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Site quality for Araucaria angustifolia plantations at subtropical Cambisol is driven by soil organisms' assemblage and the litter and soil compartments

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Abstract

Soil quality is a driver for biodiversity enrichment, soil fertility, and soil organic matter dynamics. Different soil quality levels at *Araucaria angustifolia* plantations may influence the soil organisms, and the interaction between litter and soil compartments by providing habitat and nutrients in different pathways. Our aim was to present a deeper view of the litter-soil compartments, and soil organisms community composition associated with three degrees of site quality (low-, average-, and high-quality sites), which reflect productivity levels, at the highlands of southern Brazil. The non-metric multidimensional scaling (NMDS) grouped the influence of soil quality degrees in three groups considering the dissimilarities on the soil organisms among each other. The ordination of the soil organisms, richness, and Shannon's diversity in each studied soil quality degree had a stress value of 0.08. The structural equation models indicated that the loss of soil quality showed a negative relationship among soil organisms' assemblage, and soil-litter compartments. Our results highlighted the importance of considering soil biotic and abiotic attributes for achieving high productivity levels from *A. angustifolia* plantations within its natural occurrence range.

Introduction

It is well reported that soil quality significantly influences soil food web (soil organisms' assemblage), and soil-litter compartments through positive plant-soil-litter interactions (Banerjee et al. 2023). However, it remains unclear how soil quality degrees may change the interaction among these three soil compartments (organisms, litter, and soil – solid phase) in 30-years monospecific plantations of *Araucaria angustifolia* (Bert.) O. Kuntze (Dobner Jr. et al. 2019). The role of soil quality remains far from being understood, primarily because of a wide range of soil functions, and the different interactions among soil compartments. We also must take in consideration the lack of scientific studies gathering dataset from long-term field experiments considering the interaction of organisms, litter, and soil as influenced by soil quality degrees (Souza et al. 2022a). Soil compartments, such as: (i) litter that may be characterized by litter deposition (kg m^{-2}) and *k-factor* ($years^{-1}$) assess the input of organic matter, and the nutrient cycling process; (ii) soil – solid phase may be characterized by the chemical properties that determines the soil fertility and the soil capacity to sustain high biomass production; and (iii) soil organisms' community composition that may be characterized by the abundance of insects, arachnids, myriapods, etc. that determines the structure of the soil food web and ecosystem services, are among the most important compartments that promotes the soil quality and generate positive interaction among plant-soil-litter (Banerjee and van der Heijden 2023).

The ecological significance of these three compartments is attributed to their inner traits (e.g., litter with its decomposability, soil with its fertility, and organisms with their services) to promote habitat and energy supply that enable litter to supply the nutrient cycling process, soil to sustain plant production, and soil organisms to provide better litter trituration, bioturbation, biological control, and nutrient cycling into Subtropical soils (Deng et al. 2022). For instance, litter deposition is known to increase nutrient input, thus stimulating soil and plant nutrient bioavailability over the years (Yin et al. 2022). Nutrient input creates energy supply for soil organisms. Thus, they act by transforming and decomposing the litter residue through mechanisms such as physical trituration, and enzymatic decomposition. Finally, a robust soil biota community is created in a way similar to the nutrient content hypothesis described by Souza et al. (2022a).

Despite such positive interactions among litter, soil, and soil organisms most of the evidence on the role of soil quality is often based on only one of these aimed compartments, gathered from short-term experiments (Dudas et al. 2022; Araujo et al. 2022). Such evidence increased our understanding of the role of soil quality in processes related to litter dynamics, soil and plant nutrient cycling, *k-factor*, and soil organisms' abundance (Laurindo et al. 2021). However, these findings do not consider the whole potential of the soil quality (by the lack of studies considering well-defined soil quality degrees) as a driving factor for litter quantity and quality, soil chemical properties, and soil organisms' assemblage, and are far from representing the reality in the Subtropical ecosystems. Yet, long-term studies considering plantations of *A. angustifolia* are rare into this context (Rasmussen et al. 2019).

A. angustifolia is currently defined as a critically endangered native tree species from Southern Brazil through intense timber exploitation during the 20th century (Barbieri et al. 2023). Besides the historic interest in the productive potential of *A. angustifolia*, and the quality of its wood (de Mattos et al. 2022), the soil fertility characterization that are one of the main factors contributing for *A. angustifolia* growth and yield are still little known. Moreover, due to the lack of knowledge about the ecology of *A. angustifolia*, mistakes were made firstly by selecting sites for establishing plantations of this endangered tree species (Souza et al. 2022a), and secondly by the lack of soil management practices inside these sites to conditioning soil ecosystem (Ortiz et al. 2022).

Our aim here was to understand site quality levels as affected by the interaction among litter, soil – solid phase, and organisms' assemblage at *A. angustifolia* cultivated on Subtropical Cambisols. To this end, we analysed the soil's main chemical properties (Souza et al. 2023a), litter properties (da Silva et al. 2022), and soil organisms' abundance (Laurindo et al. 2022) for three well-defined soil quality degrees. With this approach, we sought to shed light on how site quality levels, determined in terms of *A. angustifolia* yield, are influenced by the litter, soil, and organisms' compartments in subtropical Cambisols. We hypothesised that the high-quality sites present high litter deposition with low lignin content and high macronutrient content (N, P, and K), high soil exchangeable cations content resulting in an increased release of available nutrients as well as a concomitant increase in soil organisms' richness, and diversity through a positive interaction among the three studied soil compartments (litter, soil, and organisms).

Material and Methods

Experiment design overview

We conducted a field experiment with planted *A. angustifolia* by using completely randomised block design with three well-defined site quality levels: (1) low site quality (L-SQ); (2) average site quality (A-SQ, Control); and (3) high site quality (H-SQ) (Table 1). Each site-quality level was replicated eleven times by using circular plots with 500 m^2 for two consecutive years. *A. angustifolia* was selected as a model plant because this endangered tree species used to cover an area of 233,000 km^2 from Brazilian territory in 1920. Nowadays (January 2023), it has lost 97% of its original area to logging, agricultural purposes, biological invasion, and the spread of *Pinus* plantations in the States of Paraná, Santa Catarina and Rio Grande do Sul (Souza et al. 2022a).

