134.71	66.32	19.7	50.5	29.8
AGR	5.44	11.00	1.84	19.42	101.27	138.36	72.10	20.9	49.3	29.8
MIX	5.12	15.92	2.35	27.13	99.10	149.46	65.40	18.9	47.2	33.9
DIV	5.20	12.31	2.04	24.07	111.91	156.59	70.23	21.7	47.6	30.7
REF	5.62	16.99	3.13	32.63	186.60	221.20	83.47	26.0	33.3	40.7
Site 2										
CON	4.57	8.42	0.50	5.06	25.07	48.41	50.38	90.5	7.2	2.3
DSE	4.27	7.20	0.50	4.75	24.52	54.08	44.95	90.8	7.7	1.5
AGR	4.08	9.07	0.49	4.72	19.25	55.07	34.48	89.3	8.6	2.1
MIX	4.09	7.15	0.47	4.54	16.24	53.90	30.46	90.6	8.1	1.3
DIV	4.90	7.26	0.57	5.25	30.50	50.40	57.58	92.1	5.9	2.0
REF	5.06	11.70	0.69	6.31	51.11	76.65	60.11	91.7	6.4	1.9

Soils were collected to 20 cm depth in March of 2013; pH: potential of hydrogen; P_{resin} (phosphorus). van Raij et al. 2004; TN: total nitrogen and TC: total carbon (dry combustion method (CHNS/O; Perkin Elmer, Norwalk, CT, USA); SB: sum of bases; CEC: cation exchange capacity (van Raij et al. 2004); BS: base saturation; Texture (sand, clay and silt; EMBRAPA 1997)

times a year, during the first 3–4 years, and whenever necessary for the following years until canopy closure. After sowing, no other planting was undertaken in this treatment. By the time of this study, only two out of the five planted species succeeded and dominated the canopy, but an understory composed by naturally regenerated shrub, liana and tree species was already established (Supplementary Material, for tree species).

In all the other treatments apart from the control plots, nursery-raised seedlings, produced in root trainers, were outplanted one year after the direct seeding treatment (i.e. in January 1998). Weed control before planting was the same as in the direct seeding treatment, but conventional harrowing and plowing were used for site preparation for planting, instead of minimal tillage, due to operational constraints. No fertilization was done, except for the annual crops' alleys in the agroforestry treatment. Chemical and/or mechanical weeding was undertaken at least twice a year, during the first 4–5 years, as well as leaf-cutting ant control. Weeding was focused only on the exotic invader grasses, while all other regenerating species were left on site. In the agroforestry treatment, annual crops were established, starting with beans in the first and second year, corn and pumpkin in the third and fourth. Fertilization was done only in the crop alleys, following agronomic recommendation for each soil type and crop species. After the canopy closure, at 6 years, a mix of native fruit and medicinal tree species were planted in the former crop alleys, respectively in Site 1 and 2. Further details are provided in Podadera et al. (2015) and Pontes et al. (2019).

We also monitored a native forest reference ecosystem (REF) close to each experimental area. Three 50 × 50 m permanent plots were located in the reference fragments. In Site 1, we evaluated a disturbed riparian forest around 1 km away from the experimental area, because the forest closest to the experiment included numerous rock outcrops in the upper soil layers which could affect the sampling of other soil attributes that were also evaluated in another study of ours (e.g. soil fauna and soil carbon storage, in preparation). In Site 2, we sampled a late-successional remnant forest located 50 m away from the experiment.

Sampling and data collection

In each plot (including the reference forests), a 30 × 30 m subplot was established within the 50 × 50 m plot for data collection, to avoid edge effects. The control plots in Site 1 were not analyzed due to the high dominance of tall grasses and absence of trees. The plots of agroforestry and commercial mix treatments were resized due to another study that was being undertaken simultaneously, testing the effect of *Mimosa caesalpiniifolia* Benth. trees removal (Podadera et al. 2015). We sampled two out of four (10 × 10 m) subplots within each plot which, for the AGR and MIX treatments corresponded to the ones without intervention.

Tree community parameters

In March 2012 all planted and regenerating trees at least 1.3 m tall in each subplot were identified and measured. The diameter at breast height (DBH) was measured with a diametric tape and the total height with a Haglöf Vertex IV hypsometer. Plant species richness was rarefied to random samples of 100 individuals. The species deciduousness category (deciduous: deciduous + brevideciduous, and non-deciduous: evergreen) was classified following a phenological study carried out in the same area by Homem et al. (unpublished data), complemented by information from Carvalho (2003, 2006, 2008, 2010), Prado-Júnior et al. (2014) and Giselda Durigan (personal communication) (Supplementary Material). The capability of tree species to fixing nitrogen (considered putative nitrogen-fixing in this study) was classified based on USDA. ARS, National Genetic Resources Program (Germplasm Resources Information Network - GRIN 2011), Faria et al. (2011) and Canosa et al. (2012) (Supplementary Material). We calculated per plot: stem density (ind ha^{-1}), basal area (m^2 ha^{-1}), rarefied species richness (number of species), proportion of deciduous species (% individuals) and proportion of putative nitrogen-fixing trees (% individuals).

Litterfall sampling

Litter was collected in each study plot, monthly from May 2012 to April 2013, using circular traps with 0.25 m^2 area, made with mosquito netting (voile fabric) funnels, attached to circular polyethylene frames and mounted on 80 cm tall wooden stakes. We randomly distributed two traps in each 10 × 10 subplot of the agroforestry and commercial mix treatments, and four traps in the control, direct seeding, high-diversity treatment and the reference forest. Litter mass was reported as dry weight (72 h at 65 °C) for every sampling. We computed the monthly weighted averages within each plot and estimated the annual production by totaling the 12 - monthly averages.

