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Tree Species Effects on SOC and Soil Microbial Properties: Case Study From Beech and Spruce Stands in Bohinj Valley, Slovenia

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ABSTRACT

Climate change and forest management strategies in Central Europe are driving the decline of spruce in forests, while beech is expected to expand its range. Beech is seen as a key species for converting spruce-dominated forests to mixed forests, aiming to improve forest resilience. The objective of our study was to examine the long-term effects of a spruce stand and a beech stand that transitioned from a conifer-dominated stand on soil organic carbon (SOC), microbial biomass and the abundance of total bacteria, archaea and fungi. In contrast to most other studies, we used a horizon-based soil sampling approach, which provides better insights into how changes in soil chemical properties influence microbial community composition, and consequently, microbial-based processes like C-sequestration. Composite soil samples from two depths, corresponding to the A horizon (approx. 0–10 cm) and the B horizon (approx. 10–20 cm), representing the entire shallow soil profile, were collected from a European beech (*Fagus sylvatica* L.) stand and a Norway spruce (*Picea abies* [L.] Karst.) stand sharing the same soil group on limestone and dolomite. In the top A horizon, the spruce stand exhibited significantly higher levels of total organic carbon (C), total nitrogen (N), dissolved organic C and dissolved N compared to the beech stand (11.5% vs. 9.0%; 0.63% vs. 0.52%; 15.3% vs. 9.5 mg C kg^{-1} dry soil; 2.9 vs. 1.6 mg N kg^{-1} dry soil; respectively). The beech stand had significantly higher base saturation (84.6%) in the A horizon compared to the spruce stand (43.6%), primarily due to increased levels of exchangeable Ca^{2+}. The soil pH did not show statistically significant differences between the stands, indicating a strong buffering capacity of the soil and its slow response to changes in the composition of tree species in the stand. Microbial biomass C (MBC) in the A horizon was significantly higher in the spruce than in the beech stand (585 vs. 492 mg C kg^{-1} dry soil, respectively). While the abundance of bacteria and fungi did not differ significantly between the stands, a higher abundance of archaea was observed in the spruce compared to the beech stand. Total SOC stock in the entire soil profile (A and B horizons) was significantly lower in the beech than in the spruce stand (71.20 ± 3.08 t ha^{-1} and 85.35 ± 2.84 t ha^{-1}, respectively), similar to the total MBC stock (0.42 ± 0.01 t ha^{-1} and 0.48 ± 0.02 t ha^{-1}, respectively), with no significant differences observed in the B horizon. In conclusion, 20 years after the transition to a beech stand, significant differences in soil properties compared to spruce stand remain limited and confined to the A horizon. This reflects the gradual nature of changes driven by the litter input. The transition from a conifer-dominated to a beech-dominated stand leads to a reduction in SOC stocks. In comparison to beech-dominated stands, mixed forests-including both broadleaf and conifer species-may offer a promising strategy to mitigate SOC loss while enhancing forest resilience to climate change and natural disturbances.

Summary

- The transition from a conifer-dominated to a beech-dominated stand leads to a reduction in SOC stocks.
- Beech stand showed lower microbial biomass carbon compared to spruce stand.
- Spruce stand had a higher archaeal abundance; no significant differences in total bacteria and fungi between stands 20 years after transition.

1 | Introduction

Forests are globally important ecosystems, covering about 31% of the total land area, and are playing a crucial role in providing a range of ecosystem services including carbon storage, climate regulation and biodiversity conservation (FAO 2020; Morin et al. 2018). In Europe, Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) are ecologically and economically one of the most important tree species (Caudullo et al. 2016; Durrant et al. 2016). In recent centuries, large-scale planting of high-yielding coniferous tree species such as spruce began in Slovenia, as in large parts of Europe, to increase timber production. Spruce is now under pressure due to global warming and forest disturbances (Seidl et al. 2011, 2014, 2017), leading to significant mortality and a decline in growing stock (Diaci et al. 2017; Kermavnar et al. 2023; Kutnar et al. 2021). To improve forest resilience, Central European management strategies are converting spruce-dominated forests to mixed forests, with European beech being a key species for this transition (Ammer et al. 2008; Klimo et al. 2000). Climate change is also leading to changes in the habitat of forest types, with deciduous tree species expected to migrate to higher altitudes, which are currently dominated by spruce (Bircher et al. 2015; Hanewinkel et al. 2013; Lexer et al. 2015). Although a decline in the range of beech has been predicted due to climate change (Kutnar et al. 2009), the species is expected to expand its range into forest areas that meet its ecological requirements in the coming decades (Klopčič et al. 2022).

Forest soils are an important component of forest ecosystems and their importance is increasing, especially in terms of their potential for carbon sequestration and mitigation of the greenhouse effect or climate change, as they provide an extremely large stock of long-term sequestered carbon (Jackson et al. 2017; Pan et al. 2011). Soils provide water, nutrients and support for trees; and trees, in turn, change both biological and physicochemical properties of soils through variety of ways, including the input of above- and belowground litter, root exudation, influencing water dynamics, changes in microclimate, nutrient uptake, interception of atmospheric deposition, and leaching of nutrients (Augusto et al. 2002, 2015; Hagen-Thorn et al. 2004; Prescott and Grayston 2013). Understanding the relationships between tree species and the soil environment is essential for implementing sustainable forest management, increasing carbon sequestration and mitigating undesirable phenomena such as soil acidification (Stefanowicz et al. 2021). Considering the changing climate and potential shifts in forest composition, it is also crucial to assess the ecological impacts of the transition from spruce- to beech-dominated forests.

Tree species can differ in the mechanisms that affect soil, and changes in the composition of tree species composition in forests can lead to significant changes in the physicochemical and biological properties of soil (Augusto et al. 2002; Binkley and Giardina 1998; Lladó et al. 2018; Prescott and Grayston 2013). One of the primary ways tree species vary in their effect on soil properties and soil food webs is through differences in the quality and quantity of organic matter they contribute to the soil in the form of litter and root exudates (Bardgett 2005; Binkley and Giardina 1998). Spruce stands generally produce more aboveground litter than beech stands, where foliar litter accounts for the largest proportion (75%–85%) (Hansen et al. 2009). Beech leaf litter typically contains higher levels of N, Ca, Mg, and K than spruce litter (Berger et al. 2009; Berger and Berger 2012; Carnol and Bazgir 2013; Hansen et al. 2009). Beech also has a greater fine root biomass than spruce, with roots extending deeper into the soil profile (Bolte and Villanueva 2006; Finér et al. 2007). Although leaf litter is considered the main source of organic matter in forest soil, roots can contribute similar amounts (Prescott and Grayston 2023).