Table 1
Main description of the studied site quality levels at low, average, and high site qualities at Subtropical Cambisols, Campo Belo do Sul and Capão Alto, Santa Catarina, Brazil

Site	Altitude (m)	Slope (%)	Clay content (%)	No. plots	No. soil samples	Stand age (years)	Tree dominant height (m)
Low-quality	1200 (53)	12.1 (1.4)	29.5 (1.7)	99	594	27.5 (2.8)	12.7 (1.2)
Average-quality	1172 (102)	11.9 (2.1)	31.5 (3.2)	99	594	29.0 (3.2)	16.0 (2.0)
High-quality	1135 (89)	12.0 (0.9)	29.6 (2.1)	99	594	28.8 (2.6)	20.8 (3.2)
Standard deviation in parenthesis*							

From Table 1 it can be seen that despite similar stand ages, the site quality levels are substantially dissimilar in terms of tree dominant height, which is a consistent attribute to classify productivity levels of stands worldwide (Skovsgaard and Vanclay 2007).

Litter material, and greenhouse conditions to prepare the standard litter material

The standard litter material for the litter assay was prepared by considering litter from two native plant species (High C:N ratio - *Mimosa scabrella*, and low C:N ratio - *A. angustifolia*). Both plant species were grown in plastic pots containing 4 L of autoclaved sand under greenhouse conditions (25:20°C day: night temperature) for 8 weeks. Briefly, seeds of both plant species were surface sterilised with 0.5% NaOCl. Leaves were harvested and air dried at 40ºC until constant dry biomass. The standard litter material was defined as the dried leaves free of pathogens and with the same age (8 weeks). This standard material was used in the litter assay comprising freshly cut dried material free of pathogens rather than naturally senesced plant material contaminated with soil particles, fungi spores, and other opportunity decomposers. For the standard litter material, we characterised lignin content, total organic carbon (TOC), and N and P contents (Table 2).

Table 2
Lignin, and nutrient contents in each standard litter material (mean ± standard deviation, $N = 40$)

Plant material	Lignin (%)	TOC (%)	N (%)	P (mg kg^{-1})
A. angustifolia	58.6 ± 3.4	43.6 ± 1.4	0.65 ± 0.04	670.0 ± 45.8
M. scabrella	34.3 ± 1.4	20.9 ± 1.2	3.95 ± 0.23	134.8 ± 14.7

Field conditions, litter collection, and soil sampling

The experimental study was conducted in monospecific *A. angustifolia* stands on permanent plots at the Florestal Gateados Enterprise, Campo Belo do Sul, Santa Catarina, Southern Brazil (Fig. 1). The mean annual temperature of the experimental sites is + 15 ºC. We have registered a total annual precipitation of 1750 mm (from August 2021 to August 2022), within average historical records. The soil type in the experimental area was classified as Subtropical humic Cambisol (WRB 2006). Köppen's classification defines the climate of the experimental area as humid-subtropical (Cfb) type (Alvares et al. 2013).

In order to determine litter deposition, litter material was collected following a 30-day schedule from August 2021 to September 2022. We used a metallic square with 1 m × 1 m on the soil surface (da Silva et al. 2022), and three litter samples per plot were collected using plastic bags. Litter material was air dried for 48 h at 60°C until constant dry biomass. We analysed the litter nutrient contents (C, N, and P) according to Tedesco et al. (1995), and lignin content by using the Klason's method as described by Morais et al. (2010).

Monthly the soil samples were collected (from August 2021 to September 2022) using a soil auger and sampling them at 0.2 m soil depth. A total of seventy-two soil samples were collected for soil chemical characterization. All soil samples were air dried and passed through a 2-mm size sieve as described by Black (1965). The soil chemical characterization included soil pH, available P, soil organic matter, total nitrogen, exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}, and Al^{3+}), H^{+}+Al^{3+}, sulphur, and micronutrients. Soil pH was measured in a suspension of soil and distilled water (1:2.5, v:v, soil: water suspension). Available P was extracted by Mehlich-1 and determined using colorimetry. The potassium chloride extraction method was used to determine exchangeable Al^{3+}, Ca^{2+}, and Mg^{2+} (Page et al. 1982), and Mehlich-1 to determine K^{+}. Soil organic matter was estimated by rapid dichromate oxidation according to the methodology described by Okalebo et al. (1993). The total nitrogen was estimated using sulfuric acid and potassium sulphate digestion (Black 1965). Micronutrients were estimated according to the methodologies described by Black (1965).

Soil organisms' assemblage

To sample soil organisms, we have used six Provid-type traps per plot. We did not find any nests (i.e., ants and termites' nests) in the plots or nearby our experiment. During the whole experiment, Provid-type traps (each trap had four windows with 4 cm × 4 cm opening) were placed using a 2-days schedule without any disruption to collect soil fauna specimens (e.g., We placed the traps 12 times following a 30-day schedule during all the experiment), but we present the mean in our results. Into each trap, we added 200 mL of distilled water and neutral detergent solution at a concentration of 25% plus 30 mL of 70% alcohol (da Silva et al. 2022). Soil fauna specimens (macrofauna – specimens longer than 0.2 cm; and mesofauna – specimens lower than 0.2 cm) were preserved in 70% alcohol and considered for our analyses. All individuals were then sorted, counted, and classified at family level. The community structure of soil fauna in each studied treatment was characterised by the following parameters: mean abundance (ind. trap^{-1}) of soil fauna taxonomic groups, fauna richness, Shannon diversity index – H', and Simpson dominance index – C. In addition, we classified the functional group of each taxonomic unit following criteria described by Souza and Freitas (2018).