Nutrient inputs

Litter nutrient concentrations (g kg^{-1}) were analyzed in four time periods by pooling the monthly samples from each study plot: April–June 2012 (transition rainy to dry season); July–September 2012 (dry season); October–December 2012 (transition dry to rainy season) and January–March 2013 (rainy season). Total N was extracted by sulfuric acid digestion determined by the micro-Kjeldahl method. P, K, Ca and Mg were extracted by nitropercloric digestion, and P was determined by spectrophotometric with the molybdenum blue method (Malavolta et al. 1997). Annual litter nutrient inputs (kg ha^{-1} yr^{-1}) to the forest floor (referred hereafter as nutrient inputs) were quantified for each plot as the sum of the 12 monthly litterfall nutrient inputs, calculated using total litter production for each month multiplied by the nutrient concentrations determined for the respective 3-month period.

Data analysis

To assess the effects of site, restoration treatments and their interaction on tree community parameters, litter production and nutrient input (N, P, K, Ca and Mg) we used two-way ANOVA. The most parsimonious models were determined by sequential backward removal of non-significant terms ($p > 0.05$). The unplanted control plots in Site 1 were not analyzed due to the high dominance of tall grasses and absence of trees; thus, to compare annual litter production or nutrient inputs between restoration treatments and control in Site 2 we used one-way ANOVA. Multiple comparisons of means were performed using Tukey's HSD test and we considered $p \leq 0.05$ as significant. To compare annual litterfall production or nutrient inputs between restoration treatments and reference forest we used Student's t test ($p \leq 0.05$), since the reference forest was not part of the experimental design. We calculated the ratios of mean values of each variable (annual litter production and annual nutrient inputs) between each restoration treatment and, both, unplanted control [ln (Restoration treatment/Control)] and reference [ln (Restoration treatment/Reference)]. We used stepwise multiple regressions, to test the effect of tree community parameters (rarefied richness, stem density, stand basal area, proportion of individuals of deciduous and nitrogen-fixing tree species) on annual litter production and nutrient inputs. We tested the relationships among tree community parameters using variance inflation factors (VIF) (Zuur et al. 2010). We selected the best multiple regression models based on Akaike information criteria (AIC) (Burnham and Anderson 2002). We checked the homoscedasticity (Bartlett test) and normal distribution (Shapiro-Wilk test) of the residuals for each statistic model. All analyses were performed in R programming environment (R Core Team 2018) using the interface RStudio (RStudio Team 2016).

Results

Tree community parameters

Sixteen years after the experiment establishment, the main differences in plant community parameters among treatments were associated only with the planted trees (Supplementary Material). Sites and restoration treatments showed contrasting tree species richness, vegetation structure (basal area and stem density) and functional composition (deciduousness and N-fixing trees) (Table 2). Considering all treatments pooled together, rarefied species richness (100 individuals) was 23% higher in Site 1 ($F_{(1,17)} = 8.93$, $p = 0.0079$), but vegetation structure parameters and functional traits were similar between sites ($p > 0.05$). Rarefied species richness among restoration treatments ranged from 20 in the direct seeding to 30 in the high-diversity ($F_{(3,17)} = 4.27$, $p = 0.0192$). The latter was similar to reference forests' richness (28 in Site 1 and 34 in Site 2). Basal area was highest in direct seeding, and lowest in commercial mix; whereas high-diversity and agroforestry did not differ from the other treatments (Table 2) ($F_{(3,17)} = 6.18$, $p = 0.0045$). Proportion of deciduous species was lowest in high-diversity system ($F_{(3,17)} = 7.14$, $p = 0.0023$). Tree stem density ($F_{(3,17)} = 2.85$, $p = 0.0664$) and proportion of nitrogen-fixing ($F_{(3,17)} = 0.76$, $p = 0.53$) did not differ among treatments; however, tree stem density was two times higher in commercial mix than in high diversity. Putative nitrogen-fixing species was almost two time higher in agroforestry (25%) and commercial mix (23%) than in high-diversity

Table 2 Community parameters of planted and regenerating trees at least 1.3 m tall per site (Site 1 and 2) and per restoration system (DSE: direct seeding; AGR: agroforestry, MIX: commercial mix and DIV: high-diversity, CON: unplanted control), and for the reference forests (REF 1: reference at Site 1 and REF 2: reference at Site 2), 16 years after the experiment establishment, Botucatu, São Paulo, Brazil. Means (± SE) for each site were pooled across treatments and for each system pooled across sites, excluding controls (CON)

	Tree community parameters				
	Rarefied richness	Basal area (m^2 ha^{-1})	Stem Density (ind ha^{-1})	Deciduous (% individuals)	N-fixing (% individuals)
Site					
Site 1	$27.33^a \pm 1.84$	$22.28^a \pm 1.14$	$3612^a \pm 634$	$66.43^a \pm 2.70$	$16.32^a \pm 1.70$
Site 2	$21.08^b \pm 1.77$	$20.08^a \pm 2.60$	$3769^a \pm 526$	$60.56^a \pm 5.26$	$22.61^a \pm 5.79$
Treatment					
DSE	$19.83^b \pm 1.62$	$28.55^a \pm 2.35$	$2850^a \pm 748$	$69.35^a \pm 2.15$	$17.93^a \pm 3.34$
AGR	$23.66^{ab} \pm 3.90$	$20.39^{ab} \pm 2.05$	$4208^a \pm 936$	$72.03^a \pm 5.49$	$24.79^a \pm 8.86$
MIX	$23.17^{ab} \pm 2.59$	$15.30^b \pm 2.39$	$5217^a \pm 577$	$66.29^a \pm 3.94$	$22.66^a \pm 7.43$
DIV	$30.17^a \pm 0.96$	$20.47^{ab} \pm 1.75$	$2487^a \pm 521$	$46.31^b \pm 5.34$	$12.46^a \pm 2.33$
CON	10.37±0.53	3.01±1.21	1078±322	30.20±8.5	1.55±0.91
REF 1	27.55±0.47	29.79±8.93	6796±1600	84.77±1.7	11.10±0.90
REF 2	33.64±1.12	23.48±0.07	6318±925	74.90±1.8	1.09±0.31

Mean values ± SE. The same letters for the comparisons between sites or among restoration treatments are not significantly different at $p \leq 0.05$ (Tukey's HSD)

(~13%). The unplanted control treatment had lower values for all tree community parameters (Table 2) when compared to restoration treatments and reference forests.

