Soil biotic and abiotic characteristics as driven factors for site quality of *Araucaria angustifolia* plantations

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Research

Abstract

Purpose

The role of soil biotic and abiotic factors in crucial ecosystem services such as primary production, organic matter dynamics, nutrient cycling, and soil biota community structure in the *Araucaria* ecosystem remains poorly quantified. We aimed to quantify the role of site quality on the development of organic horizons, root growth, soil chemical properties, and the entire soil biota community in even-aged and monospecific *Araucaria angustifolia* plantations.

Methods

We collected and dissected soil monoliths to describe layers of organic matter and the complex soil food web into these layers. We determined soil pH, soil moisture, total nitrogen, available P, and total organic carbon into each layer (litter, F-layer, H-layer, and A horizon), the biomass of fine roots, the community structure of soil biota, arbuscular mycorrhizal fungi, and nematodes, as well as the microbial biomass carbon.

Results

In the high-productivity site, there was significantly higher organic matter formation, nutrient cycling (N and P), root growth, soil moisture, soil biota diversity, arbuscular mycorrhizal fungi, nematodes, and microbial activity evaluated by the microbial biomass carbon compared to the low-productivity site.

Conclusions

High-productivity sites promote the development of organic horizons, root growth on superficial layers that provide plant nutrient release, the A horizon nutrient contents, and the entire soil biota community in monospecific *Araucaria angustifolia* plantations located on humid subtropical Cambisols. This creates a positive plant-soil feedback that maintains soil quality and increases primary production, nutrient cycling, and habitat and food for the soil food web.

1. Introduction

It is well documented that biotic and abiotic factors significantly influence above- and belowground ecosystem primary production through positive plant-soil feedback (Bennett and Klironomos 2018). Even after decades of intensive research, it remains unclear and difficult to quantify such crucial ecosystem services in monodominance ecosystems such as *Araucaria angustifolia* (Bert.) O. Kuntze plantations (Marchioro et al. 2020). The role of soil biotic and abiotic factors remain far from being understood, primarily because of a wide range of complex compartments into soil ecosystems and a lack of scientific

studies gathered from long-term field experiments (Bowsher et al. 2018; Santos et al. 2018; Souza et al. 2019). Ecosystem services, such as primary production, organic matter dynamics, nutrient cycling, and soil biota activity are among the most important services that promote soil quality and generate positive soil-plant feedback (Tateno et al. 2017). The ecological significance of these services is attributed to their characteristics to promote habitat and energy that enable soil biota and microbiota to create positive soil-plant feedback into the soil ecosystem (Souza and Freitas 2018). For instance, primary production is known to increase litter deposition, thus stimulating organic horizon development past over the years (Santos et al. 2018; Santos-Heredia et al. 2018). This first pathway creates a habitat for soil biota and microbiota; thus, they act by transforming and decomposing the organic matter through mechanisms such as a "priming effect". Finally, a solid soil food web is created promoting soil biota community structure, microbial growth, and plant uptake in a way similar as to the soil quality and nutrient content hypothesis described by Souza and Freitas (2018) and Melo et al. (2019). Therefore, the abundance and diversity of soil organisms may, in turn, be regulated by primary production, further modulating plant-soil feedback (Tateno et al. 2017; Bennett and Klironomos 2018).

Despite such positive plant-soil feedback between the soil organic horizon, plants and functionally diverse groups of soil biota, arbuscular mycorrhizal fungi, and soil nematodes, most of the experimental findings on the role of abiotic and biotic factors are often based on only one of these properties, gathered from pot experiments, or often in the absence of adult tree plant species (Bennet and Klironomos 2018; Gebremikael et al. 2016;Santos et al. 2018; Souza et al. 2019; Zhang et al. 2018). Such studies have been used by soil ecologists in soil biology and have increased our understanding of the role of soil biotic and abiotic factors in the processes of organic horizon formation, nutrient cycling, primary production, and soil food web (Ojeda et al. 2018; Yang et al. 2018). However, these findings do not consider the whole potential of the soil biotic and abiotic characteristics as driven factors for site quality and are far from representing the reality in the field. Yet, long-term studies in the presence of adult tree plant species considering these aspects are rare (Rasmussen et al. 2019).

After roughly 100 years of timber exploitation during the 20th century, *A. angustifolia* is currently defined as a critically endangered species (Thomas 2013; Marchioro et al. 2020) and only in-line plantations can be economically used after governmental permission. Besides this historic interest in its timber, and the recognized productive potential (Nutto et al. 2005; Dobner Jr. et al. 2019), the soil bio-chemical factors that influence the growth of *A. angustifolia* are still little known. Moreover, due to the lack of knowledge about the ecology of the *A. angustifolia*, mistakes were made firstly in selecting sites for establishing monospecific stands of this plant species (Breuninger et al. 2008) and secondly in managing them (Seitz 1986; Nutto et al. 2005).