Litter decomposition assay

We used a hundred forty-four litterbags (10 cm × 10 cm) with 1 mm^2 mesh to determine the litter decomposition rate (k-factor, years^{-1}) of standard litter residues (e.g., *A. angustifolia*, and *M. scabrella*), according to the methodology described by da Silva et al. (2022). The use of litterbags with 1 mm^2 enabled us to assess: (i) macrofauna action on litter fragmentation (ii) and microbiota action on litter decomposition. Each litterbag received 10 g of dry litter residues. Litterbags were placed in a grid scheme per plot distributed between the topsoil and litter material. Following a 30 day-schedule, six litterbags per standard litter residue were collected and placed in individual paper bags. In the lab, the standard litter residues sampled in each litterbag were oven-dried at 60°C until reaching a constant weight for 72 h, and then the samples were weighted. The k factor (years^{-1}) was calculated as described by da Silva et al. (2022). In this assay, k-factor would indicate the rate of litter decomposition.

Statistical analyses

All variables were tested for normality and homoscedasticity by using the “shapiro.test” and the “bartlett.test” functions in the “stats” and “dplyr” packages, respectively. The “Moran.I” function in the “ape” package was used to detect spatial autocorrelation among blocks, and within each block among plots. We used an one-way ANOVA by using the “aov” function (in the “stats” package) to compare the influence of the soil quality treatments on soil chemical properties (hypothesis 1), soil fauna assemblage (hypothesis 2), and litter deposition and decomposition (hypothesis 3). Pearson’s correlation was used to test the correlation between k-factor and litter nutrient contents. To evaluate the similarities among the soil quality treatments due to the soil chemical properties, litter deposition, k-factor, and litter nutrient contents a principal component analysis (PCA) was carried out by using “vegan” package”. We performed a non-metric multidimensional scaling (NMDS) to analyse differences among the soil quality treatments in terms of soil fauna community by using the “metaMDS” function with Bray-Curtis’ matrix. A structural equation model (SEM) analysis was performed to explore the direct effect of soil quality treatments on soil fauna abundance and the indirect effects via changes in soil and litter properties (Souza et al. 2023a). The used variables in the SEM were previously selected by the PCA. To construct the measurement model, we utilised a confirmatory factor analysis to specify the number of variables and their associated observed indicators based on loading scores (Laurindo et al. 2022). The SEM approach was performed by using the “psych”, “lavaan”, “semTools”, and “MASS” packages. The maximum likelihood estimation method was used to parameterize the model. Model fit was assessed by comparative fit index (CFI) > 0.95, standardised root mean squared residual (SRMR) < 0.08, root mean square error of approximation (RMSEA) < 0.06 (Souza et al. 2023b). All statistical analysis were run using R software (R Core Team 2018).

We did not describe site-effects since our analyses did not indicate spatial dependence. An explanatory analysis of variance was performed to explore all data variability among the soil quality treatments, sampling period, blocks, and plots on soil chemical properties, soil fauna abundance, litter deposition, k-factor, and litter nutrient content. In this explanatory analysis, we have considered soil quality treatments (df = 2), sampling period (df = 11), plots (df = 10), and their interaction, respectively as sources of variation in a three-way ANOVA. Data from sampling points were nested by plots. We did not find any significant differences for sampling period, plots, and their interaction on all studied variables. Thus, we performed an one-way ANOVA considering soil quality treatments as source of variation, and the observed results are shown in the "Litter deposition, and litter nutrient content from the studied soil quality treatments", "Influence of Araucaria's soil quality on soil chemical properties", "Soil organisms' collection in a *A. angustifolia* field", and "k-factor and its correlation with litter nutrient content from low- and high C:N ratio residues in the *A. angustifolia* field" subsections.

Results

Litter deposition, and litter nutrient content from the studied soil quality treatments

The litter deposition, lignin content, litter nutrient content (N, P, K, Ca, Mg, S, and C), and C:N ratio varied among the site quality levels. For litter N, S, and C contents, we did not find any significant differences between the low site quality (L-SQ) and high site quality (H-SQ). In the high site quality level, we found the highest significant values of litter deposition, and litter Ca and Mg contents. For the low site quality level, we found the highest significant values of lignin content, and litter P content, while in the average site quality level the highest significant value of C:N ratio was observed (Table 3).

Table 3
Mean values of litter deposition, lignin, nutrient contents, and C:N ratio in each litter material inside the site quality levels.

Properties	L-SQ	A-SQ	H-SQ	F-value
Litter deposition (g m^{-2})	4416.28 (626.46) c	6518.22 (652.34) b	**8922.70 (797.89) a**	8.59**
Lignin content (%)	**63.50 (2.96) a**	51.95 (1.19) b	43.48 (0.61) c	9.85***
N content (g kg^{-1})	**10.46 (3.02) a**	8.96 (1.73) b	**10.53 (1.72) a**	16.71***
P content (g kg^{-1})	**0.82 (0.18) a**	0.74 (0.11) b	0.69 (0.12) c	18.27***
K content (g kg^{-1})	0.56 (0.02) b	**0.93 (0.20) a**	**1.11 (0.40) a**	8.64**
Ca content (g kg^{-1})	17.18 (3.62) b	15.67 (5.05) b	**19.50 (1.97) a**	10.90***
Mg content (g kg^{-1})	2.00 (0.69) c	2.48 (0.35) b	**3.60 (1.26) a**	9.25***
S content (g kg^{-1})	**2.43 (0.78) a**	2.09 (0.57) b	**2.42 (0.36) a**	9.51***
C content (g kg^{-1})	**384.30 (4.24) a**	369.05 (4.14) b	**383.60 (4.15) a**	15.45***
C:N ratio	38.45 (1.52) b	**41.80 (1.09) a**	36.86 (0.98) c	13.18***

Standard deviation in parenthesis.

Within studied site quality levels, the same letters represent no significant differences by Bonferroni's test ($p < 0.05$).

, and * represents $p < 0.01$, and 0.001, respectively.

