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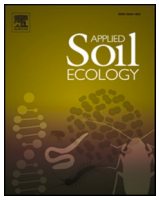

Forest density and edge effects on soil microbial communities in deciduous forests across Europe

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ABSTRACT

Forest fragmentation increases the proportion of edge area and this, in turn, induces changes in forest structure, species composition and microclimate. These factors are also strongly determined by the forest management regime. Although the interactive effects of edges and density on forest plant communities have been extensively studied, little is known about the response of the belowground communities. Here we investigated the variation of soil microbiota in 45 deciduous broadleaved forests along a latitudinal gradient from Italy to Norway at a continental scale across Europe. Phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA) were used to map the microbial community in the forest edge and interior across three forest densities (dense, intermediate, open forest). Microbial community composition was only affected by forest edge effects and not by forest density. We did not find any interaction effects between forest density and distance-to-edge. Arbuscular mycorrhizal fungi (AMF) were significantly more abundant in edges and Gram-negative bacteria more abundant in interiors, respectively. The microbial community composition was closely related to soil pH, soil potassium and nitrogen, texture (percent sand) and soil temperature. Soil pH was positively correlated with the saprotrophic fungi and potassium was positively correlated with Gram-negative bacteria but negatively correlated with Actinobacteria. In sum, we reveal the notable effects of forest edges on the soil AMF abundance. This result indicated that AMF could possess a stronger affinity with species growing in the edges, which may help to improve plant performance under hostile conditions herein.

1. Introduction

Humans have transformed forests into other land uses for thousands of years, which largely increased the level of forest fragmentation (Kaplan et al., 2009). Consequently, the proportion of interior forest habitat to the total amount of forest area has decreased steeply to the benefit of increasing forest edge area across many forested parts of the globe (Fischer et al., 2021). Based on the proportion of forest in the neighborhood of a forest pixel, an approach to define forest interior as described as Riitters et al. (1997), the global net loss rate of forest interior area is more than three times the global net loss rate of all forest habitat loss between 2000 and 2012 (Riitters et al., 2016). It has been estimated that nearly 20 % of the global forested area is positioned within 100 m of a forest edge (Haddad et al., 2015), while approximately 3.6 % of deciduous forests across Europe within 4.5 m of a forest edge (Meeussen et al., 2021).

In forest edges, the environmental conditions, including the temperature, light, soil moisture, and nutrient inputs are different from

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those away from the edges and towards the interiors of the forest fragments, and these local changes can strongly impact biological communities (Cadenasso and Pickett, 2001; Pardini, 2004). These so-called "edge-effects" within forest fragments are multi-faceted and depend on the contrasting characteristics between edges and interiors as well as edge and adjacent land (Harper et al., 2005). For example, forest edges are generally exposed to more sunlight, higher wind speed, and stronger air mixing, leading to a higher evapotranspiration and temperature variability than the interiors of the forest (Chen et al., 1993; Young and Mitchell, 1994; Didham and Lawton, 1999; Davies-Colley et al., 2000). These initial responses to edge effects will affect the recruitment, growth, mortality, and species interactions at the edge, which will have a profound influence on community structure and ecosystem functioning (Fagan et al., 1999; Harper et al., 2005).

The size of edge effects are not similar but they generally depend on the size and shape of the forest fragments (Ewers and Didham, 2007), the contrast with adjacent non-forest environments (Fletcher and Koford, 2003), and other contextual factors, such as forest structure and edge orientation (Matlack and Litvaitis, 1999; Orczewska and Glista, 2005; Remy et al., 2018). Notably, forest density can strongly affect the response of community structure to forest edges as the management practices could shape the community structure via general alterations of forest structure and its impact on the underlying microclimate, which would further affect the edge contrast with the surrounding landscapes (Aussenac, 2000; Crow et al., 2002). For instance, in open (recently thinned) forests, wind speeds, nutrient inputs, and seed dispersal of generalists into the interior of the forests is facilitated and thus a lower edge-interior contrast is found than in dense forests (Cadenasso and Pickett, 2001). Although edge effects among forests with different densities have been studied in few studies, most of them still focused on above-ground biological communities (Karraker and Welsh, 2006; Morris et al., 2010; Girona et al., 2016; Govaert et al., 2020), therefore little is known about the dual, interactive effects of forest edges and densities on belowground microbial communities.