The effects of site and restoration treatments on litter production and nutrient inputs

We found significant effects of site ($F_{(1,17)} = 21.45$, $p = 0.0002$) and restoration treatments ($F_{(3,17)} = 4.62$; $p = 0.0154$) on annual litter production (Fig. 1). Site 1 (higher fertility soil) produced 31% more litter than Site 2 (lower fertility soil) (Fig. 1a). The average annual litter production among restoration treatments, averaged across sites, was highest in high-diversity and lowest in direct seeding and agroforestry (Fig. 1b); however, commercial mix system did not differ from the other restoration treatments (Fig. 1b).

Nutrient concentrations and total litterfall nutrient inputs were significantly influenced by site ($p \leq 0.05$) and restoration treatments ($p \leq 0.05$) (Table 3). The concentrations of N ($F_{(1,17)} = 20.83$, $p < 0.001$), K ($F_{(1,17)} = 10.60$, $p = 0.0046$) and Ca ($F_{(1,17)} = 124.30$, $p < 0.001$), and the input of N ($F_{(1,17)} = 38.58$, $p < 0.001$), P ($F_{(1,17)} = 25.09$, $p < 0.001$), K ($F_{(1,17)} = 24.81$, $p < 0.001$) and Ca ($F_{(1,17)} = 124.09$, $p < 0.001$) was higher in Site 1 (Table 3). We found higher N concentrations ($F_{(3,17)} = 16.95$, $p < 0.001$) in the commercial mix and the agroforestry treatments (Table 3). The concentration of K ($F_{(3,17)} = 5.17$, $p = 0.0101$) was higher in the high-diversity, intermediate in the direct seeding and commercial mix treatments, and lower in the agroforestry treatment (Table 3). Ca concentration ($F_{(3,17)} = 3.06$, $p = 0.0562$) was higher in the high-diversity, intermediate in the direct seeding and agroforestry treatments, and lower in the commercial mix (Table 3).

Ca ($F_{(3,17)} = 7.09$, $p = 0.0027$) and Mg ($F_{(3,17)} = 5.88$, $p = 0.0061$) inputs were higher in high-diversity treatment (Table 3) and lower than in the other treatments. Annual P ($F_{(3,17)} = 12.48$, $p = 0.0001$) and K ($F_{(3,17)} = 7.60$, $p = 0.0019$) inputs were higher in the high-diversity, intermediate in the commercial mix and lower in direct seeding and agroforestry treatments (Table 3). Nitrogen inputs ($F_{(3,17)} = 4.33$, $p = 0.0192$) were highest in the commercial mix, and lowest in the direct seeding; whereas the agroforestry and the higher-diversity did not differ from the other treatments (Table 3).

The effects of tree community parameters on litter production and nutrient inputs

At Site 1 (higher fertility soil), tree stem density, basal area and proportion of deciduous species significantly affected the litter production and nutrient inputs ($p \leq 0.05$) (Table 4). Stem density positively affected N and K inputs (Table 4), while basal area negatively affected N input. Deciduousness negatively affected litter production, and P, K, Ca and Mg inputs. At Site 2 (lower fertility soil), our results indicated the positive effects of species richness and proportion of individuals of nitrogen-fixing species on all variables ($p \leq 0.05$) (Table 4). Furthermore, basal area and proportion of deciduous species influenced K input, with positive and negative effects, respectively (Table 4).

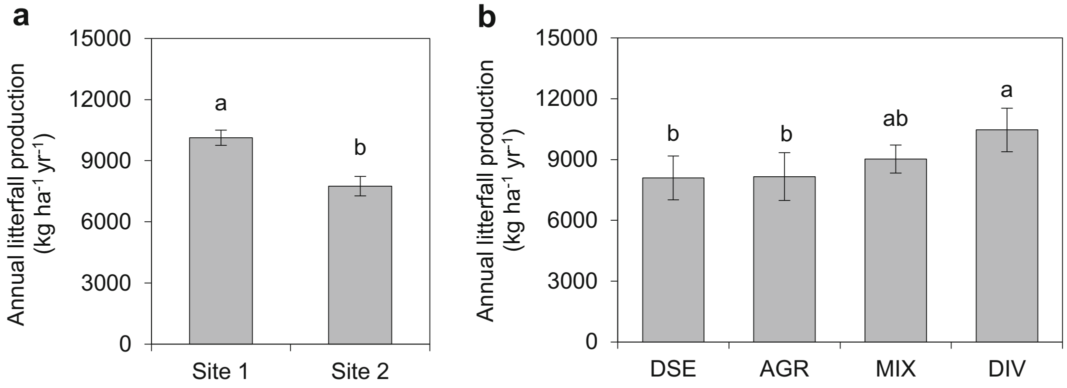

Fig. 1 Annual litterfall production (**a**) between sites and (**b**) among restoration treatments (mean values ± SE), 16 years after the experiment establishment, Botucatu, São Paulo, Brazil. Columns labeled with the same letter are not significantly different at $p \leq 0.05$ (Tukey's HSD)