Influence of Araucaria's site quality on soil chemical properties

The one-way ANOVA results showed significant differences among the studied site quality levels on soil chemical properties. The highest values of soil organic matter, soil P content, and exchangeable Ca were observed on soil samples from the high site quality level. For the low site quality, we observed the highest values of exchangeable Mg, S content, and B content. Next, we observed the highest values of exchangeable Al, H^{+}+Al^{3+}, and Zn content on plots within the average site quality. We did not find any significant differences for the soil pH, and Cu content between the low site quality and high site quality levels (Table 4).

Table 4
Soil chemical properties from the studied site quality levels, Campo Belo do Sul and Capão Alto, Santa Catarina, Brazil

Properties	L-SQ	A-SQ	H-SQ	F-value
Soil pH	**5.30 (0.42) a**	4.97 (0.17) b	**5.56 (0.87) a**	16.21***
Soil organic matter (%)	5.85 (1.48) b	5.70 (1.22) b	**7.36 (1.21) a**	20.37***
P (mg kg^{-1})	10.90 (1.25) b	9.72 (1.30) b	**12.35 (1.21) a**	13.69***
K (mg kg^{-1})	44.00 (1.27) b	**107.80 (5.09) a**	**113.35 (4.12) a**	14.50***
Exchangeable Ca ($cmol_c$ kg^{-1})	5.60 (0.30) b	4.60 (0.37) b	**8.74 (0.28) a**	14.22***
Exchangeable Mg ($cmol_c$ kg^{-1})	**2.40 (0.56) a**	1.47 (0.49) b	1.70 (0.62) b	13.67***
Exchangeable Al ($cmol_c$ kg^{-1})	0.40 (0.05) b	**1.50 (0.17) a**	0.38 (0.05) b	12.69***
H^++Al^{3+} ($cmol_c$ kg^{-1})	9.50 (0.51) b	**14.92 (0.56) a**	10.74 (0.78) b	19.87***
S (mg kg^{-1})	**20.65 (1.29) a**	18.87 (0.81) b	16.20 (0.43) c	14.91***
B (mg kg^{-1})	**0.61 (0.04) a**	0.42 (0.05) b	0.43 (0.03) b	15.63***
Cu (mg kg^{-1})	**4.05 (0.12) a**	2.57 (0.13) b	**3.30 (0.16) a**	11.08***
Mn (mg kg^{-1})	50.60 (1.32) b	**56.97 (0.42) a**	**57.68 (1.23) a**	12.55***
Zn (mg kg^{-1})	2.55 (0.63) c	**8.07 (0.75) a**	4.08 (0.25) b	16.24***

Standard deviation in parenthesis.

Within studied site quality levels, the same letters represent no significant differences by Bonferroni’s test ($p < 0.05$).

*** represents $p < 0.001$.

Soil organisms’ collection in A. angustifolia plantations

We identified 27 Families of soil biota community. In the low site quality, we found the highest significant soil organism's abundance only for the Araneidae. While in the average site quality, we found the highest significant values for Isotomidae, Nitidulidae, Neuroptera, and Halictophagidae. Finally, for high site quality, we found the highest values for Filistatidae, Acaridae, Carabidae, Scarabidae, Staphylinidae, Scutigeridae, Julidae, Formicidae, Larvae, Forficulidae, Mantidae, and Pseudoscorpiones. For the ecological indices, we found the highest significant values of biota richness ($p < 0.001$) and Shannon’s diversity ($p < 0.001$), in the high site quality level (Table 5).

Table 5

Soil organism abundance (ind. trap^{-1}, mean ± standard deviation, N = 99) and ecological indices among the studied site quality levels.

Taxonomic group	L-SQ	A-SQ	H-SQ	F-value
Araneae				
Araneidae	**15.0 (1.7) a**	11.2 (2.1) b	5.2 (1.0) c	7.83**
Filistatidae	-	**15.0 (2.1) a**	**15.8 (3.8) a**	9.85***
Acari				
Acaridae	-	18.7 (3.1) b	**55.0 (4.7) a**	8.63**
Collembola				
Isotomidae	16.5 (0.7) b	**24.0 (1.4) a**	16.0 (4.5) b	7.08*
Paronellidae	-	10.5 (1.2) b	**21.4 (3.6) a**	8.63**
Coleoptera				
Carabidae	-	12.0 (2.9) b	**16.8 (3.2) a**	6.86*
Scarabidae	-	-	**28.6 (3.2) a**	8.91**
Staphylinidae	-	-	**13.8 (4.5) a**	8.96**
Nitidulidae	10.5 (0.7) b	**18.0 (2.1) a**	12.0 (3.3) b	6.62*
Chilopoda				
Scutigeridae	-	-	**3.4 (1.1) a**	8.96**
Diplopoda				
Julidae	-	-	**2.0 (0.7) a**	9.11**
Hymenoptera				
Formicidae	12.5 (0.7) c	50.2 (2.9) b	**64.0 (8.3) a**	8.63**
Lepidoptera				
Larvae	-	-	**1.8 (0.8) a**	9.01**
Dermaptera				
Forficulidae	-	**1.7 (0.9) a**	**1.8 (0.8) a**	9.86**
Mantodea				
Mantidae	-	-	**4.4 (1.0) a**	8.91**
Neuroptera				

Taxonomic group	L-SQ	A-SQ	H-SQ	F-value
Myrmeleontidae	-	**2.0 (0.1) a**	1.4 (0.2) b	9.26**
Pseudoscorpiones				
Lechytiidae	-	-	**3.0 (0.8) a**	9.11**
Thysanoptera				
Halictophagidae	1.5 (0.7) b	**2.7 (0.9) a**	1.0 (0.2) b	8.13**
Ecological indices				
Biota richness	5.0 (1.0) c	11.0 (1.5) b	**18.0 (2.0) a**	19.25***
Shannon’s diversity	1.44 (0.25) c	**2.19 (0.51) a**	**2.31 (0.33) a**	10.12***

Standard deviation in parenthesis.