Soil microbial communities offer great potential in forest ecosystem functioning as they are actively involved in biogeochemical processes, such as soil organic matter decomposition, and nutrient immobilization (Osburn et al., 2021). Due to the different sensitivity of microbial species to environmental conditions such as light, temperature, moisture, and soil nutrients, the composition of the microbial community is expected to vary due to forest densities or edge effects. For example, increased light in thinned forests or forest edges may enhance the supply of carbohydrates from vegetation to symbiotic fungal counterparts (such as mycorrhiza), thereby enhancing the colonization and growth of fungi (Louche-Tessandier et al., 1999; Fuzy et al., 2014). Similarly, decreased topsoil moisture in edges and increased nitrogen availability can be expected to impact the biomass, community composition and activity of the soil microbial groups (Allen and Schlesinger, 2004; Malmivaara-Lamsa et al., 2008; Ushio et al., 2008; Remy et al., 2018). Although the effect of forest edge or density on the soil microbial community has been discussed in several studies (Cheng et al., 2018; Boeraeve et al., 2019), most of them were based on a molecular (metagenomic) approach. While phospholipid fatty acid (PLFA)-based analysis could quantify the total viable biomass and especially focus on the profiles of active microbial community (Orwin et al., 2018), which could expand our knowledge in the interactive effect of forest edge and density on active belowground communities.

Here we address this knowledge gap and examined the belowground community composition responses to the edge effects within forests with different densities in 45 deciduous broadleaved forest edges across Europe. The edges were situated along a latitudinal gradient from Italy to Norway. Our aim was to disentangle the effects of the distance to the edge and forest density on soil microbial community composition at the continental scale, while taking variation of environmental gradients in multiple European regions into account to increase generality. We expected that the microbial community composition would change along the forest edge-interior transect, but that these effects depended on the forest density.

2. Materials and methods

2.1. Study area

Soils were sampled in 9 different regions along a latitudinal gradient in Europe, crossing the temperate, Mediterranean and boreonemoral forest biomes. Along this north-south gradient, the selected regions were in Norway, Central Sweden, Southern Sweden, Germany, Poland, Belgium, Northern France, Switzerland and Italy (Fig. 1). In three of these regions, i.e., Norway, Belgium and Italy, three elevational belts were additionally sampled (i.e. low, intermediate and high elevation). Other regions only contained the lower elevational belt (i.e., lowland conditions). All of the 15 sampling sites (9 low elevation sites, 3 intermediate elevation sites and 3 high elevation sites) contained three distinct forest types, i.e., dense forest, intermediate forest and open forests. Dense forests were characterized by a well-developed shrub layer, high basal area and dense canopy cover. This type of forest had not been managed for >10 years and was generally not thinned during the last 30 years. Intermediate forest had lower basal areas and canopy coverage since its last thinning event, usually occurring 5 to 10 years before sampling. Open forest was characterized by a lower basal area and higher canopy openness. These forests had been thinned during the 1–4 years before sampling. A 100 m transect from the southern forest edge to the interior was established in each forest. A total of 45 transects were included in this study (15 sites × 3 forest densities). In each transect, two $3 \times 3\ m^2$ plots were set up, one at the edge (0–3 m) and one at the interior (98–101 m away from the edge). More details regarding the study design are provided in Govaert et al. (2020) and Meeussen et al. (2020).

2.2. Soil chemical and texture analysis and soil microclimate: abiotic analysis

In all 90 plots, topsoil samples (0–10 cm depth) were collected for chemical analyses of nutrients and pH, and subsurface soil samples (10–20 cm depth) were used for texture analysis. Five random subsamples from each plot were collected and then pooled together for subsequent analysis. The mixed topsoil samples were dried and sieved through 1 mm mesh, then soil pH (in H_2O), calcium, potassium, magnesium, total carbon and nitrogen, and bioavailable phosphorus (Olsen P) were measured as described by Govaert et al. (2020). The texture was determined by sieving and sedimentation with the pipet method according to ISO 11277 (2009).

Soil moisture was gravimetrically determined by air-drying the 0–10 cm soil sample at 50 °C for 48 h in a drying oven. Soil temperatures in the plot were measured by temperature data loggers (Lascar Easylog EL-USB-1) installed at a depth of 5 cm, and the mean temperatures during the summer (June–August) of 2018 were selected for the following analysis. See Meeussen et al. (2021) for details on the microclimate.

2.3. Determination of soil microbial community composition: biotic analysis

Additional soil samples (0–10 cm) for soil microbial analysis were also a subsample of selected samples within the plot during the June–August of 2018. After the sampling, the samples were immediately kept in portable cooling boxes before being transported to the laboratory. Then the samples were stored in the freezer at −18 °C for further phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA) extraction. The PLFA and NLFA were extracted and determined according to Quideau et al. (2016), and all the glassware for analysis has been thoroughly cleaned by rinsing and heating before the analysis. PLFA/NLFA analysis mainly included three steps: extraction, lipid