Plant litter is transformed into soil organic matter through the activities of soil fauna and microbes (Prescott and Vesterdal 2021). The decomposition and mineralisation of litter, essential for returning nutrients taken up by vegetation to the soil, depend on the activity of microorganisms, mainly fungi and bacteria (Baldrian 2017; Lladó et al. 2018). Microbial transformations are also crucial in stabilising litter carbon, as a significant proportion of stable organic matter consists of microbial residues and transformation products (Prescott and Vesterdal 2021). Microbial necromass, particularly from fungi, plays an important role in the accumulation of soil organic carbon (SOC) (Malik et al. 2016; Wang et al. 2021). It contributes up to 35% of SOC in forest soils and is vital for the formation of mineral-associated organic carbon, thereby aiding in the long-term stabilisation of SOC (Chang et al. 2024; Cotrufo et al. 2019; Lavallee et al. 2019; Wang et al. 2021). The contribution of microbial necromass to SOC varies due to differences in litter and rhizodeposits chemistry, as well as varying decomposition rates (Wang et al. 2021). For example, lower soil pH stimulates the accumulation of fungal and bacterial necromass, enhancing SOC sequestration (Wang et al. 2021). In spruce stands, litter chemistry slows nutrient cycling and microbial activity, which leads to lower soil pH (Berger and Berger 2012; Cotrufo et al. 2015). While microbial community composition is highly correlated with soil pH, other factors such as organic carbon, C/N ratio, nutrients, temperature and soil water content, and interactions with other organisms also play significant roles (Gupta and Tiedje 2024; Zheng et al. 2019).

It is generally accepted that low pH and low substrate quality (with a high C/N ratio) favour fungal growth, while higher pH and higher substrate quality (with a low C/N ratio) are more suitable for bacterial growth (Ananyeva et al. 2015; Högberg et al. 2006). Consequently, we might anticipate higher fungal and lower bacterial abundance in spruce stands, with the reverse expected in beech stands. Archaeal abundance, however, could be relatively stable or even higher in spruce compared to beech stands, as these microorganisms are often more resilient to extreme environmental conditions, including low pH and

nutrient-poor soils. For example, ammonia-oxidising archaea are adapted to a wide range of pH levels and play crucial roles in nitrification processes, even in acidic soils (Nicol et al. 2008).

Several studies have examined the effects of spruce and beech on soil microbial communities (Asplund et al. 2019; Bahnmann et al. 2018; Gere et al. 2022; Heděnec et al. 2020; Likulunga et al. 2021; Lu and Scheu 2021; Nacke et al. 2016; Stefanowicz et al. 2021; Uroz et al. 2016). However, these studies consistently show that although both tree species significantly influence the composition, diversity and activity of microbial communities in the soil, they differ significantly in the nature and extent of their effects. Spruce, which is typically associated with more acidic soils, tends to support fungal-dominated communities with a higher proportion of saprotrophic fungi and generally results in lower microbial diversity and activity than beech. In contrast, beech promotes more diverse and active microbial communities characterised by a greater abundance of ectomycorrhizal fungi and a more balanced ratio of fungi to bacteria, due to the higher quality of litter and less acidic soil conditions. Despite these findings, many studies use a fixed-depth sampling approach and in addition focus predominantly on the uppermost 10 cm of soil, neglecting potential variations across different soil horizons that could significantly impact microbial dynamics and soil processes. Moreover, most research has concentrated on bacterial and/or fungal communities, with only a few studies simultaneously examining archaeal, bacterial and fungal communities (Uroz et al. 2016). The effect of spruce and beech on archaeal communities (Uroz et al. 2016), as well as the effect of different tree species in general (Bomberg and Timonen 2009; Truu et al. 2020), is an area of research that has received little attention so far.

The aim of this study was to determine the long-term effects of beech and spruce on soil properties, microbial biomass and the abundance of archaeal, bacterial and fungal communities and to assess how these two tree species growing in the same soil type differ in these effects. We hypothesised that (1) the spruce stand differs from the beech stand in terms of soil organic matter content, base saturation and pH; (2) consequently the ratios of bacteria, archaea and fungi will be altered, with the ratio of bacteria-to-fungi being higher in the beech stand than in the spruce stand, without the stand having any effect on the abundance of archaea and (3) the influence of tree species on all studied properties would be more pronounced in the A horizon, where the effect of vegetation is more significant than in the B horizon, where the effect of parent material is more pronounced.

2 | Materials and Methods

2.1 | Study Site

This study was carried out in European beech (*F. sylvatica* L.) and Norway spruce (*P. abies* [L.] Karst.) stands in the Bohinj Valley in the Julian Alps, Slovenia (46°15′23″ N, 13°59′56″ E for the beech stand; 46°15′29″ N, 13°59′47″ E for the spruce stand) at an altitude of 1000 m above sea level with north aspect. The two stands are only about 275 m apart, thus excluding the influence of other factors that could have affected our results. The contact of sub-Mediterranean, continental and mountain

climates results in abundant precipitation and rapid weather changes. In the period from 1991 to 2020, the nearest weather station (Bohinjska Češnjica; 46°17′39″ N, 13°56′32″ E) recorded an average annual temperature of 8.8°C and an average annual precipitation of 2053 mm. Typically, July is the month with the highest temperatures, while November is associated with the highest levels of precipitation. Conversely, January tends to have the lowest temperatures and February is the driest month (see Figure S1; ARSO 2024). It is worth noting that the average annual temperatures have tended to increase over the years and the average annual precipitation decreased over the same period (Figures S2 and S3). The predominant natural forest type in the area is mixed mountain silver fir-European beech-Norway spruce forests. At the time of sampling, the herb layer was mostly absent in both stands. In the spruce stand, species such as *Cardamine trifolia*, *Cyclamen purpurascens*, *Daphne mezereum*, *Festuca altissima*, *Homogyne sylvestris*, *Luzula luzuloides* and *Oxalis acetosella* were present in low densities. In contrast, the beech stand had a more developed shrub layer with a low density of silver fir, beech and spruce, which was not observed in the spruce stand. The predominant soil type covering most of the Bohinj Valley is Leptosol on limestone and dolomite and moraine (TIS/ICPVO 2021).

