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

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**Abstract**

The role of soil biotic and abiotic factors in crucial soil functions such as primary production, organic matter dynamics, nutrient cycling, and soil biota community structure in the *Araucaria* ecosystem remains poorly quantified. We aimed to understand how the development of organic horizons, root growth, soil chemical properties, and the entire soil biota community affected the soil quality in even aged and monospecific *Araucaria angustifolia* plantations. We collected 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. In the high-quality site, there was significantly higher organic matter formation, nutrient cycling (N and P), root growth, soil moisture, soil biota diversity, arbuscular mycorrhizal fungi, and nematodes compared to the low-quality site. High-quality 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.

**Keywords** Cambisols · Endangered tree species · Subtropical ecosystems · Soil organic horizons · Soil food web · Soil trophic structure

**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 soil functions 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). Soil functions, 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 (e.g., here considering soil macro- 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; 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, 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 (Gebremikael et al. 2016; Bennet and Klironomos 2018; Santos et al. 2018; Zhang et al. 2018; Souza et al. 2019). 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 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 understand the role of the development of organic horizons, root growth, soil chemical properties, and the entire soil biota community on Araucaria site quality. To this end, we analyzed soil monoliths, the soil’s main chemical properties, soil biota community structure, and microbial biomass carbon for two types of A. angustifolia plantations (e.g., low-vs. high-quality sites). With this approach, we sought to shed light on how site quality influences the formation of organic matter in humid-subtropical highland soil and the macro- and microbiota that provide soil functions into this condition. We hypothesized that sites with high quality 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.

### Materials and methods

#### Species description

_Araucaria angustifolia_ belongs to the family Araucariaceae. _A. angustifolia_ is named as Araucaria, Paranâ pine, Brazilian pine, and candelabra tree (Breuninger et al. 2008). An evergreen endangered tree to 40 m with thick, tough, and triangular-like leaves and a long straight trunk. These leaves are broad at the base. However, they are razor-sharp at the edges and tip (Hoogh and Dietrich 1979). _A. angustifolia_ used to cover an area of 233,000 km² from Brazilian territory. Nowadays, it has lost 97% of its original area to logging, agriculture and _Pinus_ plantations (Dobner et al. 2019). It is tolerant of most soil types. It grows best in well drained, slightly acidic soils inside subtropical climate (e.g., with abundant rainfall more than 1200 mm). In Brazil, its seeds (called *pinhão*) are used as a food resource and medicine for the regional farmers, and it played an important role for the small population of natives in the past.

#### Study area location

The study sites are geographically located at the Florestal Gateados Enterprise in Campo Belo do Sul, Santa Catarina, highlands of Southern Brazil (Table 1). The mean annual temperature of the area is +15 ºC and receives a mean annual precipitation of 1750 mm. The experimental area was dominated by soybean in the 80’s following a conventional farming system, and after 1980 s soybean was replaced by _Araucaria_ plantation. The soil type in the experimental area was classified as Cambisols with silty-clay sediments as

| Site quality | Latitude | Longitude | Altitude (m) | Slope (%) | No. plots | No. soil samples | No. monoliths |
|--------------|----------|-----------|--------------|-----------|-----------|-----------------|--------------|
| Low          | S27º51’14” | O50º49’21”  | 1200         | 12        | 200       | 200             | 800          |
| High         | S28º01’50” | O50º51’18”  | 1135         | 6         | 200       | 200             | 800          |

Table 1 General description of the studied environments at low- and high-productivity sites.
parent material (WRB 2006). Köppen’s classification defines the climate of the experimental area as humid-subtropical (Cfb) type (Alvares et al. 2013).

Reconnaissance survey

A preliminary discussion was held with the managers of the Florestal Gateados Enterprise to get general information about the monospecific A. angustifolia plantation that covers a total area of 530 ha. Subsequently, a reconnaissance survey was conducted across the monospecific stand to have an overall impression about the study area. 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 400 sample plots (500 m²). Stands were selected as closest as possible to 30 years of age, thus representing a well-established stand. Then, two sites adjacent to each other were selected for further study (Table 2). 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.