Table 3 Nutrient concentrations (g kg^{-1}) and annual nutrient inputs (kg ha^{-1} yr^{-1}) between sites (Site 1: higher fertility; Site 2: lower fertility) and among restoration treatments (DSE: direct seeding; AGR: agroforestry, MIX: commercial mix and DIV: high-diversity), 16 years after the experiment establishment, Botucatu, São Paulo, Brazil

	Nutrient concentration				
	N (g kg^{-1})	P (g kg^{-1})	K (g kg^{-1})	Ca (g kg^{-1})	Mg (g kg^{-1})
Site					
Site 1	20.3^{a}±1.00	1.08^{a}±0.05	5.29^{a}±0.25	23.61^{a}±0.94	2.81^{a}±0.14
Site 2	17.5^{b}±0.49	1.02^{a}±0.05	4.34^{b}±0.30	13.31^{b}±0.67	3.13^{a}±0.12
Treatment					
DSE	17.7^{b}±0.77	0.94^{a}±0.06	4.69^{ab}±0.39	18.2^{ab}±4.07	2.85^{a}±0.34
AGR	20.7^{a}±1.37	1.02^{a}±0.09	4.03^{b}±0.50	18.4^{ab}±3.92	2.89^{a}±0.23
MIX	21.4^{a}±1.76	1.10^{a}±0.10	4.89^{ab}±0.68	16.7^{b}±3.05	2.83^{a}±0.20
DIV	15.9^{b}±0.67	1.14^{a}±0.09	5.64^{a}±0.56	20.6^{a}±3.14	3.33^{a}±0.26
	Amount of nutrient input				
	N (kg ha^{-1} yr^{-1})	P (kg ha^{-1} yr^{-1})	K (kg ha^{-1} yr^{-1})	Ca (kg ha^{-1} yr^{-1})	Mg (kg ha^{-1} yr^{-1})
Site					
Site 1	193.9^{a}±9.4	10.6^{a}±0.6	57.3^{a}±4.9	242.4^{a}±14.1	28.0^{a}±2.4
Site 2	131.3^{b}±8.1	7.92^{b}±0.7	35.5^{b}±3.8	106.1^{b}±10.1	24.7^{a}±1.9
Treatment					
DSE	134.8^{b}±19.2	7.34^{c}±0.9	39.9^{b}±7.3	163.5^{b}±52.6	21.8^{b}±3.4
AGR	167.3^{ab}±28.6	8.36^{bc}±1.6	35.2^{b}±8.1	154.1^{b}±41.5	23.8^{b}±3.8
MIX	185.6^{a}±27.3	9.61^{ab}±1.4	47.8^{ab}±10.6	156.7^{b}±39.5	25.1^{b}±1.5
DIV	162.8^{ab}±21.4	11.8^{a}±0.9	62.8^{a}±11.0	222.8^{a}±52.3	34.5^{a}±4.6

Mean values ± SE. The same letters for the comparisons between sites or among restoration treatments are not significantly different at $p \leq 0.05$ (Tukey's HSD)

Restoration treatments compared to the control and the reference forest

The reference forest produced 11,352 kg ha^{-1} yr^{-1} of litterfall in Site 1 and 11,718 kg ha^{-1} yr^{-1} in Site 2. Sixteen years after the experiment establishment, commercial mix ($t = -3.64$; $p = 0.0666$) and high-diversity treatments ($t = 0.41$; $p = 0.702$) produced litter biomass equivalent to the reference forest in the higher fertility soil (Site 1) (Fig. 2a); however, the direct seeding ($t = 4.00$; $p = 0.0161$) and the agroforestry treatments ($t = -3.96$; $p = 0.0166$) produced less litter than the reference. In Site 2, only in the direct seeding litter production was significantly lower than in the reference forest ($t = 3.57$; $p = 0.0233$) (Fig. 2b).

The comparison between unplanted control plots and restoration treatments in Site 1 was not possible due to the high dominance of tall grasses and absence of trees in these plots. In Site 2, litter production was 2048 kg ha^{-1} yr^{-1} in the unplanted control plots, which was significantly lower than all planted restoration systems, evidenced positive significant response ratios of litter (Fig. 2b) and all restoration treatments produced higher amounts of litter than in the unplanted control ($F = 10.49$; $p = 0.0029$).

Total nutrient inputs (kg ha^{-1} yr^{-1}) in Site 1 were generally higher in the reference forest than in the direct seeding and agroforestry treatments ($p \leq 0.05$) (Fig. 3a); whereas the inputs of P, K, Ca and Mg in the high-diversity and the inputs of P and K in the commercial mix were not significantly different to those in the reference forest ($p > 0.05$). In Site 2, the agroforestry, commercial mixed and high-diversity treatments nutrient inputs for N, P, Ca and Mg were similar to those in the reference forest (Fig. 3b). The direct seeding was the only treatment with lower nutrient inputs than the reference forest at this site (Fig. 3b). Potassium inputs were higher in the reference forest than in all other treatments in Site 2 ($p \leq 0.05$).