The selection of stands in the Bohinj Valley was based on inventory data provided by the Slovenian Forest Service (SFS 2022). Specific criteria were established to ensure optimal conditions for the study. These included a minimum tree species proportion of 90% in the growing stock, minimal slope and altitude differences between the two stands, identical aspects and developmental stages that were as similar as possible. Uniformity of parent material and soil type in both stands was verified using the 1:25.000 digital soil map (TIS/ICPVO 2021). Our primary focus was to identify stands that are on carbonate parent material (limestone and dolomite). Additional assessments of potential stands were made through on-site field assessments. Soil coring proved that the soil type at both selected sites is Leptosol on limestone and dolomite, transitioning to Cambic Leptosol and Cambisol (IUSS Working Group WRB 2015). Soil from both sites had similar soil texture, with no significant differences in the proportion of sand, silt and clay (Table 1). Bulk density, calculated using a pedotransfer function, was significantly higher in the beech stand ($0.72 \pm 0.02\,\mathrm{g\,cm^{-3}}$) compared to the spruce stand ($0.60 \pm 0.03\,\mathrm{g\,cm^{-3}}$) at a depth of 0–10 cm, whereas no significant differences were observed at a depth of 10–20 cm (0.96 ± 0.03 vs. $0.90 \pm 0.01\,\mathrm{g\,cm^{-3}}$, respectively).

Historical inventory data from permanent sample plots was analysed to track changes in tree species composition, growing stock and stand structure over time. However, the sampling sites used in this study were selected in more representative parts of the stands, distinct from the permanent sample plots. Stand parameters at these sampling sites are presented in Table 2.

The inventory data for selected two plots of our study were first collected in 1972, which with consecutive inventories every 10 years, revealed significant changes in the stands' tree species composition over the years. From 1972 onwards, in the selected spruce stand, spruce has consistently dominated the stand,

TABLE 1 | Soil texture of the beech stand and the spruce stand.

Stand	Soil depth (cm)	Samples (*n*)	Sand (%)	Silt coarse (%)	Silt fine (%)	Silt total (%)	Clay (%)
Beech	0–10	5	8.3 ± 0.7a	20.4 ± 1.1ab	36.6 ± 0.2a	57.0 ± 1.2ab	34.7 ± 1.8ab
	10–20	5	8.6 ± 0.9a	17.3 ± 0.4bc	34.3 ± 1.8a	51.7 ± 1.6c	39.7 ± 1.3a
Spruce	0–10	5	8.1 ± 1.1a	23.3 ± 0.8a	36.1 ± 1.0a	59.4 ± 0.9a	32.5 ± 0.7b
	10–20	5	6.4 ± 0.7a	15.8 ± 1.6c	38.3 ± 2.1a	54.0 ± 1.1bc	39.5 ± 1.1a

Note: Results are shown as mean ± standard error (SE). Significant ($p < 0.05$) differences between stands and soil depths according to Tukey's HSD test are marked with different letters.

TABLE 2 | Stand parameters captured with MOTI mobile app in the beech stand (B) and the spruce stand (S).

Plot	Basal area (m²/ha)	Dominant height (m)	Growing stock (m³/ha)	Tree species composition (%)		
				Beech	Spruce	Other
B 1	34	15	177	100	0	0
B 2	32	14	166	100	0	0
B 3	34	14	177	100	0	0
B 4	24	14	125	100	0	0
B 5	30	15	157	93	0	7
Average	31	14	160	99	0	1
S 1	66	33	1002	0	97	3
S 2	54	29	717	0	93	7
S 3	62	29	824	0	90	10
S 4	66	32	877	0	91	9
S 5	62	25	671	0	90	10
Average	62	30	818	0	92	8

comprising over 90% of the total growing stock. By 2022, this dominance further increased, with spruce accounting for 98% of the growing stock. In contrast, in the selected beech stand, beech started to take over the stand only after 2002, when the mature stand was harvested, and by 2022, it constituted 72% of the growing stock. Prior to this transition, the stand consisted of a mix of fir, spruce, and beech trees, with fir being the dominant species at that time. The estimated age range of the analysed spruce stand was between 50 and 60 years, while the beech stand falls within the range of 20–30 years. By 2022, the growing stock in the beech stand measured 92 m³ ha⁻¹, while in the spruce stand it was 165 m³ ha⁻¹. However, the low growing stock in the spruce stand can be attributed to harvesting activities that occurred between 2012 and 2022 in the area where the permanent sample plot is located. In 2012, the growing stock in the spruce stand was measured at 696 m³ ha⁻¹.

The current tree density in the beech stand was 1025 trees ha⁻¹, while in the spruce stand it was 250 trees ha⁻¹. In 2012, however, the tree density in the spruce stand was measured at 1475 trees ha⁻¹. The age difference between the two stands is reflected in the tree diameters. In the beech stand, most of the trees had a smaller diameter at breast height due to their younger age, mainly

between 10 and 20 cm. The spruce stand, on the other hand, consisted mainly of trees with breast height diameters of 20–35 cm.

Furthermore, the mobile application MOTI (version 1.0.10; MOTI 2023) was used to record stand parameters, including basal area, dominant height, growing stock and tree species composition at each sampling site in both beech and spruce stands (Table 2). The results showed that the spruce stand had higher basal area, dominant height and growing stock, indicating that the spruce stand was older. In both stands, the selected tree species strongly dominated, accounting for more than 90% of the tree species composition, and both stands can be classified as pure stands.