Within studied site quality levels, the same letters represent no significant differences by Bonferroni’s test ($p < 0.05$).

*, **, and *** represents $p < 0.05$, 0.01, and 0.001, respectively.

Multivariate analysis

According to the NMDS analysis, the soil organisms’ abundance in the study sites were significantly dissimilar. The ordination of the soil organisms (Formicidae, Isotomidae, Carabidae, Acaridae, Scarabaeidae, Julidae, Scutigeridae, Staphylindae, and Mantidae) and ecological indices (biota richness and Shannon’s diversity) in each studied site quality level had a stress value of 0.08. Formicidae was highly correlated with the low site quality stands, whereas Isotermidae, Carabidae, and Acaridae were highly correlated with the average site quality. Scarabaeidae, Julidae, Scutigeridae, Staphylindae, Mantidae, and ecological indices (biota richness and Shannon’s diversity) were highly correlated with the high site quality stands. Together, the soil organisms’ abundance and ecological indices explained 91.2% of the dataset variance (Fig. 2).

k-factor low- and high C:N ratio residues in the A. angustifolia plantations

The two-way ANOVA results showed significant differences among the studied site quality levels and litter residues (high- vs low C:N ratio) on *k*-factor ($p < 0.05$). On one hand, by comparing the *k*-factor between litter residues with high- and low C:N ratio, the residue with low C:N ratio (*M. scabrella*) was significantly higher in all studied site quality levels. On the other hand, by comparing the *k*-factor among the studied site quality levels, the low site quality was useful to show the highest values of *k*-factor on litterbags that received litter residues with a high C:N ratio. While, when residues with low C:N ratio were added in the studied site qualities, the highest values were found in the high site quality (Fig. 3).

The SEM model showed that the low site quality in the *A. angustifolia* plantations presented a negative relationship among soil, litter, and biota compartments. In the soil compartment, we observed an increase in soil pH, and Mg^{2+}. Next, in the litter compartment we observed an increase in *k*-factor, lignin, and C:N ratio. Finally, in the biota compartment we observed an increase in the abundance of Araneidae, Carabidae, and Mantodea (Fig. 4). Regarding litter, soil, and biota compartments at low site quality, we observed that all soil and litter properties from plots where we tested the effect of low site quality decreased the exchangeable Ca content, and abundance of Acaridae (Fig. 4).

Discussion

Our results emphasised the effects of contrasting *A. angustifolia* plantations life-history on litter traits (deposition, nutrient content, lignin content, and *k*-factor), soil chemical properties, and soil biota community (e.g., soil biota abundance, Shannon's diversity, and biota richness. Essentially, we wanted to understand how site quality for *A. angustifolia* plantations can change the litter traits, soil chemical properties, and soil biota composition by promoting negative changes on the soil ecosystem using a long-term field experiment represented by the monodominance of *A. angustifolia* in three site quality levels. In the low site quality stands, we found a significant decrease in litter deposition, litter K, Ca, and Mg contents, and C:N ratio (Borges et al. 2019; Yang et al. 2022) that in turn reduced the soil pH, soil organic matter, soil nutrient content (P, K, Ca, Mg, Mn, and Zn) (Manral et al. 2022), and soil biota abundance, richness, and diversity (Souza et al. 2022b). These changes on litter factors, and soil properties may disrupt the soil biota community composition by altering habitat provision (e.g., when reducing the litter deposition, and litter lability), soil organic matter, and resources' availability (litter and soil nutrients) (Souza et al. 2023a). The habitat and nutrient dependency hypothesis describe that the soil biota is dependent on nutrient-rich compounds provided through litter decomposition that build a soil food web composed by high trophic levels of soil organisms (Li et al. 2022a). There is scientific evidence proving the importance of soil quality, and litter compartment as key factors for nutrient cycling in some worldwide subtropical ecosystems (Li et al. 2022b; Long et al. 2023). Low site quality in subtropical ecosystems can cause rapid land degradation (by decreasing soil organic matter, increasing the content of low labile residues, and nutrient loss by run-off), which overtime reduces soil organic matter decomposition and nutrient cycling (Sadeghi et al. 2022).

Into the context of *A. angustifolia* plantations, the soil biota is important by promoting ecosystem services, such as litter transformation (by incorporating litter on soil profile), soil organic matter decomposition (by improving nutrient cycling), and biological control (through the activity of macro- and microregulators, also described as predators such as Arachnids, Myriapods, and some insects like Mantodea Order) (Auclerc et al. 2022). The soil biota also helps the soil ecosystem and plant community by providing habitat, organic matter, and nutrients (Guhra et al. 2022). The results of this study revealed that there were significant differences among the site quality levels (especially the low site quality) on soil biota abundance, richness, and Shannon's diversity (Gruss et al. 2021). On one hand, it could be considered that the low site quality can significantly alter the soil biota composition by reducing the abundance of predators (Filistatidae, Acaridae, Carabidae, Scutigeridae, Forficulidae, Mantidae, and Pseudoscorpiones), and improving the abundance of ants (Formicidae) (Manu et al. 2022). On the other hand, average and high site quality stands through its characteristics regarding litter and soil compartments have promoted a wide range of soil biota groups (Araujo et al. 2022). The groups of Arachnids (Acaridae, Araneidae and Filistatidae - both classified as predators), Insects (Formicidae, Isotermidae, Carabidae, Scarabaeidae, Staphylindae, and Mantidae that are classified as ecosystem engineer, microregulator, predator, litter transformer, and predators, respectively), and Myriapods (Scutigeridae - predator, and Julidae - litter transformer) were the most affected soil organisms by reducing the soil quality (Zhou et al. 2022). These changes on soil biota community structure promoted negative chances on soil ecosystem (Lu et al. 2023). *A. angustifolia* stands present a wide dissimilarity among the site quality levels (Souza et al. 2022a), and when we decided to start our field study, we expected to find a high impact of site quality on all soil biota functional groups. However, we just observed a significant impact on the predators' abundance after performing the SEM analysis (Sánchez et al. 2022).