This study aimed to quantify the role of *Araucaria* site quality on the development of organic horizons, root growth, soil chemical properties, and the entire soil biota community. To this end, we analyzed soil monoliths, the soil's main chemical properties, soil biota and microbiota community structure, and microbial biomass carbon for two types of *A. angustifolia* plantations (e.g., low- vs. high-productivity sites). With this approach, we sought to shed light on how soil quality/productivity influences the

formation of organic matter in humid-subtropical highland soil and the macro- and microbiota that provide ecosystem services into this condition. We hypothesized that sites with high productivity are the ones characterized as follows: high biological activity in soil and with high cation exchange capacity resulting in an increased release of available nutrients as well as a concomitant increase in fine roots production and plant growth, thus creating a positive plant-soil feedback.

2. Material And Methods

Soil samples were collected inside even-aged and monospecific *Araucaria angustifolia* plantations of the Florestal Gateados Enterprise. The experimental area is located at the highlands of Southern Brazil (800–1,200 m.a.s.l.). The climate is humid-subtropical (Cfb type according to the Köppen climate classification), with 1,750 mm of total annual precipitation and annual mean air temperature of +15°C (Alvares et al. 2013). Soils in the area were classified as Cambisols (WRB 2006). In July 2019, fifty soil samples were collected at the 0–20 and 20–40 cm soil depths. The samples were homogenized, air-dried, and organic residues were removed manually by each layer. Then, soil samples were dried in an oven at 60°C, sifted in a 2-mm mesh sieve, and subjected to analyses. Clay content was 540 and 405 g kg^{-1} at the 0–20 and 20–40 cm of soil depths, respectively. Soil pH (H$_2$O) was 5.6 to 6.3 at 0–20 cm, and 5.2 to 5.7 at the 20–40 cm soil depth; cation exchange capacity values at soil pH were 16.4 and 19.3 cmol$_c$ kg^{-1} at the 0–20 and 20–40 cm soil depths, respectively. Total organic carbon and available P (Mehlich 1) ranged from 20.6 to 14.5 g kg^{-1} and from 3.8 to 1.4 mg kg^{-1}, at the 0–20 and 20–40 cm soil depths, respectively (EMBRAPA 1997; Tedesco et al. 1995).

Within the 530 ha of plantations, seventy-five sample plots with the highest and seventy-five plots with the lowest quality were selected. At this point, site quality was selected only in terms of dominant height, i.e., according to the accumulated productivity. The relationship between dominant height (h$_{100}$) and age as a measure of site quality (Skovsgaard and Vanclay 2008) was obtained from 460 sample plots (500 m²). Stands were selected as closest as possible to 30 years of age, thus representing a well-established stand. Additional stand characteristics are given in ESM_1. In terms of dominant height, at the age of 30 years, an 8-m difference was verified, which, when translated to mean annual increment (MAI) in volume, represents 14 to 31 m³ ha^{-1} yr^{-1}. Both stands were not thinned and thus allowed robust comparisons in terms of growth and yield.

To characterize the litter compartment and layers of organic matter at intermediate stages of decomposition (F-layer and H-layer), four soil monoliths in each studied plot were collected accordingly to Fassbender (1993). Before collecting the soil monoliths, an area of 20 × 20 cm on the soil surface was delimited for separately sampling the litter layer. After that, we extract soil monoliths with the following dimensions 20 × 20 × 20 cm. Next, we wrapped them with plastic film and transported all the monoliths with minimal disturbance until analysis. During our analysis, the monoliths were dissected into the litter, F-layer, H-layer, and A horizon. We considered the F-layer to be the material composed of partly decomposed litter, the H-layer the material with well-decomposed litter, and the A horizon composed

exclusively of mineral material (Toutain 1987). The ratio of organic matter layers was calculated using the following equation: $ROML_i = dm_i/Tm$, where dm_i is the dry mass of each layer (e.g., litter, F-layer, H-layer, and A horizon), and Tm are both the total dry mass of the soil monolith (20 × 20 × 20 cm) and dry biomass of litter.

To estimate fine root (diameter: <2 mm) dry biomass, we collected roots from the soil samples of each layer (e.g., litter, F-layer, H-layer, and A horizon) during the monoliths processing described above. Fine roots in these layers were washed using a 0.5-mm nylon mesh bag. We sorted fine roots into living and dead roots based on morphology and condition. Only living roots were considered to estimate dry biomass. Fine roots included both tree and herbaceous species because it was difficult to distinguish between these precisely. Fine root dry biomass (g) was determined after drying the samples for 48 h at 70°C. Samples of each layer (litter, F-layer, H-layer, and A horizon) from monoliths were air-dried and passed through a 2-mm sieve. We determined soil pH in a suspension of soil and distilled water (1:2.5 ratio) (Black 1965). Total soil nitrogen and soil organic carbon were estimated according to the methodology described by Okalebo et al. (1993). Phosphorus (P_{sbe}) was determined using the Olsen's P protocol (Olsen et al. 1954). The soil moisture was measured by the gravimetric method, where a fresh soil sample was weighed, oven-dried until no further mass loss, and then reweighed (Black 1965).