2.2 | Soil Sampling

Soil samples were collected in late October 2021. At the time of sampling, soil temperature at a depth of 10 cm averaged 5.6°C in the beech stand and 5.7°C in the spruce stand. We selected five dominant trees in each stand that stood out from the surrounding trees in terms of their dimensions. We then sampled the soil around each tree within a 5 m radius. For each selected

dominant tree, we measured the total thickness of the organic horizons (O), which averaged 5.0 cm in the beech and 4.9 cm in the spruce stand. The organic horizons were excluded from analysis as they consist mainly of organic material, which is subject to rapid changes due to decomposition processes. By focusing on the mineral soil, the study aims to examine long-term effects of tree species on soil properties that are less affected by short-term fluctuations. The mineral soil was sampled using a soil corer (diameter 3 cm). The soil sample in the soil corer was separated by a visual assessment of horizons and depth, accounting for spatial variability (A horizon at approx. 0–10 cm; B horizon at approx. 10–20 cm). Throughout the text, we refer to the 0–10 cm layer as 'A horizon' and the 10–20 cm layer as 'B horizon'. Ten soil cores were collected around each selected tree, specifically targeting micro-locations where the B horizon was present. Soil samples of the same horizon from all soil cores around a single tree were merged into one composite sample per depth. Due to the high proportion of skeleton and/or the presence of parent material at the 20 cm depth, we could not take deeper soil samples. Fresh soil samples were homogenised and 2 mm sieved and then divided into four parts: for (i) gravimetric water determination; (ii) physicochemical analysis (dried at 40°C for 24 h), (iii) microbial biomass determination (fresh) and (iv) molecular analysis (shock-frozen on dry ice and stored at −20°C).

2.3 | Soil Physicochemical Analyses

Soil texture was determined using the sedimentation pipette method (ISO 11277 2009). Soil pH was measured in 0.01 M calcium chloride ($CaCl_2$) suspension (ISO 10390 2005). Total soil C (TC) and nitrogen (TN) were quantified with an elemental analyser (Vario MAX, Elementar, Langenselbold, Germany) using the dry combustion method (SIST ISO 10694 1996). Soil mineral carbon (carbonates) was determined using the volumetric method (ISO 10693 1995) with a Scheibler calcimeter. SOC was calculated from the difference between the TC and the mineral C. Dissolved organic carbon (DOC), dissolved total nitrogen (TDN), nitrate (NO_3-N) and ammonium nitrogen (NH_4-N) were extracted with 1:10 (w/v) soil/0.01 M $CaCl_2$ solution. Plant-available P and K were extracted using amon-lactate according to Egner-Riehm-Domingo (Egnér et al. 1960). DOC and TDN were analysed by oxidation and gas analysis with NDIR and EC detector, respectively (Vario TOC cube, Elementar, Langenselbold, Germany). Extracted NO_3-N, NH_4-N and AL-P were determined using a Gallery Automated Photometric Analyser (Thermo Scientific, Waltham, Massachusetts, USA) and extracted AL-K using atomic adsorption spectrometry (AA240FS, Varian, Palo Alto, USA). Potential cation exchange capacity (CEC) was determined by summing the base cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+) extracted with 1 M ammonium acetate (pH 7) and the acidic cations determined using the modified Mehlich method (Soil Survey Staff 1992). Extracted Na^+ and K^+ were analysed with a flame emission spectrometer and extracted Ca^{2+} and Mg^{2+} with an atomic absorption spectrophotometer. Base saturation was calculated as the percentage of CEC occupied by base cations.

Soil bulk density was calculated using a pedotransfer function developed for Slovenian forest soils by Kobal et al. (2011). Soil

organic and microbial biomass carbon (MBC) stocks (t ha^{-1}) were then calculated using the equivalent soil mass approach described by Lee et al. (2009), where the sample with the lowest bulk density in both the A and B horizons was chosen as the reference soil mass. These stocks were then additionally corrected for the percentage of skeletons.

2.4 | Microbial Biomass and Molecular Analyses

Soil MBC and microbial biomass nitrogen (MBN) were determined by chloroform fumigation extraction method using 0.01 M $CaCl_2$ as extracting solution (ISO 14240-2 2011). Soil DNA was extracted using the DNeasy PowerSoil Pro Kit (Qiagen GmbH, Hilden, Germany) according to the manufacturer's instructions. The quality and concentration of DNA extracts were determined spectrophotometrically (NanoDrop 2000 UV–vis Spectrometer; Thermo Scientific, Waltham, Massachusetts, USA). Quantitative polymerase chain reaction (qPCR) was then used as described in Govednik et al. (2023) to quantify the total bacterial, archaeal and fungal communities in total extracted DNA by targeting bacterial and archaeal 16S rRNA gene and fungal ITS region, respectively. Primers used for bacteria were 341F/534R (Muyzer et al. 1993), for fungi ITS3F/ITS4R (White et al. 1990) and for archaea Crenar771F/Crenar975R (Ochsenreiter et al. 2003).

The 15 μL qPCR reaction mixture contained 2 ng of DNA sample, 1 μM forward and reverse primers specific for each gene and 7.5 μL of Master Mix (ABsolute Blue qPCR SYBR Green Low Rox, Thermo Scientific, Waltham, Massachusetts, USA). The PCR cycling conditions set in a qPCR system (QuantStudio 5, Applied Biosystems, Waltham, USA) for primer pair 341F/534R were 95°C for 15 s, 60°C for 30 s, 72°C for 30 s, followed by acquisition step at 80°C for 18 s (35 cycles); 95°C for 15 s, 55°C for 30 s, 72°C for 30 s, followed by acquisition step at 80°C for 18 s (35 cycles) for primer pairs ITS3F/ITS4R and Crenar771F/Crenar975R. Efficiencies for bacterial 16S and ITS were 95% and 93%, respectively, while for archaeal 16S the efficiency was 65%. All R^2 for the standard curves were 0.999 or higher. The calculation of the target gene copies of each sample was performed using Design & Analysis Software (Thermo Fischer Scientific, Waltham, Massachusetts, USA).

2.5 | Statistical Analysis

The statistical analyses were performed using the SPSS Statistics (version 22, IBM, Armonk, NY, USA). The data were checked for normal distribution and homogeneity of variances using Shapiro–Wilk test and Levene's test, respectively. Based on five replicates in each stand, we used analysis of variance (ANOVA) and a *post hoc* Tukey HSD test for comparison of means to test for the effect of forest stand and horizon on soil chemical properties, MBC, MBN and abundances of bacteria, archaea and fungi. The difference in total SOC and MBC stocks in the entire soil profile between the two stands was tested using a Student's *t*-test. The level of significance of $p = 0.05$ was accepted in all cases. Graphs were made with R software (R Core Team 2024) by using 'ggplot2' package (Wickham 2016).