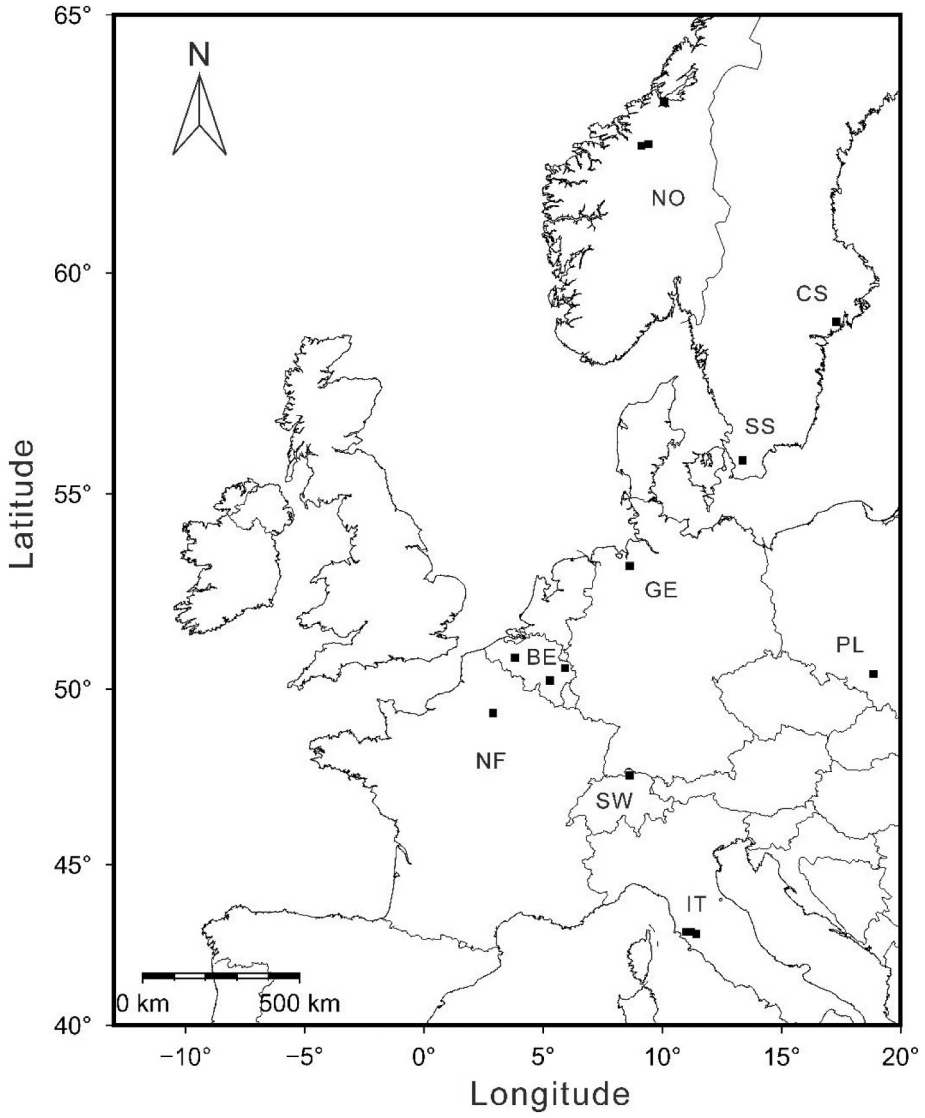

Fig. 1. Overview of study regions along the latitudinal gradient in Europe. Norway (NO), Central Sweden (CS), Southern Sweden (SS), Germany (GE), Poland (PL), Belgium (BE), Northern France (NF), Switzerland (SW) and Italy (IT).

fractionation and lipid methylation. Firstly, 3 g freeze-dried soil samples were extracted with Bligh and Dyer extractant, which comprised of a citrate buffer, chloroform and methanol with a ratio of 0.8:1:2 (v/v/v). After 2-hour shaking, the supernatant were drawn off and the retaining liquid were transferred to another glass vial. With a second round of extraction, the same phases were collected. Following the addition of chloroform and citrate buffer (1:1, v/v) and thorough mixing, the samples were kept overnight at room temperature in the dark. The lower phase was carefully transferred to a new vial and chloroform was evaporated off slowly (under compressed N_2). Secondly, the samples were re-dissolved with chloroform and then transferred to the solid-phase extraction (SPE) columns. Glycolipids were washed off from the polar lipids with acetone, and neutral lipids and phospholipids were eluted and collected from polar lipids by adding chloroform and methanol to the SPE columns, respectively. The collected neutral lipid and phospholipid were dried at room temperature under compressed N_2 (to avoid oxidation). Thirdly, the separated neutral lipids and phospholipids were transformed to fatty acid methyl esters (FAMEs) with methanolic KOH. More specifically, chloroform, methanol and methanolic KOH (daily prepared) were added to the neutral lipid and phospholipid fractions (1:1:2, v/v/v), and then the vials were placed in 37 °C bath for 30 min. Subsequently, hexane and acetic acid were added to the samples and phase separation become visible. After the vortex and centrifuging, the top phase was transferred to a clean vial and a second of round hexane addition and top phase separation was performed. Finally, N_2-dried FAMEs were resolved by adding 1 ml hexane before the gas chromatograph analysis, and the identification and quantification of each PLFA/NLFA were accomplished by gas chromatography–mass spectrometry (GC–MS, Trace GC-DSQ, Thermo Fisher, USA). Methyl nonadecanoate (MeC19:0) was used as internal standard and the concentration of each biomarker was expressed in μg/g.