At the end of the summer, we sampled four soil monoliths (20 × 20 × 20 cm) to extract and characterize the soil fauna community per studied plot (e.g., low- and high-productivity sites), and collected the organisms manually using metal clips. They were stored in containers with 70% alcohol until identification as recommended in Tropical Soil Biology and Fertility (Anderson and Ingram 1989). These were later counted and identified under a stereoscopic microscope, at the level of a major taxonomic group. The term "taxonomic group" was used in the soil macroarthropod study, meaning either a Class, as Order or even Family, to comprise a set of individuals with a similar life form. The communities were characterized based on the following parameters: (a) richness and (b) Shannon Diversity Index (H) (Shannon and Weaver 1949). We assessed the frequency of occurrence of each taxonomic group by both studied sites. In addition, we classified the taxonomical groups according to their functional groups as described by Souza and Freitas (2018). The frequency of occurrence was calculated using the following equation: $FO_i = n_i/N$, where n_i is the number of times an organism was observed, and N is the total arbuscular mycorrhizal fungi (AMF) spores observed from each studied ecosystem.

To sample the spores of arbuscular mycorrhizal fungi and soil nematodes, we sampled undisturbed soil cores ($n = 6$ per studied plot and 300 g of soil each core), wrapped them, and stored them with minimal disturbance until specimen's extraction as recommended by Souza and Freitas (2018). For AMF extraction, spores and sporocarps from the field were extracted by the wet sieving technique (Gerdemann and Nicolson 1963) followed by sucrose centrifugation (Jenkins 1964). Initially, the extracted spores were examined in water under a dissecting microscope and they were separated based on morphological characteristics. Subsequently, they were mounted in polyvinyl alcohol in lacto-glycerol (PVLG) with and without the addition of Melzer's reagent (Walker et al. 2007). Species identification was based on the descriptions provided by Schenck and Perez (1987), and by consulting the online AMF collection of the

Department of Plant Pathology, the University of Agriculture in Szczecin, Poland (http://www.agro.ar.szczecin.pl/~jblasxkowski/) and the International Culture Collection of Arbuscular Mycorrhizal Fungi Database—INVAM (http://invam.caf.wvu.edu). The AMF communities were characterized based on the following parameters: (a) richness and (b) Shannon Diversity Index (H) (Shannon and Weaver 1949). We assessed the frequency of occurrence of each taxonomic group at both studied sites.

Soil nematodes were extracted as described for the AMF spore extraction. Additionally, we used the method described by Buchan et al. (2013), to separate free-living nematodes from soil components (e.g., organic matter and clay). We counted the soil nematodes under a binocular microscope. Next, the soil nematodes were fixed with a 4% hot (70ºC) formaldehyde solution. Finally, nematode identification using trophic groups was carried out according to Yeates et al. (1993).

Soil samples were put into pots. They were brought to and maintained at ca. 50% water-filled porosity and incubated at 18°C for 45 days. The amount of distilled water was based on the bulk density and initial moisture content of the soil. Water reposition was calculated weekly using a mass balance of each pot. Four replications from each studied site were sampled after 5, 15, 30, 45, and 60 days of incubation. Microbial biomass carbon (C_{mic}) was determined using the fumigation-extraction protocol described by Vance et al. (1987). We divided the soil (20 g of fresh soil per pot) into fumigated and non-fumigated controls. The C_{mic} was extracted with 40 mL of 0.5 M K_2SO_4 and stored at − 18°C until analysis. Organic carbon contents of the extracts were determined by the rapid dichromate oxidation method described by Okalebo et al. (1993).

Before analysis, all the variables were tested for normality (e.g., by Shapiro-Wilk test) and homoscedasticity (e.g., by the Bartlet test), and log transformations were applied to meet both required criteria. To find possible spatial autocorrelation, we used the Moran.I function (Gittleman and Kot 1990). We did not detect any relationship between the variables and the sampling points, indicating spatial independent samples. Soil properties, soil biota, and microbiota community composition, and microbial biomass carbon were analyzed with a non-parametric paired t-test followed by the Monte Carlo test (1000 permutations). The dissimilarities between the productivity sites (e.g., by Bray-Curtis distance measure) were analyzed using non-metric multidimensional scaling (NMDS), which provided a graphical ordination of the variables that when presenting a measure of stress less than 0.01, indicate an excellent fit of the model (Zuur et al. 2007). It also enables us to reduce the number of the variables used to determine which abiotic or biotic variable explained most of the variation in the productivity sites (Oksanen et al. 2013). All analyses were run using R 3.4.0 statistical software (R Core team 2018).

3. Results

The ratio of litter and organic matter layers (e.g., F-layer and H-layer) on soil monoliths was significantly higher in the high-productivity site ($n = 16$, $t = 11.54$, $p < 0.01$, $n = 16$, $t = 17.33$, $p < 0.001$; $n = 16$, $t = 21.45$, $p < 0.001$, respectively), while the A horizon was significantly higher in the low-productivity site ($n = 16$, $t =$