3 | Results

3.1 | Soil Chemical Properties

The soil of the spruce stand had significantly higher levels of total and dissolved organic C (SOC and DOC) and total and dissolved N (TN and TDN) in the A horizon (0–10 cm) than that of the beech stand (Table 3). In the A horizon, base saturation was significantly higher in the beech stand than in the spruce stand (84.6% vs. 43.6%) due to the Ca^{2+} content, which was significantly higher in the A horizon in the beech stand than in the spruce stand (26.24 $mmol_c$ 100 g^{-1} vs. 14.90 $mmol_c$ 100 g^{-1}, Table 3). In the B horizon (10–20 cm), no significant differences in chemical properties were observed between the two stands.

Total SOC stock in the entire soil profile (sum of both depths) was significantly higher in the spruce stand (85.35 ± 2.84 t ha^{-1}) compared to the beech stand (71.20 ± 3.08 t ha^{-1}). In the A horizon, the SOC stock was significantly higher in the spruce stand

than in the beech stand; however, no differences were observed in the B horizon (Figure 1A; Table 3).

3.2 | Microbial Biomass

MBC, determined by chloroform fumigation extraction, was on average significantly higher in the A horizon compared to the B horizon in both stands (Figure S4A). In the A horizon, we found a significantly higher MBC content in the spruce compared to the beech stand (Figure S4A; Table S1). Total MBC stock in the entire soil profile was significantly higher in the spruce stand (0.48 ± 0.02 t ha^{-1}) compared to the beech stand (0.42 ± 0.01 t ha^{-1}). In the A horizon, the MBC stock was significantly higher in the spruce stand than in the beech stand, while no significant differences were observed in the B horizon (Figure 1B). Both MBN and total extracted DNA were on average significantly higher in the A horizon, but significant differences between the means of the two stands were not detected (Figure S4B,C; Table S1). Mean levels of total extracted

TABLE 3 | Soil chemical properties of the beech stand and the spruce stand.

Stand	Beech		Spruce	
Soil depth (cm)	0–10	10–20	0–10	10–20
pH (CaCl$_2$ 0.01 M)	5.08 ± 0.23 a	5.11 ± 0.30 a	4.49 ± 0.10 a	5.01 ± 0.15 a
Carbonates (%)	0.56 ± 0.10 a	0.74 ± 0.31 a	0.40 ± 0.09 a	0.56 ± 0.10 a
SOC (%)	9.00 ± 0.39 b	4.00 ± 0.36 c	11.54 ± 0.67 a	4.94 ± 0.28 c
SOC stock (t ha^{-1})	44.81 ± 1.92 b	26.38 ± 1.42 c	57.46 ± 3.33 a	27.89 ± 1.42 c
Organic matter (%)	15.52 ± 0.67 b	6.90 ± 0.63 c	19.88 ± 1.14 a	8.54 ± 0.48 c
TN (%)	0.52 ± 0.02 b	0.23 ± 0.02 c	0.63 ± 0.03 a	0.29 ± 0.01 c
C/N	17 ± 0.47 a	18 ± 0.58 a	18 ± 0.44 a	17 ± 0.57 a
DOC (mg kg^{-1} dry soil)	9.45 ± 0.99 b	4.58 ± 0.47 c	15.30 ± 1.66 a	6.42 ± 0.83 bc
TDN (mg kg^{-1} dry soil)	1.65 ± 0.31 b	0.87 ± 0.32 b	2.90 ± 0.26 a	1.63 ± 0.13 b
P$_2$O$_5$ (mg 100 g^{-1})	1.06 ± 0.16 a	0.44 ± 0.02 b	1.38 ± 0.14 a	0.52 ± 0.06 b
K$_2$O (mg 100 g^{-1})	11.02 ± 1.05 a	8.54 ± 1.69 a	12.90 ± 0.58 a	8.64 ± 0.63 a
Ca^{2+} ($mmol_c$ 100 g^{-1})	26.24 ± 2.92 a	14.80 ± 2.68 b	14.90 ± 1.57 b	14.90 ± 1.96 b
Mg^{2+} ($mmol_c$ 100 g^{-1})	0.78 ± 0.03 ab	0.41 ± 0.04 b	1.49 ± 0.31 a	1.05 ± 0.38 ab
K$^+$ ($mmol_c$ 100 g^{-1})	0.24 ± 0.03 a	0.16 ± 0.04 a	0.26 ± 0.02 a	0.18 ± 0.02 a
Na$^+$ ($mmol_c$ 100 g^{-1})	0.08 ± 0.01 a	0.05 ± 0.01 bc	0.07 ± 0.00 ab	0.04 ± 0.00 c
H$^+$ ($mmol_c$ 100 g^{-1})	18.30 ± 0.57 ab	15.95 ± 0.72 b	22.24 ± 1.07 a	18.59 ± 1.50 ab
S ($mmol_c$ 100 g^{-1})	27.32 ± 2.93 a	15.44 ± 2.73 b	16.74 ± 1.64 b	16.18 ± 2.08 b
CEC ($mmol_c$ 100 g^{-1})	32.38 ± 1.28 a	32.35 ± 2.91 a	38.77 ± 1.16 a	39.37 ± 1.19 a
Base saturation (%)	84.60 ± 7.88 a	49.40 ± 10.49 b	43.60 ± 5.23 b	41.00 ± 5.13 b
NH$_4$-N (mg 100 g^{-1})	0.35 ± 0.04 a	0.46 ± 0.24 a	0.49 ± 0.06 a	0.31 ± 0.03 a
NO$_3$-N (mg 100 g^{-1})	0.16 ± 0.04 ab	0.07 ± 0.03 b	0.21 ± 0.05 a	0.12 ± 0.01 ab

Note: Significant ($p < 0.05$) differences between stands and soil depths according to Tukey's HSD test are marked with different letters. Results are shown as mean ± standard error (SE).