A total of 23 PLFAs and 7 NLFAs were detected in this study. Only 19 PLFAs and one NLFA, which showed a high-frequency and well-recognized identity here, were selected as useful biomarkers to calculate the total microbial biomass. The PLFA biomarkers iC 14:0, iC 15:0, aC 15:0, iC 16:0, iC 17:0 and aC 17:0 were assigned to Gram-positive bacteria (Farrell et al., 2013; Kaiser et al., 2015); 16:1ω7c, cy 17:0 and cy 19:0 were assigned to Gram-negative bacteria (Mitchell et al., 2015); 10MeC16:0, 10MeC17:0 and 10MeC18:0 were assigned to Actinobacteria (Xu et al., 2019); C14:0, C15:0, C16:0 and C17:0 were assigned to non-specific bacteria (general bacteria lacking valid identification) (Steinbeiss et al., 2009; Willers et al., 2015); while 18:2ω6c and 18:1ω9c were assigned to saprophytic fungi (Zhang et al., 2014). To minimize the influence of the background amounts (from bacteria) of

PLFA16:1ω5c on the estimation of arbuscular mycorrhizal fungal biomass in soil, the ratio of NLFA and PLFA 16:1ω5c was used to represent arbuscular mycorrhizal fungi (Olsson, 1999; Ngosong et al., 2012). The relative abundance of each microbial group was calculated as the sum of representative PLFA/NLFA biomarkers divided by the total microbial biomass.

2.4. Statistical analyses

All statistical analyses were carried out in R (ver.4.0.3) (R Core Team, 2008). To explore correlation within the data, we first calculated a Spearman correlation matrix between pairs of edaphic properties (% sand, % silt, % clay, pH, total C and N, Olsen P, K, Mg, Ca, C/N, soil moisture and temperature) using the *rcorr* function in the *Hmisc* package (Harrell and Dupont, 2016). We used linear mixed-effects models (LMMs) to test factor variables distance-to-edge and forest density effects on edaphic properties and microbial composition, respectively. When fitting LMMs on edaphic properties, we used log transformations for response variables: % sand, % silt, % clay, total C, Olsen P, Mg, Ca, C/N; while we used sqrt transformations for response variable total N (Table S1). When fitting LMMs on microbial composition, we used log transformations for response variable- total microbial biomass (Table 1). We tested the interaction between distance-to-edge and forest density as fixed effect in our LMMs, while the "region" factor variable (with 15 levels) was included as a random effect (random intercept) in our LMMs. The *lmer* function in *lme4* package was used to fit LMMs (Bates et al., 2014). Additionally, the magnitude of edge influence (MEI) was calculated per forest density type for each microbial group. The MEI was estimated for edge plots for each transect as $(e\text{-}i)/(e+i)$, wherein e represents the relative abundance of each microbial group in the edge plot and i represents those in the interior plot (Harper et al., 2005).

Models were run for each microbial group as well as total microbial biomass separately to test the multiple edaphic properties effects on microbial composition. First, a model including predictor variables soil pH, % sand, % silt, % clay, C, N, Olsen P, K, Mg, Ca, C/N, moisture, temperature was assessed for each response variables, i.e., relative abundance of each microbial group as well as total microbial biomass. We controlled for collinearity among response variables with Spearman correlation coefficients (Fig. S1) and used $r > 0.7$ as a threshold to remove explanatory variables that are too much correlated to limit multicollinearity issues in the models (Dormann et al., 2013). Soil C, Mg, Ca, silt % and clay % were highly correlated with other edaphic properties (Fig. S1) and thus were not used as explanatory variables in these LMMs. A LMM with the remaining explanatory variables and random effect "region" was fitted for each response variable. Second, the generated models were simplified using the *dredge* function of the *MuMIn* package based on Akaike's Information Criterion (AIC) and the single best model was selected for the following analyses.

To explore the variability of the microbial community composition along the distances-to-edge and forest density gradients, non-metric multidimensional scaling (NMDS) based on the Bray Curtis distance matrix were conducted in the *metaMDS* function in the *vegan* package (Oksanen et al., 2012). The Shepard diagram of NMDS can be found in Fig. S2. Permutational multivariate analysis of variance (PERMANOVA) was used to test the significance in the microbial community composition (for 999 permutations) along the distance-to-edge and forest density gradients (function *adonis* in *vegan* package).