Our hypothesis that low site quality promotes negative effects on the soil biota community composition was supported (Aguilar-Paredes et al. 2023). The soil biota community in this condition was characterised with a significant abundance of ants (Formicidae - ecosystem engineers). The decrease in the litter deposition and litter quality (nutrient content) decreased the soil biota abundance, and diversity, since litter deposited on soil surface is considered as the main source of habitat, and the first stage of the soil organic matter with initial degree of decomposition (Vaupel et al. 2023). For the low site quality, the lowest levels of soil biota diversity corresponded to the lowest values of litter deposition as described by Souza et al. (2023a). It also agrees with previous works done by Cappelli et al. (2022), Lozano et al. (2022), and Wang et al. (2022) that reported positive correlations with: i) soil biota diversity, and litter deposition; ii) soil biota abundance, and soil organic matter content; and iii) litter quality, and soil biota richness.

For litter deposition, litter traits (lignin, and litter macronutrients content), and C:N ratio, the high site quality stands showed higher values of litter deposition, litter N, K, Ca, Mg, S, and C content among the other studied site quality levels. These results support our hypothesis that high litter deposition and litter quality may improve the soil ecosystem through *k*-factor (decomposability) and nutrient cycling and the abundance of a diverse soil biota community (Yin et al. 2022). In fact, litter acts in two dissimilar pathways by: i) creating habitat for soil organisms as described by da Silva et al. (2022); and ii) providing plant and organisms' essential nutrients (Swart et al. 2022). Both pathways are supported by our results for litter traits, and soil biota abundance in the high site quality level. Our experiment was designed to directly test whether litter properties affected soil biota biodiversity, and in this context, we must consider that the highest diversity and litter properties were positively correlated by analysing our NMDS and SEM results. According to Deng et al. (2022), litter residues that present high content of macronutrients and low content of lignin are the preferred source for r- and k-strategists that provide the litter biochemical decomposition (Greff et al. 2022). Thus, we must consider that litter residues deposited aboveground with high contents of N, K, Ca, Mg, and S may be positively correlated to their high N, K, Ca, Mg, and S cycling into the soil ecosystem (Marco et al 2022). We cannot exclude the habitat quality and nutrient hypotheses described by Forstall-Sosa et al. (2020), and Melo et al. (2019), in which litter residue drives the soil biota diversity in tropical and subtropical, which can be supported by results on the plots from high site quality. These results agree with previous studies done by Wang et al. (2022), and Wang et al. (2022), which reported that a constant input of high-quality litter may directly influence the nutrient cycling, and soil biota community composition by improving the abundance of some soil organisms, such as: Formicidae, Isotomidae, Carabidae, Acaridae, Scarabaeidae, Julidae, Scutigeridae, Staphylindae, and Mantidae.

The three groups formed on NMDS supported our hypothesis that different site quality levels create different habitats with specific values of litter deposition, litter quality, and soil organic matter that in turn may change the abundance of soil biota community composition. According to the study done by Zheng et al. (2022), the site quality levels and the soil biota community may create a specific pairing between them. This specific pairing can also: i) promote the dominance of some groups such as Formicidae in the low site quality stands (Remke et al. 2022); ii) reduce the abundance of predators (Long et al. 2022); iii) changes litter dynamics, litter nutrient quality, and its decomposability that directly affects the nutrient cycling and the soil biota community diversity (Huangfu et al. 2022); and iv) changes soil chemical properties, that contributes to create negative a tripartite relationship among the soil properties, the abundance of biota, and litter traits as influenced by site quality for *A. angustifolia* stands (Oliva et al. 2023). This study was not designed to estimate root activity, but another study that was performed in the same experimental area has provided evidence for high root activity in the high site quality stands (Souza et al. 2022a). These authors have reported that the high root activity in the high site quality may positively influence the soil biota near the rhizosphere of *A. angustifolia*, and may alter the soil reaction through root exudation, and H^{+} extrusion processes (Ulbrich et al. 2022; Fan et al. 2022). Interestingly these phenomena are indirectly shown by the NMDS and SEM analysis, where dissimilarities among the site quality sites on soil biota community composition, and the correlations among the soil ecosystem, the abundance of some soil organisms, and the litter traits were observed. Based on our results, we must assume that different site quality levels can promote different habitats for root growth, and specific soil food-webs near the rhizosphere of *A. angustifolia* (Chen et al. 2022).

The soil ecosystem, the abundance of some soil biota organisms, and litter traits were three important drivers to soil biota community structure, nutrient cycling, lignin content, *k*-factor, and soil organic matter dynamics (Hopkins et al. 2023). The soil chemical properties, especially soil acidity, and the contents of exchangeable Ca and Mg were found with low values into the low site quality stands, due to the litter traits with high contents of lignin (low decomposability), high *k*-factor, and high C:N ratio. Both compartments combined reduced the refuge for predators such as Araneidae, Acaridae, Carabidae, and Mantidae (Deng et al. 2022; Lü et al. 2023). Considering some relationships among the soil biota organisms, the soil ecosystem, and the litter traits that we observed in our study, we found negative effects on these three compartments as influenced by the site quality reduction (Kang et al. 2021). In the low site quality stands, we found a significant decrease in the abundance of predators Araneidae, Acaridae, Carabidae, and Mantidae, which may be related to active biological control. These results agree with the studies done by Souza et al. (2023b), and Queiroz et al. (2022), who reported low abundance of predators, especially Arachnids in soils with low content of soil organic matter, and low litter deposition. In low-quality sites, we usually found an ecological impact described as habitat simplification. Into this context, the soil and litter traits may act promoting habitats for predators. Once the abundance of this functional group is reduced, the abundance of other groups is directly and indirectly increased such as the abundance of Formicidae (Souza et al. 2022b).