Abbreviations: CEC, cation exchange capacity; DOC, dissolved organic carbon; S, sum of base cations; SOC, soil organic carbon; TDN, total dissolved nitrogen; TN, total nitrogen content.
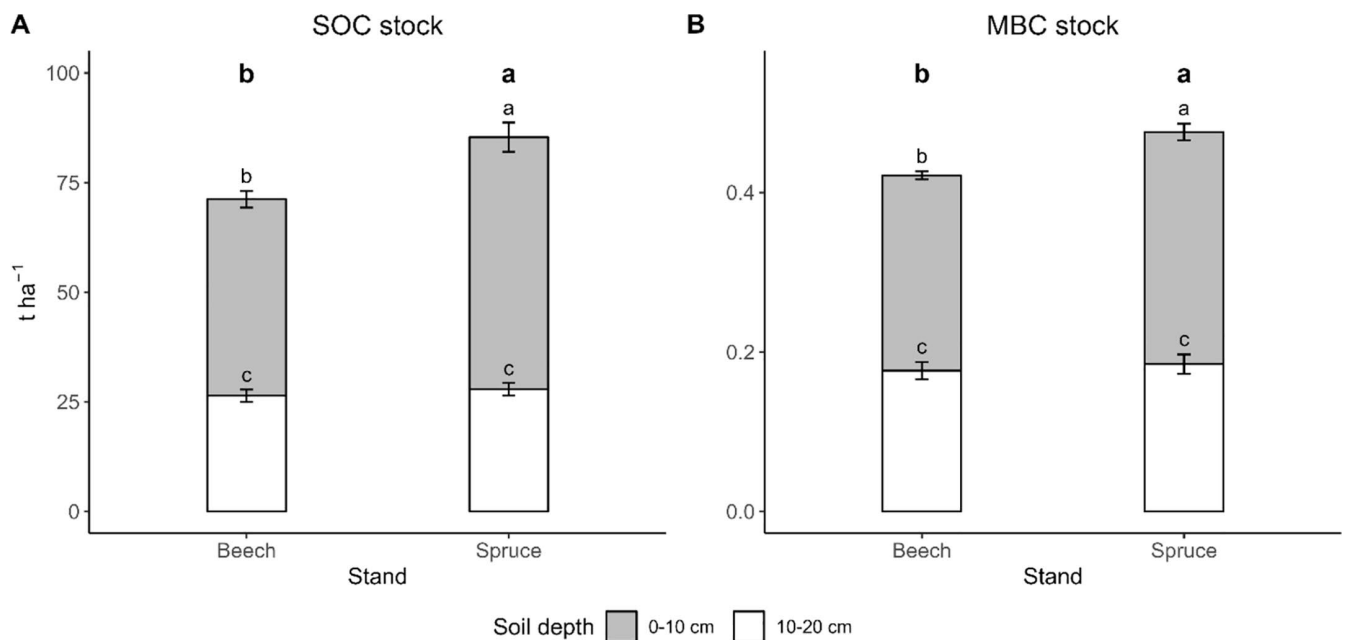
FIGURE 1 | Soil organic (A) and microbial biomass (B) carbon stocks in beech and spruce stand at two sampling depths (cm), which corresponds to soil horizons A and B, and total C stock in the soil profile. Averages and standard errors of five replicates are shown. Different letters indicate significant differences according to Tukey's HSD test ($p < 0.05$) for the depths and a Student's t-test for the total values in bold. Please note the different scales of Y-axes.
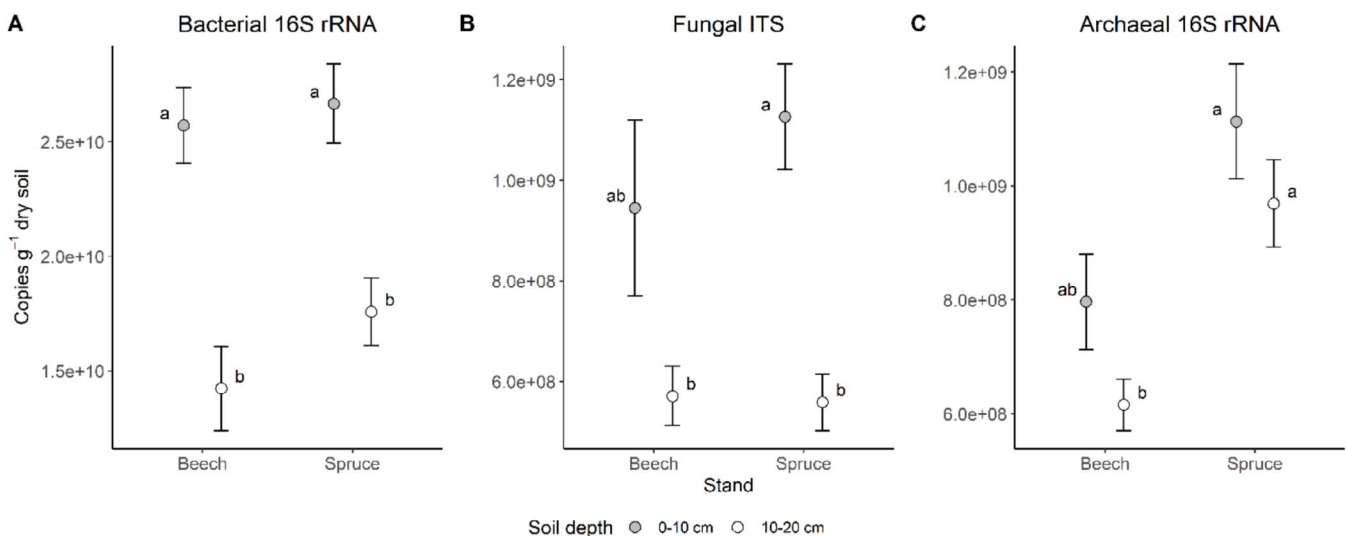

FIGURE 2 | Relative abundance of bacteria (A), fungi (B) and archaea (C) determined by quantitative PCR in beech and spruce stand at two sampling depths (cm). Averages and standard errors of five replicates are shown. Different letters indicate significant differences according to Tukey's HSD test ($p < 0.05$). Please note the different scales of Y-axes.

DNA at depths 0–10 cm and 10–20 cm were 155.5 ± 9.0 and $93.8 \pm 3.8\,\mu g\,g^{-1}$ dry soil for the spruce stand and 145.0 ± 6.6 and $73.6 \pm 7.2\,\mu g\,g^{-1}$ dry soil for the beech stand, respectively.