Scheme of sample plot

A systematic sampling approach was implemented to conduct the field study. A total of two hundred plots, 20 × 25 m were established in each site. The first plot was laid out systematically using a compass, 250 m away from the edge to avoid an edging effect. The transect lines (five transects per site) were made along the centre of each studied site and 50 m away from each other. Soil samples were taken in the centre of the plots at the 0–20 and 20–40 cm soil depths. This helped us to understand the soil environment inside and beyond the monoliths studied perimeter. The samples were homogenized, air-dried, and organic residues were removed manually. 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 soil depths, respectively. Soil pH (H₂O) was 5.6 to 6.3 at 0–20 cm, and 5.2 to 5.7 at the 20–40 cm soil depth; CEC values at soil pH were 16.4 and 19.3 cmolc 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 (Tedesco et al. 1995; Embrapa 1997). The inventories were conducted in July and December 2019.

Soil organic matter formation

To characterize the litter compartment and layers of organic matter at intermediate stages of decomposition (F-layer and H-layer), four soil monoliths by each studied plot were collected accordingly to Fassbender (1993) at the same period to avoid soil moisture variation into each monolith. 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: ROML₄ = dm₄/Tm, where dm 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.

Fine roots

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

| Table 2 | Site characteristics including age, site index (SI) stocking (N), quadratic mean diameter at breast height (d₄₅), dominant diameter at breast height (d₄₀), dominant height (h₁₀₀), basal area (G), standing volume (V), and mean annual increment (MAI) in volume |
|---|---|---|---|---|---|---|---|---|---|
| Site quality | Age Years | SP | N trees ha⁻¹ | d₄₅ cm | d₄₀ cm | h₁₀₀ m | G m² ha⁻¹ | V m³ ha⁻¹ | MAI m³ ha⁻¹ yr⁻¹ |
| Low | 31 | 16 | 2281 | 17.7 | 28.0 | 14.2 | 56.6 | 420.2 | 13.6 |
| High | 30 | 26 | 1488 | 26.0 | 40.2 | 22.0 | 79.0 | 922.7 | 30.9 |
| Amplitude | 11-51 | 60–2560 | 11–50 | 17–78 | 7–23 | 4–53 | 19–556 | – |

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

**Soil chemical properties**

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$_{soi}$) 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).

**Soil fauna**

At the end of the winter and summer, we sampled four soil monoliths (20×20×20 cm) per plot 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 1993). 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 at both studied sites. For soil nematodes, 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 (70 °C) formaldehyde solution. Finally, nematode identification using trophic groups was carried out according to Yeates et al. (1993).

**Arbuscular mycorrhizal fungi and soil nematodes**

To sample the spores of arbuscular mycorrhizal fungi and soil nematodes, we sampled undisturbed soil cores (n = 4 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/~jblasxkowskij/) 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. For soil nematodes, 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 (70 °C) formaldehyde solution. Finally, nematode identification using trophic groups was carried out according to Yeates et al. (1993).

**Microbial biomass carbon**

Microbial biomass carbon

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 (Cmic) 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 Cmic was extracted with 40 mL of 0.5 M K2SO4 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).

**Statistical analysis**

Before analysis, all the variables were tested for normality (e.g., by Shapiro-Wilk test) and homoscedasticity (e.g., by the Bartlett 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 site quality (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).