20.56, $p < 0.001$). There were significant differences on total nitrogen ($n = 16$, $t = 21.28$, $p < 0.001$), and P by sodium bicarbonate extraction ($n = 16$, $t = 20.19$, $p < 0.001$) between low- and high-productivity sites, reaching the lowest average of total nitrogen and P by sodium bicarbonate extraction (P_{sbe}) in the A horizon. For all studied layers (litter, F-layer, H-layer, and A horizon), the total N and P_{sbe} were higher at high-productivity site than at the low-productivity site. Differently than observed for the soil layers, at least numerically, we did not find any significant differences between the studied sites on total organic carbon ($n = 16$, $t = 2.07$, $p = 80.798$) by analyzing soil monoliths. Overall, litter presented 206% and 6% more total nitrogen and P_{sbe} at the high-productivity site than at the low-productivity one. For the A horizon, total nitrogen and available P_{sbe} tended to be higher (135% and 166%) at the high-productivity site than at the low-productivity one. Fine root dry biomass was significantly higher in litter ($n = 16$, $t = 11.34$, $p < 0.01$) and the A horizon ($n = 16$, $t = 14.82$, $p < 0.01$) at the high-productivity site that at the low-productivity one. Whereas, for the H-layer, we found the significant highest fine root dry biomass at low-productivity site ($n = 16$, $t = 14.27$, $p < 0.01$). The soil pH was not observably different for the litter at both low- and high-productivity sites. There were significant differences between sites for the soil pH of the F-layer ($n = 16$, $t = 8.13$, $p < 0.05$), H-layer ($n = 16$, $t = 8.02$, $p < 0.05$) and A horizon ($n = 16$, $t = 7.45$, $p < 0.05$). For moisture, we found significant differences between low- and high-productivity sites in the litter ($n = 16$, $t = 17.38$, $p < 0.01$), H-layer ($n = 16$, $t = 15.37$, $p < 0.01$), and A horizon ($n = 16$, $t = 19.81$, $p < 0.01$) (Table 1).

Table 1

Variation in the soil productivity site on the ratio of organic matter layers (%), total nitrogen (g kg⁻¹, b), available P (mg kg¹), total organic carbon (g kg⁻¹, d), fine roots dry biomass (g), soil pH (1:2.5 v:v), and soil moisture (%)

Sites[a]	Ratio of organic matter layers (%)	Total nitrogen (g kg⁻¹)	Available P (mg kg⁻¹)	Total organic carbon (g kg⁻¹)	Fine root dry biomass (g)	Soil pH (1:2.5 v:v)	Moisture (%)
	Litter						
Low	1.4 ± 0.3	3.01 ± 0.02	10.2 ± 0.5	89.3 ± 0.2	1.9 ± 0.4	5.0 ± 0.5	37.9 ± 5.4
High	3.5 ± 0.5**	9.57 ± 0.09**	15.3 ± 0.4**	90.5 ± 0.1	47.4 ± 2.2**	5.0 ± 0.5	70.2 ± 11.2**
	F-layer						
Low	5.0 ± 0.5	2.56 ± 0.22	5.5 ± 0.1	41.4 ± 0.2	11.8 ± 0.9	4.7 ± 0.1	11.0 ± 1.2
High	7.4 ± 0.7**	6.77 ± 0.17**	13.5 ± 0.3**	45.5 ± 0.3*	11.0 ± 0.8	6.6 ± 0.2*	11.0 ± 1.0
	H-layer						
Low	19.1 ± 1.2	1.99 ± 0.43	4.3 ± 0.3	39.7 ± 0.4*	44.9 ± 5.4**	4.7 ± 0.3	14.6 ± 1.3
High	36.5 ± 2.3**	3.97 ± 0.19*	10.5 ± 0.2**	35.6 ± 0.2	21.0 ± 4.3	6.3 ± 0.2*	22.9 ± 3.6**
	A horizon						
Low	74.5 ± 5.1**	0.99 ± 0.17	3.7 ± 0.2	25.7 ± 0.5	16.5 ± 3.9	4.1 ± 0.1	3.6 ± 0.6
High	52.6 ± 3.7	2.01 ± 0.05*	6.9 ± 0.5*	30.5 ± 0.4*	34.6 ± 0.9**	5.9 ± 0.3*	15.9 ± 0.2**

[a]Litter height (Low: +3.5−0.0 cm; High: +4.2−0.0 cm); F-layer depth (Low: 0.0−2.7 cm; High: 0.0−3.2 cm); H-layer depth (Low: 2.7−16.5 cm; High: 3.2−17.1 cm); A horizon depth (Low: 16.5−20.0 cm; High: 17.1−20.0 cm); *, ** significant at 5% and 1% by paired t-test, respectively.

Our results about soil fauna revealed the general effects of soil quality on the average fauna abundance, occurrence of functional groups, richness, and diversity. The high-productivity site had the highest richness and diversity. In this site, we identified exclusively soil organisms from Blattidae, Scarabaeidae, Spirobolidae, Enchytraeidae, Acaridae, Acerentomidae, Filistatidae, Scutigeridae, Forficulidae, and Procampodeidae. The results from functional groups showed a similar pattern for ecosystem engineers, litter transformers, microregulators, and predators, with the high-productivity site having the highest values of soil fauna abundance and the exclusive presence of some families of these groups (Table 2).

Table 2
Soil fauna abundance (of individual monoliths), richness, diversity (Shannon's index), and functional groups at low- and high-productivity sites.