3.3 | Abundances of Bacteria, Archaea and Fungi

Bacterial abundance was higher in the A horizon than in the B horizon in both stands but did not differ between the stands. A similar pattern was observed for fungal abundance; however, the difference between depths was observed only in the spruce stand (Figure 2A,B; Table S1). No significant differences were observed in the bacteria-to-fungi ratio between stands (Table S1).

Interestingly, fungal abundance decreased more rapidly with depth than bacterial abundance in the spruce stand, resulting in a broader ratio in the B horizon. In contrast, the opposite pattern was observed in the beech stand, but both differences were insignificant. Depth stratification was less pronounced for archaea, as no differences between depths were observed in either stand (Figure 2C; Table S1).

4 | Discussion

Beech and spruce are widespread in the study area (Bončina et al. 2001; Kutnar et al. 2021), and it is expected that beech

will expand its range due to climate change. Their current dominance in the selected stands reflects past forest management, while large ungulates influence forest development through browsing (Diaci et al. 2022; Klopčič et al. 2017; Klopcic and Boncina 2011; Roženbergar et al. 2019). There is no clear pattern of beech expansion either nationwide or in the study area (Klopčič et al. 2022; Kutnar et al. 2021; Poljanec et al. 2010), although climate change in Slovenia is well underway (Bertalanič et al. 2018).

The significantly higher SOC content in the A horizon of the spruce stand compared to the beech stand (Table 3) can be attributed to several factors. A higher SOC content in spruce stands, primarily in the topsoil (0–15 cm), was reported by previous studies (Clesse et al. 2022; Cremer et al. 2016; Desie et al. 2019; Steffens et al. 2021) and could be due to a slower decomposition rate of spruce litter, which is more recalcitrant due to its higher lignin and lower nutrient content, leading to a greater accumulation of organic matter. DOC leaching from the organic horizons is one of the pathways by which C enters the mineral soil horizons, and it has been found to be high under tree species with higher C stocks in the organic horizons, such as spruce (Prescott and Vesterdal 2021; Vesterdal et al. 2013), which was confirmed in our study (Table 3). Consequently, total and A horizon SOC stocks were significantly higher in spruce stand compared to beech stand (Figure 1A; Table 3). Higher total SOC stocks as well as higher C stocks in organic horizons in spruce stands compared to beech stands have been reported in previous studies (Cremer et al. 2016; Galka et al. 2014; Prietzel and Bachmann 2012; Vesterdal et al. 2008, 2013). In mineral horizons, there is a trade-off, species that accumulate more C in the organic horizons tend to store less C in mineral horizons (Vesterdal et al. 2013), but this was not the case in our study. While aboveground litter, particularly leaf litter, is considered as the main source of organic matter in forest soils, roots can make a similar contribution. Although there is limited literature on this topic, fine root production in forests averages between 3.1 and 6.0 t ha^{-1} year^{-1}, which is comparable to average rates of leaf litter production, typically ranging from 1 to 9 t ha^{-1} year^{-1} (Finér et al. 2011; Prescott and Grayston 2023). The largest amount of living fine root biomass in spruce is found at a depth of 0–10 cm, while the fine root biomass of beech at a depth of 20–40 cm can be about four times higher than that of spruce (Achilles et al. 2021; Bolte and Villanueva 2006). Although we could not sample deeper than 20 cm due to the high proportion of skeleton and/or the presence of parent material, differences in SOC stock between the beech and spruce stands may exist also in deeper soil layers. The contributions of roots to soil organic matter are particularly critical, as noted by Prescott and Vesterdal (2021), who highlight that root-derived organic matter contributes more to stable soil organic matter than aboveground litter due to its slower decomposition and chemical complexity.

Microbial biomass, expressed as MBC, was significantly higher in the A horizon of the spruce stand than in the beech stand (Figure S4A; Table S1), likely due to the higher SOC content, which is an important substrate for microbial communities. This finding aligns with previous studies that reported positive relationships between SOC and microbial biomass (Peng et al. 2020; Stefanowicz et al. 2021). The observed decrease in microbial biomass with depth in both stands is likely due to the limited

C sources available to microbes in deeper, mineral soil horizons (Ekschmitt et al. 2005; Wardle 1992). Contradictions exist in the literature regarding microbial biomass under deciduous and coniferous trees. Gere et al. (2022) reported findings similar to ours, showing higher MBC in spruce stands compared to beech stands in Slovakia. However, some studies report higher microbial biomass under deciduous trees, while others find no significant differences (Augusto et al. 2015; Lorenz and Thiele-Bruhn 2019). PLFA-based studies on fungal and bacterial biomass have also produced mixed results. Some studies reported higher bacterial biomass in beech compared to spruce stands (Heděnec et al. 2020), while others found no significant differences (Stefanowicz et al. 2021; Zheng et al. 2022). Similarly, variations in fungal biomass have been observed, with some studies reporting higher values in beech stands (Bahnmann et al. 2018; Zheng et al. 2022), while others found no significant differences (Heděnec et al. 2020; Stefanowicz et al. 2021). These discrepancies are likely attributable to site-specific factors (e.g., soil type, parent material, climate, tree age, management history) and methodological differences (e.g., experimental setup—natural forest vs. common garden design; sampling depth, seasonality, methods for quantifying microbial biomass).

In forest soils, the contribution of slowly decomposable plant residues to SOC is greater than that of microbially derived C (Cotrufo et al. 2019; Lavallee et al. 2019). However, higher MBC stock in the spruce stand (Figure 1B) could increase SOC content through the accumulation of microbial necromass. Since microbial biomass serves as a source of microbial residues that form mineral-associated organic carbon, this could potentially lead to higher SOC levels in spruce compared to beech stands, contributing to the long-term stabilisation of SOC. Generally, mineral-associated organic carbon, which originates from microbial necromass or plant decomposition products and exudates, is better protected from microbial decomposition, resulting in longer mean residence times than particulate organic carbon (Cotrufo et al. 2019; Hansen et al. 2024; Lavallee et al. 2019). Therefore, the stability of organic carbon is also highly dependent on soil properties, especially texture (Angst et al. 2018). The amount and composition of microbial biomass and the accumulation of necromass are also influenced by mean annual temperature and precipitation through their effects on vegetation and litter composition, soil pH and SOC content, as well as by microbial C use efficiency and turnover rate (Wang et al. 2021). Consequently, higher temperatures and lower precipitation in the study area (Figures S2 and S3) due to climate change could reduce microbial necromass accumulation and thus lower carbon sequestration potential.