Table 4 Multiple stepwise regressions to test effects of rarefied species richness, basal area (m^2 ha^{-1}), stem density (ind ha^{-1}), and the proportion of deciduous (% of individuals) and nitrogen-fixing (% of individuals) on annual litter production (kg ha^{-1} yr^{-1}) and annual nutrient inputs (kg ha^{-1} yr^{-1}) for different forest restoration treatments, Botucatu, São Paulo, Brazil. Significant effects at $p \leq 0.05$ in bold

	Amount of litter and nutrient inputs											
	Litter		N		P		K		Ca		Mg	
	Slope	*p*	*Slope*	*p*	*Slope*	*p*	*Slope*	*p*	*Slope*	*p*	*Slope*	*p*
Site 1												
Richness	---	---	1.15	0.2805	0.12	0.1741	---	---	---	---	---	---
Basal area	---	---	-4.95	**0.0124**	---	---	---	---	---	---	---	---
Stem Density	---	---	0.013	**0.0058**	0.0005	0.0751	0.005	**0.0481**	---	---	---	---
Deciduous	-89.7	**0.0214**	-0.84	0.2819	-0.15	**0.0409**	-1.75	**0.0065**	-3.04	**0.0453**	-0.51	**0.0480**
N-fixing	---	---	2.13	0.1291	---	---	1.49	0.0923	---	---	---	---
	R^2=0.43		R^2=0.86		R^2=0.67		R^2=0.63		R^2=0.34		R^2=0.34	
Site 2												
Richness	424.8	**0.0012**	7.84	**0.0005**	0.58	**0.0125**	3.41	**0.0028**	10.36	**0.0137**	1.82	**0.0071**
Basal area	---	---	0.89	0.1697	0.086	0.2945	0.87	**0.0349**	2.84	0.0715	0.42	0.0876
Stem Density	---	---	---	---	---	---	---	---	-0.007	0.2360	---	---
Deciduous	---	---	0.36	0.2725	-0.049	0.2475	-0.42	**0.0459**	-1.06	0.1097	0.14	0.2369
N-fixing	136.1	**0.0009**	2.78	**0.0006**	0.19	**0.0162**	1.22	**0.0027**	4.03	**0.0170**	0.65	**0.0066**
	R^2=0.73		R^2=0.88		R^2=0.71		R^2=0.83		R^2=0.78		R^2=0.73	

The ratio of mean values of nutrient input among restoration treatments and unplanted control were all positive (Fig. 3c). All treatments had higher N, Ca and Mg inputs than the control; whereas P input was higher only at the high-diversity, and K input was higher at the high-diversity and commercial mix treatments, in comparison to the control (Fig. 3c).

Discussion

In this study, regardless of the site effects, the most species-rich restoration treatment (i.e. high-diversity), in general, produced the highest amounts of litter and nutrients. Furthermore, higher litter production and nutrient inputs were also related to a greater proportion of

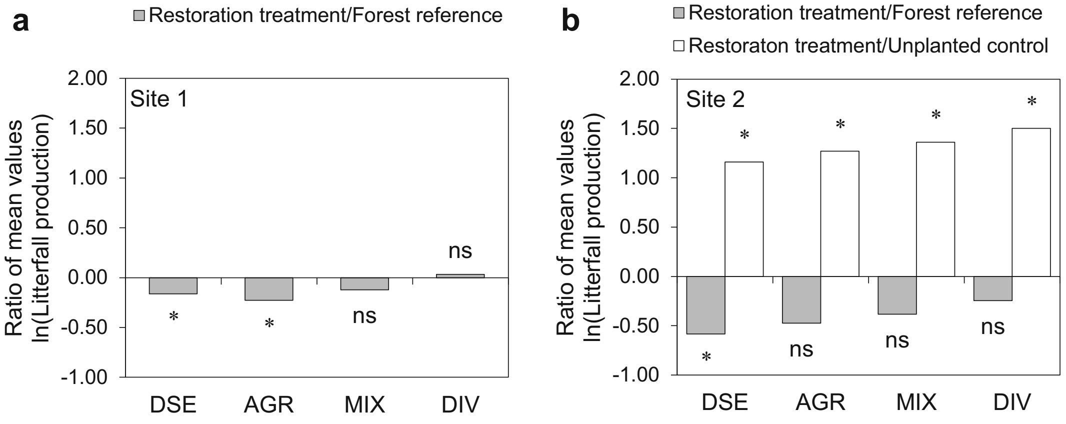

Fig. 2 Ratio of mean values of annual litterfall production (kg ha^{-1} yr^{-1}) of restoration treatments compared to reference forest [ln(Restoration treatment /Reference)] and restoration treatments compared to unplanted control [ln(Restoration treatment/Control)] in (**a**) Site 1 and (**b**) Site 2, Botucatu, São Paulo, Brazil. * represents significant differences ($p \leq 0.05$; ns: not significant) between original means of restoration treatments and reference (t test), and restoration treatments and control (Tukey's HSD). In Site 1 Control plots were not included due to the high dominance of tall grasses and absence of trees