Taxonomic group / Family	PRODUCTIVITY LEVELS		Functional groups
	Low	High	
Blattodea / Blattidae	-	2	Ecosystem engineer
Blattodea / Termitidae	1	8**	Ecosystem engineer
Hymenoptera / Formicidae	17**	9	Ecosystem engineer
Coleoptera / Scarabaeidae	-	3	Litter transformers
Diplopoda / Spirobolidae	-	2	Litter transformers
Enchytraeidae	-	17	Litter transformers
Acari / Acaridae	-	1	Microregulator
Collembola / Isotomidae	2	27**	Microregulator
Protura / Acerentomidae	-	3	Microregulator
Araneae / Filistatidae	-	8	Predator
Chilopoda / Scutigeridae	-	3	Predator
Dermaptera / Forficulidae	-	5	Predator
Strepsiptera / Myrmecolacidae	2	-	Predator
Diplura / Procampodeidae	-	3	Herbivore
Larvae of Coleoptera	6	-	Herbivore
Richness	5	13**	-
Diversity (Shannon index)	1.12	2.15**	-

Soil monolith dimensions: 20 × 20 × 20 cm; Functional groups classification was done according to Souza and Freitas (2018); ** Significant at 1% by paired t-test.

Collectively, we identified eight arbuscular mycorrhizal fungi (AMF) species in all samples. Eight AMF species were found at the high-productivity site, and four at the low-productivity one. There were differences between the AMF frequencies of occurrence between low- and high-productivity sites. Across all the samples, *Funneliformis mosseae* was the most abundant identified AMF species. *Acaulospora morrowiae, C. pellucida, G. gigantea*, and *R. coralloidea* were AMF species found exclusively at the high-productivity site (Table 3).

Table 3

Frequency of occurrence (%) of arbuscular mycorrhizal fungi at low- and high-productivity sites.

Arbuscular mycorrhizal fungi species	Productivity levels	
	Low	High
Acaulospora morrowiae Spain & N.C. Schenck	-	12.33
Cetraspora pellucida (T.H. Nicolson & N.C. Schenck) Oehl, F.A. Souza & Sieverd.	-	8.03
Claroideoglomus claroideum (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler	16.30**	9.63
Funneliformis mosseae (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler	53.60**	25.39
Glomus sp.	14.90*	10.90
Gigaspora gigantea (T.H. Nicolson & Gerd.) Gerd. & Trappe	-	5.34
Racocetra coralloidea (Trappe, Gerd. & I. Ho) Oehl, F.A. Souza & Sieverd.	-	21.33
Rhizophagus intraradices (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler	15.20**	7.05
Richness	4	8**
Diversity (Shannon index)	1.19	1.94*
*, ** Significant at 5% and 1% by paired t-test, respectively.		

The abundance and functional composition of nematodes in the low-productivity site were dissimilar (36 *vs.* 76 ind. g^{-1} soil) to the high-productivity site. In the site with low productivity, we did not find Carnivores and Omnivores. The total abundance and abundances of bacterivores, carnivores, omnivores, and fungivores were significantly higher ($p < 0.01$) at the high-productivity site than at the low one. Only, the abundance of herbivores was significantly higher ($p < 0.01$) at the low-productivity site than at the high one (Fig. 3A). Microbial biomass carbon showed similar dynamics between low- and high-productivity sites. The highest values were at 5 days of incubation, and then they started to decline until reaching a stable line after 45 and 30 days for high- and low-productivity sites, respectively. In our study,

C_{mic} was lower at the low-productivity site than at the high- one, and was significantly different ($p < 0.001$) (Fig. 3B).

According to the NMDS analysis, the soil productivity sites were significantly dissimilar (Fig. 4). The ordination of the soil chemical characteristics (e.g., ratio of A horizon, ratio of H-layer, P contents in A horizon, F-layer, and H-layer, and N content in litter), soil biota abundance (e.g., Formicidae, and Isotomidae), soil microbiota abundance (e.g., *F. mosseae*, and Bacterivores) and microbial biomass carbon in each productivity site had a good fit (stress value = 0.18). Formicidae, the ratio of the A horizon, and *F. mosseae* were highly correlated with the low-productivity site, whereas Isotomidae, Bacterivores, microbial biomass carbon, litter N content, P content in the A horizon, F-layer, and H-layer, and the ratio of H-layer were highly correlated with the high-productivity site. Formicidae, the A horizon, *F. mosseae*, P_{A-H}, C_{mic}, Bacterivores, Isotomidae, N_L, H-layer, P_{F-L}, and P_{H-L} explained 87.2, 79.8, 0.94, 0.90, 0.91, 0.94, 0.94, 0.95, 0.86, 0.82, and 0.76 of the variation in the productivity sites (Fig. 4).