The relationship between microbial community composition and edaphic properties was determined by canonical correspondence analysis (CCA). Before the analysis, edaphic properties were log- or sqrt-transformed (same with Table S1) to reduce the influence of a skewed data distribution on the results. The best model was selected using the *step* function, which uses AIC for the model choice. The collinearity among the constraining variables were checked by Variance Inflation Factor (VIF) using *vif.cca* function and the variables with high VIF (>10) was excluded in the final model. The CCA model and the permutation test for CCA were performed within function *cca* and *anova.cca* in the *vegan* package.

3. Results

3.1. Abiotic environmental properties

We first tested the interactive effects of distance-to-edge and forest density on the edaphic properties. Based on the LMMs, we found no significant interactions on the edaphic properties we tested (Table S1). Then, we tested the main effects of distance-to-edge and forest density on those properties, respectively. We found that the distance to the forest edge significantly influenced soil K, Mg and Ca, which were 34.37 %, 48.52 %, and 63.63 % higher in forest edges than in forest interior, respectively ($p < 0.01$). These observations were in line with those for soil pH, as a higher soil pH was observed in edges (5.30 ± 0.90) than in the interiors (5.01 ± 0.82). Besides, distance-to-edge also had an impact on soil temperature, with a significantly higher temperature in forest edges than in interiors ($p < 0.05$). Forest density did not affect edaphic properties significantly, with an exception that soil temperature was significantly higher in open forest than in dense and intermediate forest ($p < 0.05$).

3.2. Soil microbial abundance

Most of the obtained biomarkers of soil samples were indicative for Gram-negative bacteria (ranging from 21.47 % to 44.43 %), followed by Gram-positive bacteria (19.49 % in average), non-specific bacteria (17.26 % in average), saprotrophic fungi (10.05 % in average), arbuscular mycorrhizal fungi (AMF, 9.53 % in average) and Actinobacteria (8.84 % in average). Consistent with the edaphic property patterns, we found no significant interactions of distance-to-edge and forest density on the relative abundance of microbial groups as well as the total microbial biomass based on the LMMs (Table S2). Then we tested the main

Table 1
Effects of forest density and distance from the edge on the relative abundance of microbial groups and total microbial biomass based on linear mixed-effect models. Chi-square values of each specific microbes and total microbial biomass were calculated based on ANOVA results of each model. Statistically significant Chi-square values were highlighted in bold.

	Distance from edge			Forest density		
	Chi-square value	Conditional R^2 (%)	Marginal R^2 (%)	Chi-square value	Conditional R^2 (%)	Marginal R^2 (%)
Gram-positive	1.7105 ns	4.73	1.92	1.8681 ns	4.66	2.10
Gram-negative	**3.8504*↑**	10.60	4.06	0.078 ns	6.24	0.09
Actinobacteria	2.5482 ns	16.61	2.51	1.3623 ns	15.05	1.36
Non-specific bacteria	0.1645 ns	8.77	0.18	0.8328 ns	9.81	0.88
Arbuscular mycorrhizal fungi	**5.3332*↓**	5.90	5.90	1.0751 ns	1.25	1.25
Saprotrophic fungi	3.0074 ns	12.18	3.12	0.2355 ns	8.64	0.25
Total microbial biomass §	2.6376 ns	11.31	2.76	1.6341 ns	10.01	1.73

Asterisks indicate significance (*$p < 0.05$; ns, non-significant). §, log-transformed. The formulas used for distance from edge and forest density were 'Y ~ distance from forest edge + (1|region)' and 'Y ~ forest density + (1|region)', respectively.

effects of forest density and distance from edges (without interaction term) on the soil microbial abundance. We found that the distance-to-edge exerted a significant impact on soil microbial abundance, in which arbuscular mycorrhizal fungi (AMF) showed a significantly higher relative abundance in the forest edges than interiors, while Gram-negative bacteria showed a significantly higher proportion in the forest interiors than edges instead (Fig. 2, Table 1). In contrast, the microbial abundance was not significantly affected by the forest density ($p > 0.05$, Table 1). However, when further investigating the magnitude of edge influence on the microbial composition in different forest density gradients, we still found some contrasting edge effects among different microbial groups and forest densities. In general, we found the greatest MEI in AMF groups, irrespective of forest density gradients (dense forest, intermediate forest and open forests) (Fig. 3). When compared with dense forests, the absolute MEI of AMF tends to decrease (close to zero) in open forests, while it tends to increase in intermediate forests. In contrast, the absolute MEI in Gram-negative bacteria increased after the thinning practice (see intermediate and open forest), while the largest effect size was also found in intermediate forests. Notably, other microbes only changed to a minor degree or highly variable between the positive and negative MEI, indicating the unstable status of edge effects.