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-quality site \((t = 11.54, p < 0.01; t = 17.33, p < 0.001; t = 21.45, p < 0.001,\) respectively), while the A horizon was significantly higher in the low-quality site \((t = 20.56, p < 0.001).\) There were significant differences on total nitrogen \((t = 21.28, p < 0.001),\) and P by sodium bicarbonate extraction \((t = 20.19, p < 0.001)\) between low- and high-quality 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-quality site than at the low-quality site. Differently than observed for the soil nitrogen and P by sodium bicarbonate extraction, the H-layer depth \((t = 11.34, p < 0.01)\) and A horizon \((t = 14.82, p < 0.01)\) at the high-quality site that at the low-quality one. Fine root dry biomass was significantly higher in litter \((t = 11.34, p < 0.01)\) and the A horizon \((t = 14.27, p < 0.01)\). The soil pH was not observably different for the litter at both low- and high-quality sites. There were significant differences between sites for the soil pH of the F-layer \((t = 8.13, p < 0.05),\) H-layer \((t = 8.02, p < 0.05)\) and A horizon \((t = 7.45, p < 0.05)\). For moisture, we found significant differences between low- and high-quality sites in the litter \((t = 17.38, p < 0.01),\) H-layer \((t = 15.37, p < 0.01),\) and A horizon \((t = 19.81, p < 0.01)\) (Table 3).

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-quality site had the highest richness and diversity. In this site, we identified exclusively soil organisms from Blattidae, Scarabaeidae, Spirobolidae, Enchytraeidae, Acaridae, Acradidae, 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 4).

Collectively, we identified eight arbuscular mycorrhizal fungi (AMF) species in all samples. Eight AMF species were found at the high-quality site, and four at the low-quality site (AMF = 206% and 6% more total nitrogen and \(P_{sbe}\) at the high-quality 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-quality site than at the low-quality one. Fine root dry biomass was significantly higher in litter \((t = 11.34, p < 0.01)\) and the A horizon \((t = 14.82, p < 0.01)\) at the high-quality site that at the low-quality one. Whereas, for the H-layer, we found the significant highest fine root dry biomass at low-quality site \((t = 14.27, p < 0.01)\). The soil pH was not observably different for the litter at both low- and high-quality sites. There were significant differences between sites for the soil pH of the F-layer \((t = 8.13, p < 0.05),\) H-layer \((t = 8.02, p < 0.05)\) and A horizon \((t = 7.45, p < 0.05)\). For moisture, we found significant differences between low- and high-quality sites in the litter \((t = 17.38, p < 0.01),\) H-layer \((t = 15.37, p < 0.01),\) and A horizon \((t = 19.81, p < 0.01)\) (Table 3).

Table 3 Variation in the soil productivity site on the ratio of organic matter layers (%), total nitrogen (g kg\(^{-1}\)), available P (mg kg\(^{-1}\)), total organic carbon (g kg\(^{-1}\)), fine roots dry biomass (g), soil pH (1:2.5 v:v), and soil moisture (% w/w)

| 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 (% w/w) |
|------------|-----------------------------------|-------------------------------|-----------------------------|-------------------------------|--------------------------|-------------------|------------------|
| 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
There were differences between the AMF frequencies of occurrence between low- and high-quality sites. Across all the samples, *Funneliformis mosseae* was the most abundant identified AMF species. *Acaulospora morrowiae*, *C. pellicida*, *G. gigantea*, and *R. coralloidea* were AMF species found exclusively at the high-productivity site (Table 5).

The abundance and functional composition of nematodes in the low-quality site were dissimilar (36 vs. 76 ind. g⁻¹ soil) to the high-quality site. In the site with low-quality, 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-quality site than at the low one. Only, the abundance of herbivores was significantly higher (*p < 0.01*) at the low-quality site than at the high one (Fig. 1A). Microbial biomass carbon showed similar dynamics between low- and high-quality 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-quality sites, respectively. In our study, *Cmic* was lower at the low-quality site than at the high one and was significantly different (*p < 0.001*) (Fig. 1B).