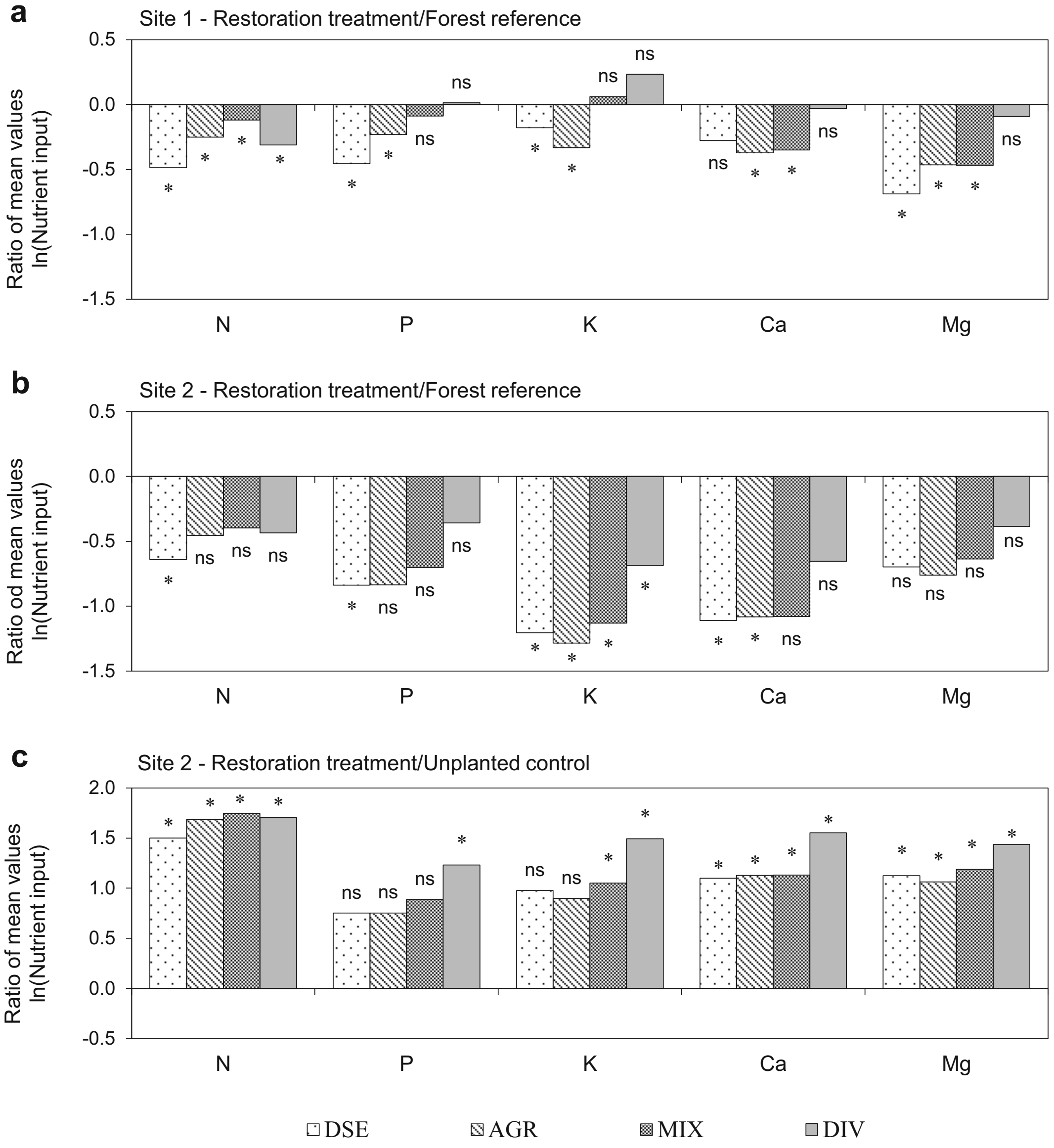

Fig. 3 Ratio of mean values of annual nutrient (kg ha^{-1} yr^{-1}) inputs of restoration treatments compared to reference forest [ln(Restoration treatment/Reference)] and restoration treatment compared to unplanted control [ln(Restoration treatment/Control)] in (**a**) Site 1 and (**b**, **c**) Site 2, Botucatu, São Paulo, Brazil. * represents significant differences ($p \leq 0.05$; ns: not significant) between original means of restoration treatments and reference (t test), and restoration treatments and control (Tukey's HSD). In Site 1 Control plots were not included due to the high dominance of tall grasses and absence of trees

individuals of putative nitrogen-fixing species (i.e. commercial mix treatment). Thus, our results indicated the importance not only of the species richness on the biogeochemical cycling of nutrients but also of some species' functional traits (e.g. nitrogen-fixing tree capability).

Site conditions differentially affected the relationships among plant species, therefore influencing the vegetation structure and functional parameters of the communities, which are responsible for nutrient cycling. In the higher fertility site, stem density was the most important community parameter related to nutrient inputs; however, in the lower fertility site, species richness and proportion of putative nitrogen-fixing species were the tree community parameters most strongly related to higher litter production and nutrient inputs.

Effects of site on litter production and nutrient inputs

Our results suggest strong effects of site conditions on litter production and nutrient inputs. These effects might have been mediated indirectly by the effects of soil conditions on vegetation (e.g. demographic process and biomass productivity of trees), as reported by van der Sande et al. (2017, 2018) and Guo et al. (2020). The effects of soil conditions on litter production and nutrient inputs agree with patterns described by Vitousek and Sanford (1986), in their extensive review about nutrient cycling in tropical rain forests from different regions of the world. Tissue nutrient concentrations increase with soil fertility because species use nutrients less efficiently (Hobbie 1992). Other studies found the same pattern, as Chave et al. (2010) for 81 sites in South America tropical forests, and Heineman et al. (2015), in Panamanian Lower Montane Forest.

Indeed, soil physical and chemical properties can affect all aspects of plant community development (Ehleringer and Sandquist 2006), including species survival and growth, and thus species filtering (Baker et al. 2003; Park et al. 2010; van Breugel et al. 2011; Li et al. 2014; van der Sande et al. 2018). This may consequently affect the plant community dynamics and nutrient cycling processes. Indeed, our results did indicate differences in species richness between sites (Table 2): species richness was higher in Site 1, although landscape context is more favourable in Site 2 (Pontes et al. 2019) (with larger areas of neighboring intact, diverse, native forests), suggesting that site factors might be important for species filtering from the local species pool (Hobbs and Norton 2004).

Litter production and nutrient inputs among restoration treatments

Litter production was much higher in the high-diversity treatment than in the direct seeding and agroforestry, whereas commercial mix produced intermediate amount of litter. In general, litter production in the high-diversity treatment appears to be associated with species richness, and intermediate values in commercial mix with proportion of nitrogen-fixing species, especially in Site 2 (with lower fertility soil).