We also analyzed effects of edaphic properties on the relative abundance of different microbial groups (Table 2), and found that soil K was the most influential factor, which was retained in most of the models. However, soil K was positively correlated with the abundance of saprotrophic fungi but negatively correlated with the abundance of Gram-negative bacteria and Actinobacteria. Other edaphic factors, for example, % sand also had significant correlations with microbial groups, which was positively correlated with Gram-negative bacteria while negatively correlated with Actinobacteria. Finally, the total microbial biomass was larger in soils with higher N but decreased with Olsen P concentrations.

3.3. Soil microbial community composition

The NMDS revealed the effects of multiple groups on the soil microbial community composition (Fig. 4). The NMDS ordination of PLFA/NLFA profiles produced a two-dimensional ordination with low stress ($S = 0.0827$) after 20 iterations. Although not significant, distance-to-edge still had an impact on the soil microbial composition to a large degree (PERMANOVA, $p = 0.078$), while neither forest density nor the interaction between distance-to-edge and forest density had observable effects on the microbial community composition ($p = 0.736$ and $p = 0.631$, respectively; Table S3).

CCA were performed to investigate which edaphic properties contributed to explain the variation in soil microbial community composition (Fig. 5). According to the CCA, the first two axes explained 24.54 % of the variance in microbial community composition. Variation