4. Discussion

The soil quality of even-aged *A. angustifolia* plantations on the highlands of Southern Brazil impacts the soil biotic and abiotic properties. Our results indicate a promotion in soil organic matter formation (e.g., litter, F- and H-layers), plant nutrient release (e.g., total N and P_{sbe}), and fine root production at the litter and A horizon of high-productivity sites. This can be explained by the high productivity amplitude observed in *A. angustifolia* plantations in southern Brazil. While high productive sites and stands are available, with mean annual increments ~ 25 m³ ha^{-1} yr^{-1} (Nutto et al. 2005), or even > 30 m³ ha^{-1} yr^{-1} as was the case for the evaluated one, there are also sites and stands where productivity is negligible by Brazilian standards (< 10 m³ ha^{-1} yr^{-1}). Unfortunately stands with low productivity are way more common than highly productive ones. In low-productivity sites, the low cover rate leads to decrease both the soil organic matter, and nutrient cycling by the exposure of soil to wind and rainfall. This is the reason for the low commercial interest in t *A. angustifolia* and why many *A. angustifolia* plantations were converted into other land uses. It is important to note that the site quality classification proposed by Schneider et al. (1992), and employed for the classification of the 530 ha of plantations regarded for stand selection, shows that the productivity level of *A. angustifolia* can be even lower than the low-productivity stand evaluated in the present study (14 m³ ha^{-1} yr^{-1}). On the other hand, the studied high-productivity site had a dominant height at age of 30 years beyond the values given by Schneider et al. (1992), indicating that this site delivered an impressive production even beyond those authors' best stands. Recent results of *A. angustifolia* genetic breeding started in the 1970s by EMBRAPA are now delivering promising perspectives (Silva et al. 2018; Sousa and Aguiar 2012), which will probably be the genetic base of a new plantation wave. Nevertheless, this new enhanced genetic material will only deliver its maximum potential if accompanied by a deeper understanding of site quality. Thus, the abiotic and biotic characterization of the studied sites delivers a wider understanding of which factors are the drivers for the productivity of *A. angustifolia* plantations over a long period (30 years), as discussed in detail as follows. The decrease in soil organic matter formation and nutrient cycling is consistent with the findings

of previous studies for cultivated tree species in the highland of southern Brazil (Hoogh and Dietrich 1979; EMBRAPA 1988; Horst et al. 2018; Koehler et al. 2010).

As we originally hypothesized, the productivity level of the soil was explained by the biotic and abiotic properties, which were likely caused by an increase in the soil organic matter formation (e.g., by providing habitat), plant nutrient release (e.g., by improving N and P contents on litter, F-layer, and H-layer) as described by Eslamdoust and Sohrabi (2018), which promoted soil biota, arbuscular mycorrhizal fungi, and soil nematode abundance (Gebremikael et al. 2016; Moreira et al. 2007). However, differently than hypothesized, a soil depth of ≥ 1 m is not a crucial factor for *A. angustifolia* or, at least, it could be compensated for by other soil properties, such as N and P content and soil biota abundance and activity. Here we presented important evidence on the effects of soil history and quality sites on a variety of compartments into the soil profile in a long-term subtropical *Araucaria* ecosystem. Our results support the evidence that soil quality promotes the formation of layers of organic matter at the intermediate stage of decomposition (F- and H-layer), and nutrient cycling, which may influence the soil food web. Most of the variables analyzed in this study (e.g., layers of organic matter, nutrient cycling, and fine roots production) responded positively to the high-productivity site (Mishra et al. 2019). Productivity level (e.g., high- and low-productivity sites) was an important variable to understand all studied variables, indicating that site quality influences the nutrient cycling, fine root production, and soil biota diversity and activity.

Site differences considering soil biodiversity were discussed in previous studies performed around the world (Bennett and Klironomos 2018; Beretta-Blanco et al. 2019). Our study provided evidence that high-productivity sites, when compared to low-productivity sites, had the highest values of organic matter layers, total N, P_{sbe}, fine root production, and soil moisture. Considering all these variables, we may consider that ecological processes, such as litter deposition, soil organic matter formation, primary production, and nutrient cycling, were dissimilar between the studied sites, indicating robust associations regardless of the soil quality on high-productivity sites and land degradation on low-productivity sites (Bini et al. 2013; Huangfu et al. 2019; Mauda et al. 2018; Roy et al. 2018; Mishra et al. 2019). This indicates that the abundance of soil biota, arbuscular mycorrhizal fungi, and functional-groups of soil nematodes might be playing an important role in high-productivity site sustainability (Gebremikael et al. 2016; Souza et al. 2019). The high-productivity site showed a better-quality residue and, consequently, the cycling of nutrients is faster in this environment, which can influence the productivity of *A. angustifolia*. In addition, the higher N and P contents in the monoliths may be due to the greater accumulation of residues in the high-quality site, since the litter in reforestation of *A. angustifolia* may be higher than the litter in native forests of southern Brazil (Bini et al. 2013). The N content in the araucaria residue is 13 g kg^{-1} (Pereira et al. 2013), which can bring about 200 kg of N to the soil per hectare.