The high-diversity treatment, established using a higher number of tree species belonging to different ecological and silvicultural groups, produced higher amounts of litter when compared to the less diverse direct seeding and agroforestry treatments. Similar patterns of positive species richness effects on litterfall and leaf-litter production were found in plantations with 1 to 16 species in subtropical China (Huang et al. 2018a; Huang et al. 2018b); while a higher litter production was observed in intermediate species richness treatments, varying from 1 to 6 species (Scherer-Lorenzen et al. 2007). Nevertheless, contrasting results regarding the effects of planted forest parameters structure and diversity on litter production have been reported elsewhere. The only comparable study in Brazil testing the effect of planted species richness (20, 60 and 120 tree species) on litter production found that 6 years after implementation, no differences among treatments were found (Gazell et al. 2012; Duarte 2018). Also, in a study comparing tree monocultures and mixed plantations (Montagnini 2000) and another comparing different restoration strategies (Celentano et al. 2011), both in Costa Rica, no effects of species richness on litter production were found; although Celentano et al. (2011) did find effects of tree density and canopy cover on litter production.

The commercial mix treatment, with intermediate species richness, produced the same amount of litter as the other treatments, due probably to the high population density of one single dominant putative nitrogen-fixing species (*M. caesalpiniifolia*). In fact, we did not find differences in litter production between the treatments with 40 (high-diversity) and 25 species (commercial mix). Complementary resources used by species might have been resulted from different functional traits of the high-diversity system, hence increasing litter production (Huang et al. 2018b). On the other hand, the equivalent litter production of the commercial mix treatment can suggest a selection effect of *M. caesalpiniifolia,* given the potential of this species in fixing nitrogen (Reis-Júnior et al. 2010) and its ability of producing high amounts of leaf biomass (Fernandes et al. 2006; Ferreira et al. 2007). Celentano et al. (2011) reported similar effects by *Inga edulis*, a nitrogen-fixing species, which contributed with up to 70% of leaf-fall in the plantations, demonstrating the influence that one single species might have on litter quantity.

In our study, nutrient inputs, in general, were higher on high-diversity treatment, intermediate on commercial mix and agroforestry, and lower on direct seeding. Only for nitrogen did the treatment with intermediate richness (commercial mix) have the highest input, along with the agroforestry, which can be attributed to the high density of nitrogen-fixing trees, as also reported by Celentano et al. (2011). The highest values of nutrient inputs on high-diversity can be associated with species richness (Huang et al. 2018b); whereas higher values of nitrogen inputs on commercial mix and agroforestry is due the high proportion of nitrogen-fixing trees in these stands.

Effects of tree community parameters on litter production and nutrient inputs

We have found distinct effects of tree community parameters on nutrient inputs depending on the site. In Site 1, where stem density positively affected nitrogen, phosphorus ($p = 0.07$) and potassium inputs. The high-diversity treatment had a higher stem density of planted individuals than other treatments (Supplementary Material). These results are consistent with the positive effects of dense planting on nutrient cycling reported in other forest restoration studies in Brazil (Alonso et al. 2015; Villa et al. 2016). These authors argued that higher dense planting usually results in more rapid canopy closure (Alonso et al. 2015), with higher natural pruning of litter fractions (i.e. branches and leaves) and, therefore, higher litter and nutrient inputs (Villa et al. 2016).

An additional possible explanation for the observed effects is that the higher stem density in combination with the high number of planted species with different functional traits (e.g. growth rate, canopy architecture, leaf area index, nitrogen-fixing tree capability) may have increased structural complexity in the high-diversity treatment and, consequently, higher nutrient inputs. Therefore, we can hypothesize that the higher stem density of different species in Site 1 might have resulted in a complementarity effect, probably due to the higher number of species with traits that favored nutrient inputs. Huang et al. (2017), studying a subtropical forest, found effects of richness species on both litterfall and litter quality. These authors as well as Baruffol et al. (2013) hypothesized that the larger number of individual trees in more diverse plots resulted from complementarity among species. Additionally, the positive diversity-productivity relationships may result from the high vertical occupation of available space within a canopy, which in turn allows for greater light capture, thus, light-use efficiencies (Forrester 2014; Guo et al. 2020), and recent studies have shown out that crown spatial complementarity between trees drive the positive tree species diversity-litterfall productivity relationships (Willians et al., 2017; Zheng et al. 2019).

Deciduousness negatively affected litter production and P, K, Ca and Mg inputs in Site 1 (with higher fertility soil). Deciduous species, which have short-lived leaves generally with high specific leaf area (Villar et al. 2006; Araújo and Haridasan 2007; Silva et al. 2015), lose all their leaves during the dry season to reduce water loss and optimize growth rates during the rainy season (Tomlinson et al. 2013). Additionally, some studies have shown that deciduous species with short leaf lifespans have relatively high nutrient concentrations (Chen et al. 2013; Rossato et al. 2015). Thus, although we expected to find positive effects of proportion of deciduous individuals on nutrient cycling, this hypothesis was not supported by our data. Our results might be explained by differences in nutrient resorption prior to leaf abscission (Reich et al. 1992), which would result in lower nutrient concentrations in senesced leaves of deciduous species. Siddique et al. (2008), studying nutrient cycling in both direct seeding and high-diversity treatments in the Site 2, found that the proportion of P resorption in the direct seeding was approximately 60% higher than in the high-diversity treatment. These authors also found high phosphorus resorption for the most abundant species in the direct seeding, the *Schizolobium parahyba* and *Enterolobium contortisiliquum*. It is also very possible that our results are confounded by the fact that treatments that were less complex in terms of structure and diversity (i.e. the direct seeding) have the highest proportion of deciduous species (100%) and the lower litter and nutrient inputs. The canopy of the direct seeding treatment plots at both sites are strongly dominated by a single species *S. parahyba* (Pontes et al. 2019), which represents 60% of its tree density and 77% of the basal area. Indeed, when we re-analyzed our data eliminating the data of the direct seeding plots in Site 1, the significantly negative effect of deciduousness on nutrient inputs disappeared. Therefore, these results might have affected the negative effects of deciduousness proportion on litter production and, consequently, on nutrient inputs in Site 1.