According to the NMDS analysis, the soil productivity sites were significantly dissimilar. 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,

| Taxonomic group / Family | Site quality | Functional groups |
|--------------------------|-------------|-------------------|
| Blattodea / Blattidae     | -           | 2 Ecosystem engineer |
| Blattodea / Termitidae    | 1           | 8** Ecosystem engineer |
| Hymenoptera / Formicidae  | 17**        | 9 Ecosystem engineer |
| Coleoptera / Scarabaeida  | -           | 3 Litter transformers |
| Diplodota / Sphirobolidae | -           | 2 Litter transformers |
| Enchytraeidae             | -           | 17 Litter transformers |
| Acari / Acaridae          | -           | 1 Microregulator |
| Collembola / Isotomidae   | 2           | 27** Microregulator |
| Protura / Acrentomidae    | -           | 3 Microregulator |
| Araneae / Filistatidae    | -           | 8 Predator |
| Chilopoda / Scutigeridae  | -           | 3 Predator |
| Dermaptera / Forficulidae | -           | 5 Predator |
| Strepsiptera / Myrmecolaidae | 2       |  - Predator |
| Diplura / Procampeodeida | -           | 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

| Arbuscular mycorrhizal fungi species | Site Quality |
|-------------------------------------|--------------|
| *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*        | 16.30**      |
| (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler | 9.63        |
| *Funneliformis mosseae*             | 53.60**      |
| (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler | 25.39        |
| *Glomus sp.*                        | 14.90*       |
| *Gigaspora gigantea*                | -            |
| (T.H. Nicolson & Gerd.) Gerd. & Trappe | 10.90       |
| *Racocetra coralloidea*             | -            |
| (Trappe, Gerd. & I. Ho) Oehl, F.A. Souza & Sieverd. | 5.34        |
| *Rhizophagus intraradices*          | 15.20**      |
| (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler | 7.05        |
| Richness                            | 4            |
| Diversity (Shannon index)           | 1.19         |

* *, ** Significant at 5% and 1% by paired t-test, respectively
and the ratio of H-layer were highly correlated with the high-productivity site. Formicidae, the A horizon, F. mosseae, PA−H, Cmic, Bacterivores, Isotomidae, NL, H-layer, PF−L, and PH−L explained 87.2, 79.8, 0.94, 0.90, 0.91, 0.94, 0.95, 0.86, 0.82, and 0.76 of the variation in the productivity sites (Fig. 2).

**Discussion**

The high soil quality of even-aged *A. angustifolia* plantations on the highlands of Southern Brazil exhibit the high values soil biotic and abiotic traits than the low soil quality sites. Our results indicate a higher soil organic matter formation (e.g., with more than 2.1, 2.4, and 17.4% litter, F- and H-layers, respectively), plant nutrient release (e.g., total N and P with more than 57.28 and 49.47%, respectively), and fine root production at both litter and A-horizon (e.g., with more than 96.03 and 52.31%, respectively) in the high-quality sites when compared with the low-quality 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-quality sites, the low litter deposition overtime leads to decrease organic horizon formation (e.g., with less 3.5% year⁻¹ when compared with high-quality sites). Also, its litter quality (ESM_1) with low contents of N, P, K, Ca, Mg and S, and high contents of lignin (that reduces litter decomposition rate) lead to reduce nutrient cycling, thus creating negative plant-soil feedback. This is the reason for the low commercial interest in *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

![Fig. 1 Mean nematode abundance of each trophic group (A) and microbial biomass carbon (B) at low- and high-quality sites](image-url)
the 530 ha of plantations regarded for stand selection, shows that the productivity level of *A. angustifolia* can be even lower than the low-quality stand evaluated in the present study (14 m³ ha⁻¹ yr⁻¹). On the other hand, the studied high-quality 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 (Sousa and Aguiar 2012; Silva et al. 2018), 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).

As we originally hypothesized, the quality level of the soil was explained by the biotic (e.g., soil biota richness, diversity, and abundance) and abiotic properties, which were likely caused by an increase in the soil organic matter formation (e.g., by providing habitat), and plant nutrient release (e.g., by improving nutrient contents on litter, F-layer, and H-layer) as described by Esalamdoust and Sohrabi (2018), which promoted soil biota (with more 160 and 91.9% of richness and diversity, respectively), arbuscular mycorrhizal fungi (with more 100 and 63.02% of richness and diversity, respectively), and soil nematode abundance (with more 164.3%) (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 litter quality with high nutrient content (ESM_1) 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 overtime soil quality was influenced by the formation of layers of organic matter at the intermediate stage of decomposition (F- and H-layer), and nutrient cycling, which have influenced the entire soil food web thus affecting plant productivity. Based on our results about the entire soil food web, we have proposed a schematic view that described how it works in both low- and high-quality sites (ESM_2).