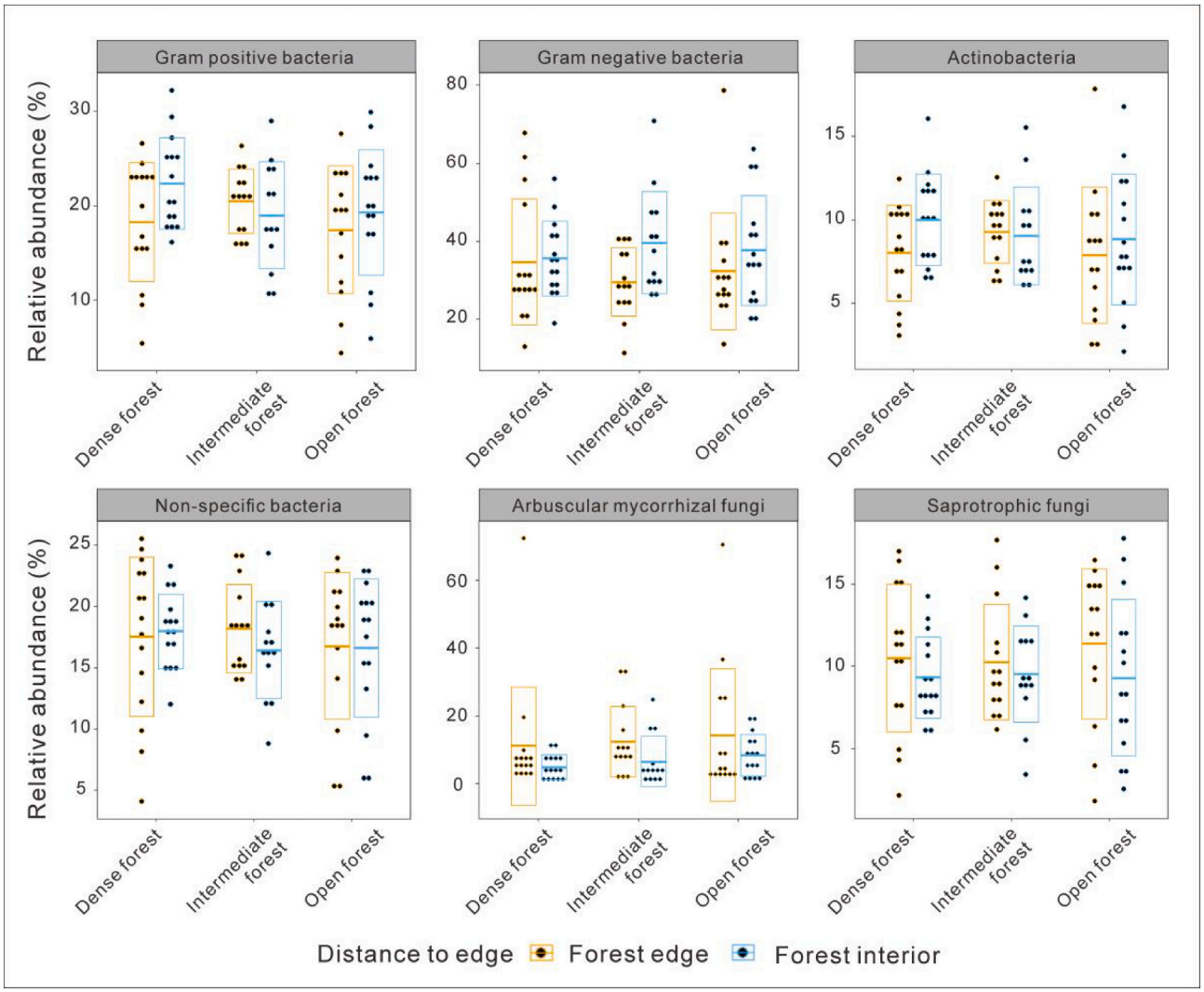

Fig. 2. Relative abundances of microbial groups in the three forest density gradients (dense, intermediate and open forests) and at the edge or in the interior. The relative abundance of each microbial group was calculated as the sum of representative PLFA or NLFA biomarkers divided by the total microbial biomass.

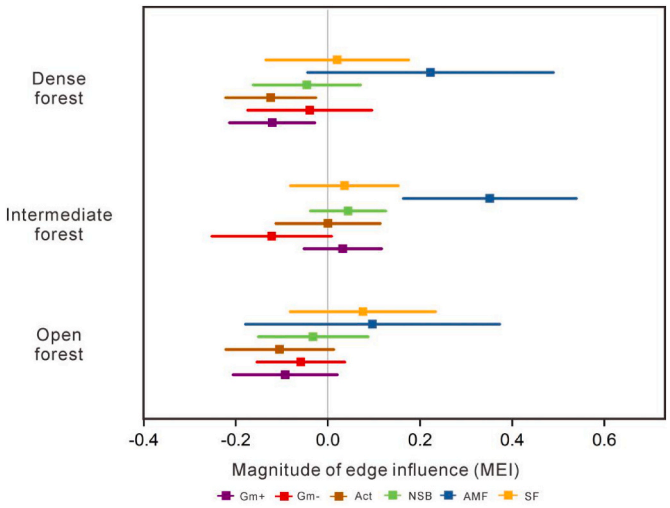

Fig. 3. Magnitude of edge influence (MEI) of each microbial group in three forest densities. Error bars indicate 95 % confidence intervals. Gm+: Gram-positive bacteria; Gm−: Gram-negative bacteria; Act: Actinobacteria; NSB: Non-specific bacteria; AMF: Arbuscular mycorrhizal fungi; SF: Saprotrophic fungi.

in the microbial community was significantly related to soil pH, K, N, % sand and temperature (Table S4). Among them, soil pH and K were positively correlated with PLFA iC 14:0, 16:1ω5c, 18:2ω6c and NLFA 16:1ω5c, while soil temperature and % sand were positively correlated with PLFA Cy 19:0. The first CCA axis was strongly correlated with soil K and pH but negatively correlated with % sand and temperature, and the second CCA axis was positively correlated with soil N.

4. Discussion

4.1. Distance-to-edge effect

A different microbial PLFA/NLFA community was observed between forest interiors and edges, which could be mainly attributed to edge-to-interior gradients in soil pH, N and K concentration (Fig. 5a). It is known that forest edges that border a non-forested habitat can exhibit increased aboveground productivity due to the greater light exposure (Malanson and Kupfer, 1993), therefore the altered litter input and quality in edges might increase the soil pH and fertility (see Hamberg et al., 2008 and Table S1). These results are also in line with the study of Malmivaara-Lamsa et al. (2008), who showed that edge-to-interior gradients induced alterations on soil pH and nutrient levels that could make significant contributions to shifts in the microbial community composition of boreal urban forest soils. As shown in previous literature, microclimate, including soil temperature and moisture, could also affect the microbial composition and activity (Castano et al., 2018). Studies examining the influence of soil moisture on the microbial community are consistent in that increased moisture would accelerate the decomposition rates of soil organic matter to a certain level (Wang et al., 2016; Luis Moreno et al., 2019), at least in temperate forests. However, the soil moisture tested here was a snapshot in time, therefore it is possible that there isn't a visible correlation between the soil moisture and microbiota. In contrast, we found a significant correlation between microbial composition and soil temperature, which is positively correlated with several bacterial groups such as Gram-positive and Gram-negative bacteria (Fig. 5a, Tables 2 & S4). This is in agreement with the findings of a meta-analysis (Zhou et al., 2016), showing that the temperature is an important determinant of the composition of bacterial and fungal communities by analyzing soil samples from a wide range of temperature gradients in North America. In addition, we found that texture (% sand) also played a significant role in driving the different composition of the microbial PLFA community. This may be linked to plant communities in oligotrophic sandy soils, which exhibited an alternative resource acquisition strategy to promote their nutrient and water capture from soil (Kochsiek et al., 2013), and the changes in soil nutrient supply induced by those plants may in turn affect the composition of soil microbial community.