Conclusion

The low-quality sites showed the highest impacts on litter factors, soil chemical properties, and soil biota abundance, richness, and diversity on Cambisols in field conditions from *A. angustifolia* plantations. Our findings suggest that the site quality decreases as a result of decreases in litter quantity and quality (nutrients content), soil fertility, and the abundance and diversity of soil organisms classified as predators. The results of our study highlighted the importance of considering high-quality sites for establishing *A. angustifolia* plantations for both productive and conservation purposes, based on a sustainable way that builds a positive relationship among litter, soil, and organisms. Thus, the use of high-quality sites may exploit positive feedback among litter (by improving litter deposition, k-factor, and exchangeable Ca and Mg contents), and soil properties (by improving soil organic matter, soil P content, Mn and Cu contents, and exchangeable Ca), and soil biota (by improving biota richness, diversity, and the abundance of Scarabaeidae, Julidae, Scutigeridae, Staphylindae, and Mantidae).

Declarations

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Consent to publish We confirm that this manuscript has not been published elsewhere and is not under consideration by another journal. All Authors have approved the manuscript and agree with submission to the final version of the manuscript. We have read and have abided by the statement of ethical standards for manuscripts submitted as a scientific manuscript.

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Figures

Figure 1

Location of our field experiment at the highlands of Santa Catarina, southern Brazil, to assess the influence of site quality levels on soil organisms, litter, and soil compartments. Litterbags with 1 mm^2 mesh to determine the litter decomposition rate of standard litter residues. Plots have considered monoespecific and evenaged *A. angustifolia* stands; an average site quality with 30-years-old trees is shown.

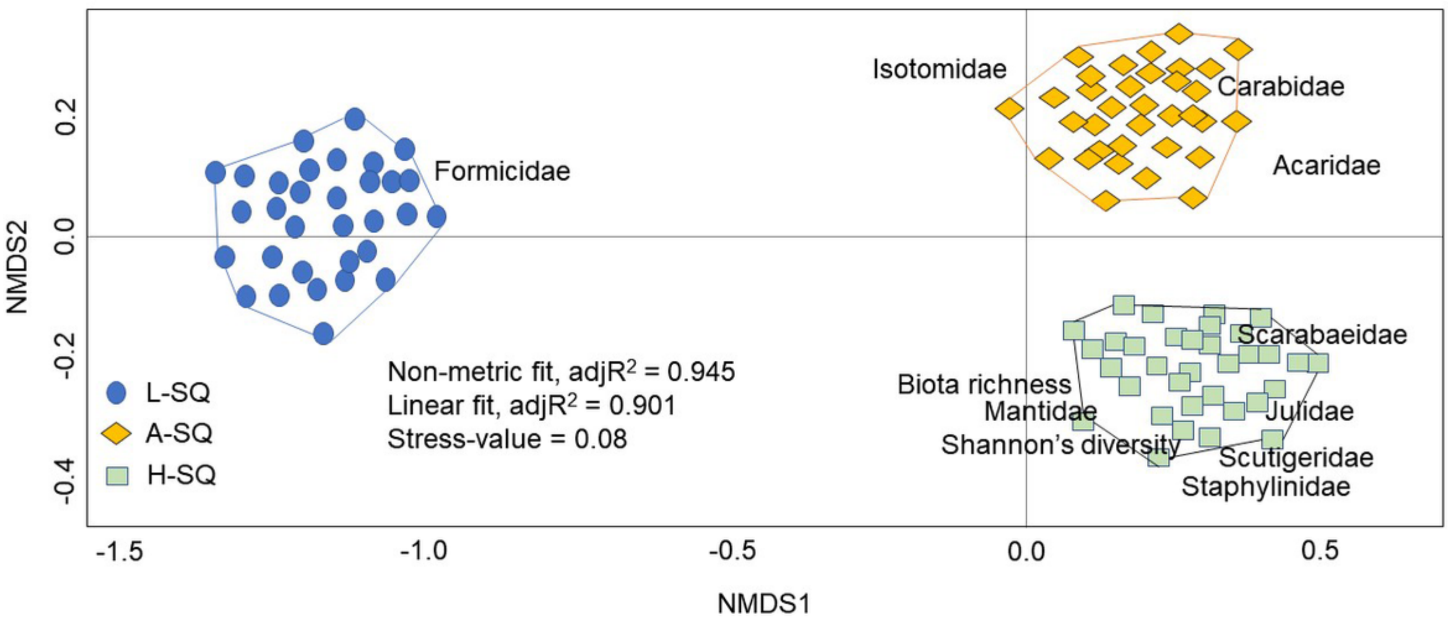

Figure 2

Site quality dissimilarities based on soil biota abundance plotted as non-metric multidimensional scaling (NMDS) of the dataset from all studied site quality levels (L-SQ = Low site quality; A-SQ = average site quality; and H-SQ = high site quality). Polygons represent the studied plots by each site quality, and non-metric fit explains 91.2% of the dataset variance.