Most of the variables analyzed in this study (e.g., layers of organic matter, soil nutrient contents, and fine roots production) responded positively to the high-productivity site (Mishra et al. 2019). We found at the high-quality sites a high deposition of litter with more N, P, K, Ca, Mg and S contents when compared with the litter deposited at the low-quality sites. It acted as habitat and energy provision to a wide range of soil fauna organisms. We found at the high-quality sites 13 families classified as ecosystem engineers, litter transformers, predators, microregulators, and herbivores as proposed by Souza and Freitas (2018). On the other hand, we have just found 5 families at the low-quality sites (e.g., Formicidae, Isotomidae, Larvae of Coleoptera, Myrmecolacidae, and Termitidae), which are related with disturbed ecosystems as described by Mishra et al. (2019), Souza et al. (2019), and Forstall-Sosa et al. (2020). Thus, productivity level (e.g., high- and low-quality sites) was an important variable to understand all studied variables, indicating that soil biotic traits overtime influences the quality sites, thus affecting the fine root production (with more 34.41% of fine roots at high-quality sites than in the low-quality ones), and soil biota diversity (with more 61.53% of fauna’s diversity at high-quality sites than in the low-quality ones).

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, Pabs, 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; Mauda et al. 2018; Roy et al. 2018; Huangfu et al. 2019; 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, and nutrient contents in the litter 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., with 47.05% less of Formicidae, and with more 88.9 and 87.5% Isotomidae, and Termitidae abundance, respectively), arbuscular mycorrhizal fungi (e.g., with less 40.9, 52.6, 26.8, and 53.6% of C. claroideum, Funneliformis mosseae, Glomus sp., and Rhizoglomus intraradices abundance, respectively), functional-groups of soil nematodes (e.g., with more abundance of bacterivores, carnivores, fungivores, and omnivores, and with less abundance of herbivores), microbial biomass carbon, and ecological indexes (e.g., with more 160 and 100% richness, and 91.9 and 63.0% diversity by soil fauna and AMF, respectively) when compared with the low-productivity sites. These results emphasize the influence of site quality on soil biodiversity, which in turn affected productivity levels in a specific layer, and plant growth, and thus, creating 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 (Dobner Jr et al. 2019; Jones et al. 2019).

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 (Gebremikael et al. 2016; Mauda et al. 2018; Beretta-Blanco et al. 2019; Mishra et al. 2019) that reported high litter deposition and rhizodeposition as the main factors increasing nutrient availability, microbial activity, and abundance of higher trophic 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 Pₜₐₑ). These conditions would be responsible to promote soil nematode and microbial activity, especially by microbial biomass carbon, as well as herbivorous 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 positive plant-soil feedback was supported. So, the high-quality sites showed more 0.6 cm of an organic horizon than the low-quality sites. Here we must consider that we needed 40 years to produce just 0.6 cm of an organic horizon in a warming Brazilian biome (e.g., Atlantic Forest biome) that comprises areas with an endangered tree species, Araucaria angustifolia. We found into a soil layer of 20 cm a content of 85.5% of an organic horizon that sustain a diverse soil biota community (e.g., macroarthropods, soil nematodes, and AMF). We also have strong evidence that shows in the high-quality sites a better-quality residue and high nutrient cycling. 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 (Melo et al. 2019; Forstall-Sosa et al. 2020); (ii) a low abundance of symbionts (e.g., Claroideoglomus 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 (Zhang et al. 2018; Barel et al. 2019; Ge et al. 2019; Cuassolo et al. 2020; Jo et al. 2020).

Conclusions

High-quality sites exhibit high thickness 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-quality 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.

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