Results on the high-productivity site were significant for soil biota abundance (e.g., Formicidae, Isotomidae, and Termitidae), arbuscular mycorrhizal fungi (e.g., *C. claroideum, Funneliformis mosseae, Glomus* sp., and *Rhizoglomus intraradices*), functional-groups of soil nematodes (e.g., bacterivores, carnivores, fungivores, herbivores, and omnivores), microbial biomass carbon, and ecological indexes (e.g., richness and diversity by soil fauna and AMF). These results emphasize the influence of site quality

on soil biodiversity, which in turn affected productivity levels in a subtropical *Araucaria* ecosystem (Gebremikael et al. 2016; Forstall-Sosa et al. 2020; Souza et al. 2019). Essentially, we wanted to understand how dissimilar sites (e.g., chosen by their productivity levels) promotes the soil food web in a long-term field experiment, considering a monodominance of *Araucaria angustifolia*. A pioneer study considering site quality for *A. angustifolia* was conducted by Hoogh and Dietrich (1979). These authors reported that the best growth performance was obtained in soils where *A. angustifolia* was planted immediately after the clear-cutting of the native forest. To our knowledge, our study is the first report in a subtropical *Araucaria* ecosystem showing the role of nutrient cycling, soil fauna diversity, AMF diversity, an abundance of soil nematodes, and microbial activity in sustain a positive plant-soil feedback as we found in the high-productivity site. The significant differences between the studied sites for soil properties may influence the soil biota community structure and function, consequently altering nutrient cycling and plant productivity (Jones et al. 2019; Romanowicz et al. 2016). Allied to this, it is also important to maintain soil moisture, adequate contents of plant-nutrients, and a constant supply of residues promoted by litter deposition, which is common in the *A. angustifolia* ecosystem.

The results observed in this study revealed that there were significant differences between the studied sites on soil biodiversity. Therefore, we may consider that the soil food web of the study sites is completely different as proposed by Anyango et al. (2020). According to Roy et al. (2018) and Parsons et al. (2020), soil organisms (e.g., here considering macro- and microbiota) may influence soil health, plant growth, and litter palatability. These authors also report that litter palatability may attract a high diversity of soil fauna functional groups (e.g., ecosystem engineers, and decomposers), which in turn may fuel higher trophic levels (e.g., bacterivores, fungivores, omnivores, and predators). These results agree with previous works (Beretta-Blanco et al. 2019; Gebremikael et al. 2016; Mauda et al. 2018; Mishra et al. 2019) that reported high litter deposition and rhizodeposition as the main factors increasing nutrient availability, microbial activity, and abundance of higher tropic levels as observed in the high-productivity site. By changing these two processes in the rhizosphere of *A. angustifolia*, a quality site may be improved over the years, generating high productivity levels because of increased release of plant-available nutrients (total N, and P_{sbe}). These conditions would be responsible to promote soil nematode and microbial activity, especially by microbial biomass carbon, as well as microbivorous nematodes (e.g., bacterivores and fungivores (Gebremikael et al. 2016; Impastato and Carrington et al. 2020; Jo et al. 2020). Our hypothesis that a high-productivity site presents high biological activity resulting in an increased release of available nutrients and a concomitant increase in fine roots production in a specific layer, and plant growth, and thus, creating a positive plant-soil feedback was supported. Overall, soil fauna community composition in the high-productivity site was characterized by i) a high abundance of ecosystem engineers (e.g., Termitidae) and predators (e.g., Isotomidae), which give us evidence of sites with a high degree of bioturbation, organic matter decomposition, and biological control (Forstall-Sosa et al. 2020; Melo et al. 2019); ii) a low abundance of symbionts (e.g., e.g., *Claroideiglomus claroideum, Funneliformis mosseae, Glomus* sp., and *Rhizoglomus intraradices*) which reflect a high content of plant-available nutrients, creating an independence of *A. angustifolia* plants in this site (Souza et al. 2019); and iii) a high abundance of higher trophic levels of soil nematodes, which indicate that soil nematode

community are promoting nutrient cycling, plant biomass, net N, and net P (Rosenfield and Müller 2020). These three characteristics created a positive effect in the trophic structure by promoting some important ecological processes such as nutrient cycling, biological control, mutualism, parasitism, and soil organic matter formation (Barel et al. 2019; Cuassolo et al. 2020; Ge et al. 2019; Jo et al. 2020; Zhang et al. 2018).

5. Conclusions

High-productivity sites promote the development of organic horizons (e.g., F- and H-layers), root growth on superficial layers which provide plant nutrient (e.g., P and N) release, soil chemical properties of the A horizon (e.g., contents of P and total N) and the entire soil biota community (e.g., abundance, richness, and diversity) in monospecific *Araucaria angustifolia* plantations located at humid subtropical Cambisols.

High-productivity sites are accompanied by high activity of fauna and microorganisms in the soil that can promote the nutrient cycling process, thus creating positive plant-soil feedback. Future studies could be carried out to assess which abiotic factors are more important in *A. angustifolia* plantations at different crop ages and if microorganisms could be inoculated to seedlings or sites to improve their productivity level. The results of this study contribute to a deeper view of plant-soil feedback influencing site quality that, in turn, may improve the interest in establishing new plantations of this endangered tree species. Besides the commercial and economic motivations, this would be also an important in-situ conservation strategy.

Declarations

Author's contributions

We declare that all the authors made substantial contributions to the conception, design, acquisition, analysis, and interpretation of the data. All the authors participate in drafting the article, revising it critically for important intellectual content, and finally, the authors gave final approval of the version to be submitted to the *Forest Ecosystems*.

Compliance with Ethical Standards

Conflict of Interest: The authors declare that they have no conflict of interest.