Our data suggest that, at the lower fertility soil (Site 2), the higher species richness and proportion of individuals of nitrogen-fixing species might have triggered a complementarity effect, leading to a higher niche partitioning among species. In this case, the positive effect of species richness on nutrient inputs might be more consistent and stronger. Once species use different resources or at different times or different points in space, a higher share of the total pool is expected to be used by the community as a whole, increasing complementarity among species and reducing interspecific competition through niche partitioning (Hooper et al. 2005). Complementary resource use of the most species rich treatment (i.e. high-diversity), with species having different ecological traits, might have favored the higher nutrient inputs in the system (Huang et al. 2018a; b). Moreover, the high nitrogen concentration, mainly in the agroforestry and commercial mix treatments, can be related to some species' particular traits in these treatments (Macedo et al. 2008; Wang et al. 2010; Hoogmoed et al. 2014), mainly the nitrogen fixing capacity (Celentano et al., 2011). Nitrogen-fixing trees might affect the nitrogen dynamics in the community, increasing the concentration of this element in plant tissues (Parrotta 1999; Piotto 2008; Siddique et al. 2008) and, therefore, increasing nutrient inputs (Siddique et al. 2008; Celentano et al. 2011).

Besides the importance of species richness for ecosystems functioning, studies have indicated effects of particular traits on some aspects of nutrient cycling (Celentano et al. 2011). Nitrogen input in the agroforestry and commercial mix treatments were mainly related to the significant contribution of the nitrogen-fixing species *M. caesalpiniifolia* for the system's litter production, once it can produce up to 20% of the total leaf biomass production (Camargo and Engel, unpublished data). Nitrogen concentration in these treatments was almost 25% higher than in high-diversity treatment (Table 3). Furthermore, another research about the effect of *M. caesalpiniifolia* trees removal (Podadera et al. 2015) in the same area, indicated a decrease in total litter production and nutrient inputs in managed plots, compared to unmanaged plots (Oliveira et al. in preparation). These results demonstrate the important role that this species plays in nutrient cycling. However, we emphasize, that *M. caesalpiniifolia* is a non-native species and the tradeoff between its beneficial effect to the system (e.g. framework-species, Lamb et al. 1997) and its potential negative effects must be taken into account, particularly if it becomes an invasive species (D'Antonio and Meyerson 2002).

Restoration treatments compared to control and reference forest

Sixteen years after the restoration treatments were established, the annual litter production was comparable to that reported by several studies carried out in active restoration experiments in Tropical Semideciduous Forest (Arato et al. 2003; Costa et al. 2004; Gazell et al. 2012), tropical forest plantations in Central America (Montagnini 2000; Ruiz-Jaén and Aide 2005; Scherer-Lorenzen et al. 2007; Celentano et al. 2011) and different Atlantic Forest phytophysiognomies (Martinelli et al. (2017). Martinelli et al. (2017) found an overall litterfall average of 8.0 ± 2.5 Mg ha^{-1} (values among 3.5–15.0 Mg ha^{-1}). The nutrient inputs are also comparable to those measured in different tropical forest formations (Costa et al. 2004; Ruiz-Jaén and Aide 2005; Ferreira and Lira Jr, 2007; Celentano et al. 2011; Lanuza et al. 2018).

The commercial mix and high-diversity treatments did not differ from the reference neither in litter production nor in nutrient inputs. As discussed above, stem density in the Site 1, and species richness and the proportion of nitrogen-fixing trees in the Site 2, were the most important community parameters positively associated with litter production and nutrient inputs. Indeed, species richness in the high-diversity (30 species) was intermediate between the reference forests (28 species in Site 1 and 34 in Site 2). In the high-diversity treatment the greater species richness might have been associated with greater functional diversity (in terms of, e.g. growth rate, canopy architecture, leaf area index), providing a canopy stratification more similar to the reference forests (Ruiz-Jaén and Aide 2005). Thus, these characteristics of the high-diversity system associated with its high stem density contributed with highest values of litter and nutrient inputs in this treatment.

All restoration treatments produced more litter and nutrient inputs than the unplanted control (passive restoration), especially the high-diversity treatment. This strong biogeochemical effect of active restoration was probably exacerbated by the dominance of weed grasses (mainly *Urochloa decumbens* Stapf.) all control plots, thereby delaying succession and thus litter production. As we expected, grasses seem to represent an important barrier for tree establishment (Holl 2002) and hence for certain ecosystem functions, such as litter production (Celentano et al. 2011).

Conclusions

Our study showed that restored forests on higher fertility soils had higher levels of litterfall and associated nutrient inputs than on lower fertility soils. However, the effects of tree community parameters on litter production and nutrient inputs depended of on site conditions. Our findings suggest that it may be possible to restore litter production and nutrient inputs in lower fertility sites by establishing restoration plantations with lower species richness, as long as a higher proportion of nitrogen-fixing tree species are used. It is possible to increase nutrient inputs in naturally fertile soils by establishing restoration treatments at high stem densities. Both the commercial mix (established using 25 plant species, with a relatively high proportion of putative nitrogen-fixing trees, i.e. *M. caesalpiniifolia*) and high-diversity treatments (established using 40 plant species) restored litterfall and nutrient inputs after 16-years. Nitrogen-fixing trees play an important role in restoring higher levels of nutrient cycling in forest ecosystems.

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Author's contributions VLE and JAP designed and implanted the original experiment. DLM and VLE designed this study. DLM, DSP and LMS collected field data. DLM and RGMG analyzed the data. DLM wrote the first draft of the paper. VLE, DSP, JAP, LMS, RGMG, LFDM and contributed critically to the draft. All coauthors gave final approval for publication. The authors declare that they have no conflict of interest.

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