The significant differences in several soil chemical properties observed in the A horizon (0–10 cm) are probably related to the different influences of litterfall and decomposition rates. Deciduous tree species generally have a much higher nutrient content, such as N, K, Ca and Mg, in their foliage as compared to coniferous species (Augusto et al. 2002). In the A horizon, the beech stand had almost twice the exchangeable Ca^{2+} content of the spruce stand (Table 3). Previous studies have found higher Ca^{2+} contents in beech litter compared to spruce litter (Berger and Berger 2012; Carnol and Bazgir 2013; Cremer et al. 2016). Therefore, the increased content of exchangeable Ca^{2+} in the A horizon of the beech stand can be partly attributed to a

phenomenon called base pump effect, which is typical for beech and other deciduous tree species. This process refers to the uptake of cations such as Ca, Mg and K from mineral subsoils, which are then sequestered into biomass and re-translocated to the organic horizons through litterfall, significantly affecting the chemical properties and nutrient distribution in the soil (Achilles et al. 2021; Berger et al. 2006). In addition, soils under beech stands are associated with a higher abundance of burrowing earthworms than those under spruce stands (Desie et al. 2019; Schelfhout et al. 2017), which are essential for incorporating organic material into the soil through bioturbation and influencing the activity of other soil organisms, thus contributing to a faster turnover of organic matter and a vertical distribution of Ca^{2+} cations.

No significant differences in pH were found in our study; however, the beech stand had much higher base saturation than the spruce stand (84.6% vs. 43.6%, respectively) (Table 3). Spruce is generally associated with creating more acidic soil than beech, which is supported by several authors (Bahnmann et al. 2018; Buresova et al. 2021; Hagen-Thorn et al. 2004; Perković et al. 2019; Zheng et al. 2022), while other studies have also reported nonsignificant differences in pH (Asplund et al. 2019; Gere et al. 2022; Heděnec et al. 2020; Likulunga et al. 2021; Stefanowicz et al. 2021; Uroz et al. 2016). The absence of pH differences between the two stands in our study suggests a considerable buffering capacity of the Cambic Leptosol developed on limestone, which leads to a slow response of pH to changes in tree composition. Although spruce tends to acidify the soil through the accumulation and slow decomposition of its needle litter, the deeper mineral soil beneath beech, at later stages of soil development, can also become acidified through bioacidification. This process involves the excretion of protons (H^+) as part of the base pump effect, where beech trees uptake base cations from deeper soil layers (Achilles et al. 2021).

The selected stands are located in close proximity, and it can be assumed that their initial soil properties are comparable due to the slow soil development and similar pedogenetic factors. However, recent natural disturbances and the chosen criteria for selecting optimal stands resulted in the identification of only two potentially comparable sites. Since only two stands were analysed, covariates were excluded from the analysis, representing a limitation of the study. In addition, spruce and beech stands differed in age and tree density, which could influence the effects of tree species on soil properties. Therefore, certain aspects of soil properties in the younger beech stand, such as pH, may not yet fully reflect the changes that would occur in the mature forest.

The composition of the microbial communities in forest soil is influenced by several factors, with soil pH and C/N ratio emerging as the most prominent drivers, but also other variables, such as soil water content, N and P content and SOC content play important roles. These factors are intricately associated with tree species, both directly and indirectly through the influence of litter and root exudates (Thoms et al. 2010; Kaiser et al. 2016; Nacke et al. 2016; Lladó et al. 2018; Dukunde et al. 2019; Heděnec et al. 2020; Lu and Scheu 2021; Likulunga et al. 2021). However, our study did not reveal significant differences in fungal and bacterial abundances, or in the bacteria-to-fungi ratio, between the beech and

spruce stands (Figure 2A,B; Table S1), likely due to minimal differences in soil pH and C/N ratio. Although higher fungal abundance would typically be expected in soils with higher SOC content (Malik et al. 2016; Strickland and Rousk 2010), we observed a significantly higher abundance of archaea in the spruce stand. Additionally, depth had a greater effect on bacteria and fungi than on archaea, confirming the adaptability of archaea to a wide range of conditions. Differences in soil chemical properties resulting from different tree species composition observed in our study are expected to intensify over time. These variations are likely to result in more pronounced distinctions in microbial communities between spruce and beech stands.

5 | Conclusion

This study provides insights into gradual changes in soil properties following the transition from a conifer-dominated stand to a beech-dominated stand. Twenty years after the transition, notable changes were observed in the A horizon (SOC, microbial biomass, and base saturation), where the influence of vegetation is more pronounced and becomes apparent more readily. In contrast, changes in the B horizon, which is more strongly influenced by parent material and may buffer potential changes, are expected to occur over a longer time frame.

Although no significant differences were found in fungal and bacterial abundances—likely due to minimal variation in influencing properties such as soil pH and C/N ratio—differences in archaeal abundance were observed. This finding is noteworthy, as the influence of tree species on archaeal communities remains less understood compared to bacteria and fungi, despite the crucial role of archaea in processes like the nitrogen cycle. More comprehensive studies on taxonomic and functional diversity are needed to provide deeper insights.

Furthermore, our results confirm that the transition from a conifer-dominated to a beech-dominated stand leads to a reduction in SOC stocks. Compared to purely beech-dominated stands, mixed stands with conifers may offer a promising strategy to balance SOC loss, particularly as mixed stands are known to enhance forest resilience to climate change and natural disturbances.

Author Contributions

Peter Horvat: writing – original draft, writing – review and editing, conceptualization, formal analysis, visualization, investigation. **Anton Govednik:** writing – review and editing, formal analysis, data curation, methodology. **Matija Klopčič:** conceptualization, writing – review and editing. **Marjetka Suhadolc:** conceptualization, writing – original draft, writing – review and editing, methodology, supervision, funding acquisition.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.