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Supplementary Material

Electronic supplementary material_1: Stand characteristics including age (at field measurement of 2016) site index (SI) stocking (N), quadratic mean diameter at breast height (d_g) dominant diameter at breast height (d_{100}), dominant height (h_{100}), basal area (G), standing volume (V) and mean annual increment (MAI) in volume.

Productivity level	Age Years	SI[a]	N trees ha^{-1}	d_g cm	d_{100} cm	h_{100} m	G m² ha^{-1}	V m² ha^{-1}	MAI m² ha^{-1} yr^{-1}
Low	31	16	2,281	17.7	28.0	14.2	56.6	420.2	13.6
High	30	26	1,488	26.0	40.2	22.0	79.0	922.7	30.9
amplitude	11-51		60-2,560	11-50	17-78	7-23	4-53	19-556	-

[a] Site index, the dominant height at an index age of 40 years, according to the classification proposed by Schneider *et al.* (1992).
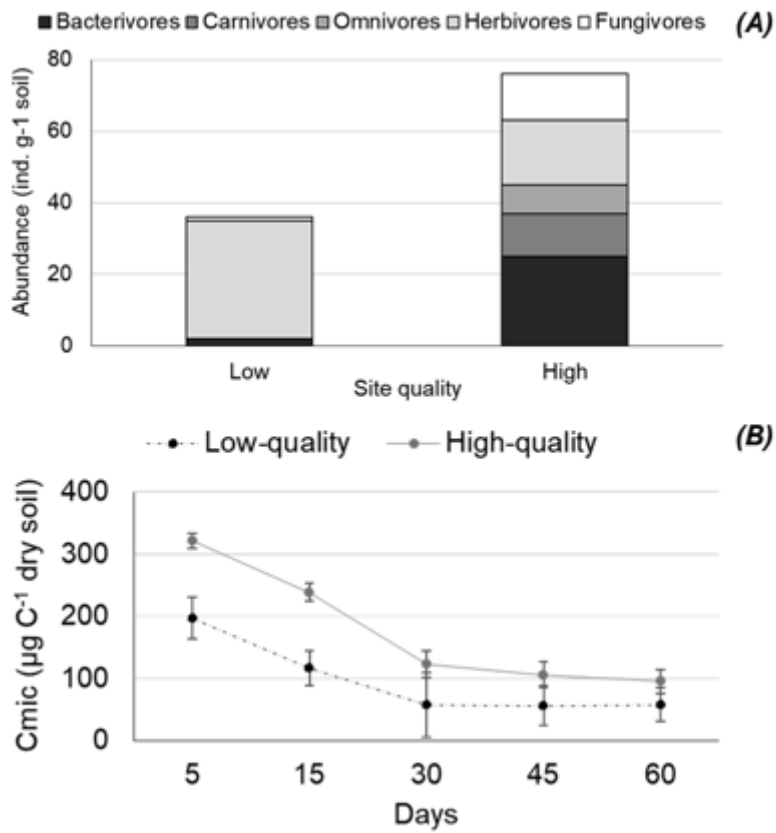
Figures

Figure 1

Mean nematode abundance of each trophic group (A) and microbial biomass carbon (B) at low- and high-productivity sites
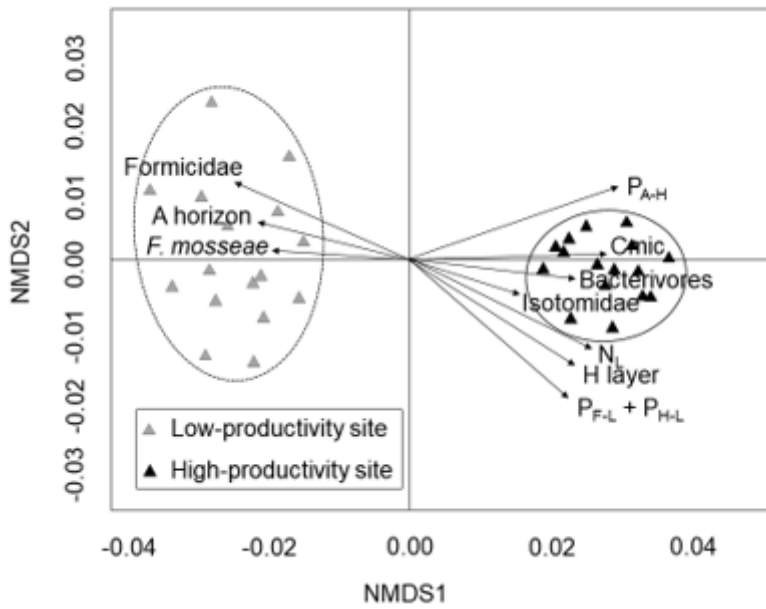

Figure 2

Productivity site dissimilarities base on soil chemical characteristics (soil organic matter layers, and nutrient cycling), soil biota and microbiota abundance, microbial C biomass (Cmic) plotted as non-metric multidimensional scaling (NMDS) of the dataset from low- and high-productivity sites. The productivity of sites is represented by the following symbols: low = gray triangles; and high = dark triangles. Vector length and direction represent only probability values less than 0.01 (p < 0.01). A horizon (A-H) = Ratio of A horizon (%); L = Litter; F-L and H-L = F- and H-layer