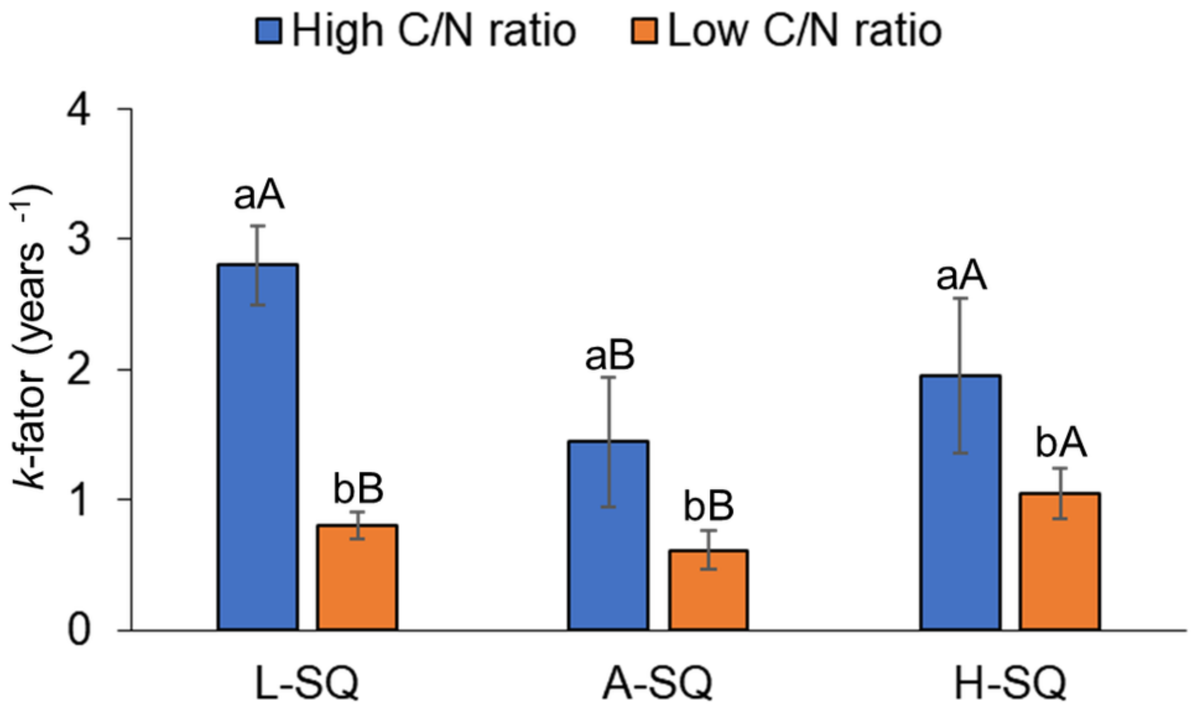

Figure 3

Litter decomposition (k-factor) determined by comparing decomposition rates in litter bags with different litter materials (high C:N ratio vs. low C:N ratio). Small letters compared the studied litter residues (high vs. low C:N ratio), while capital letters compared the site quality levels by the Bonferroni test at $p < 0.05$.

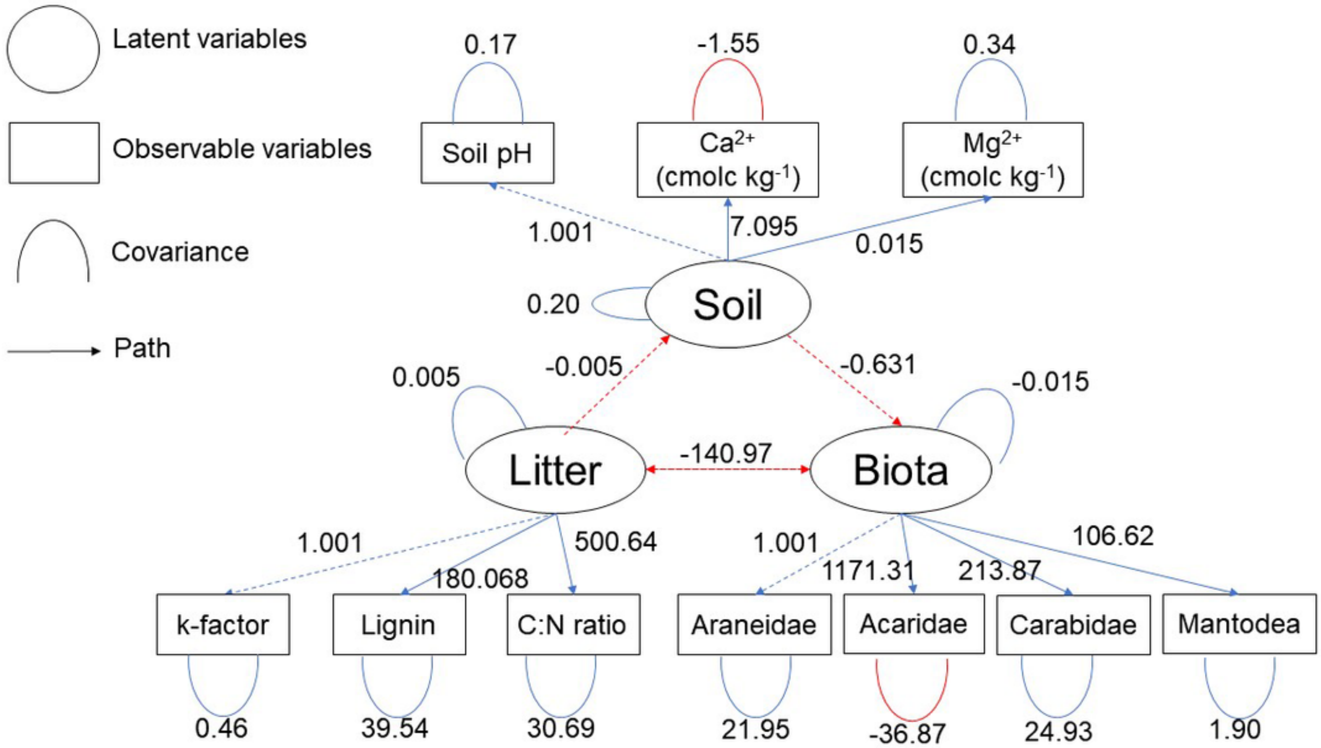

Figure 4

Structural equation model (SEM) indicating the effect paths of soil, litter, and biodiversity indices as influenced by low site quality level ($\chi2 = 152.29$, $p > 0.05$, RMSEA = 0.027, CFI = 0.92). Soil was presented by soil pH, and exchangeable Ca and Mg; Litter was presented by k-factor, lignin, and C:N ratio; and Biota was presented by Acaridae, Araneidae, Carabidae, and Mantodea. Arrows represent significant effects at $p < 0.01$ (dashed arrows) and $p < 0.001$ (full arrows). Blue (positive) and red (negative) values represent estimated values that indicate the proportion of response variation explained by relationships with other variables. Values associated with arrows indicate standardised path coefficients.