However, the magnitude and direction of the edge effect on microbial abundance varied considerably among microbial groups. We showed a higher relative abundance of AMF in forest edges than interiors (Fig. 2). Given that forest edges receive more light, wind and also present warmer and drier conditions than forest interiors (Chen et al., 1993), the amount of drought-resistant and warm-tolerant plant species are expected to increase in forest edges (Ranney et al., 1981; Tuff et al., 2016). As shown in our previous study, total species richness of plant is higher in edges, which is mainly attributed to the higher generalist richness here (Govaert et al., 2020). Generalists were defined as species that can be or mainly be found in open vegetation as well as those true open habitat species as described in Govaert et al. (2020). The higher generalist abundance in edges indicates that these plant species may form a stronger AMF affinity than the species growing in the interior (specialists in closed forests). Additionally, edges and intermediate

Table 2
Effects of soil pH, % sand, soil N, Olsen P, K content, C/N, soil moisture, and soil temperature on the relative abundance of each microbial group and total biomass based on linear mixed effect models. Chi-square values of each specific microbes and total microbial biomass were reported. Statistically significant Chi-square values were highlighted in bold.

	pH	% Sand §	N (mg/kg) £	Olsen.P (mg/kg) §	K (mg/kg) §	C/N §	Moisture %	Temperature °C	Conditional R^2 (%)	Marginal R^2 (%)
Gram-positive bacteria	1.7583						**8.3735**** ↑	2.7036	16.35	13.49
Gram-negative bacteria		**8.5289**** ↑			**6.5015*** ↓	**4.3730*** ↓		2.4495	22.59	20.05
Actinobacteria		**5.2099*** ↓	**7.5980**** ↑	**7.6963**** ↑	**9.0984**** ↓				26.25	25.24
Non-specific bacteria			**6.5811*** ↑						8.09	7.28
Arbuscular Mycorrhizal Fungi					2.2676				25.98	25.98
Saprotrophic Fungi	**5.7219*** ↑				**4.0215*** ↑				17.83	17.57
Total microbial biomass §			**14.9839***** ↑	**4.1619*** ↓					17.91	16.36

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

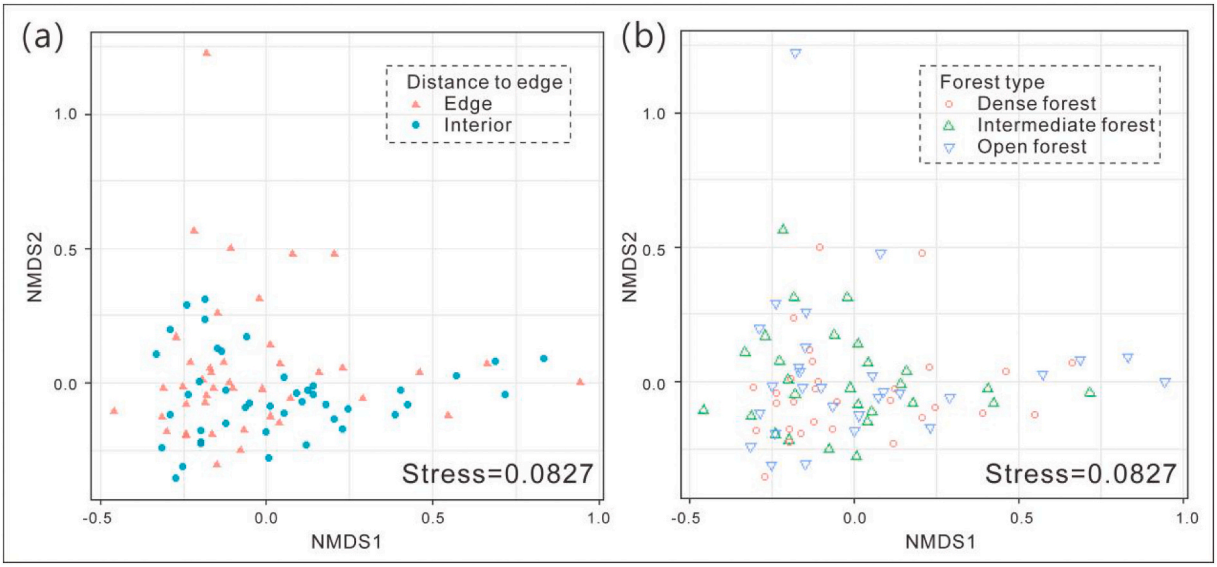

Fig. 4. Non-metric multidimensional scaling (NMDS) results of the microbial composition based on the PLFA/NLFA biomarkers. Variation of the microbial composition between different distances to forest edge (a) and forest density (b) based on the Bray-Curtis distance matrix.

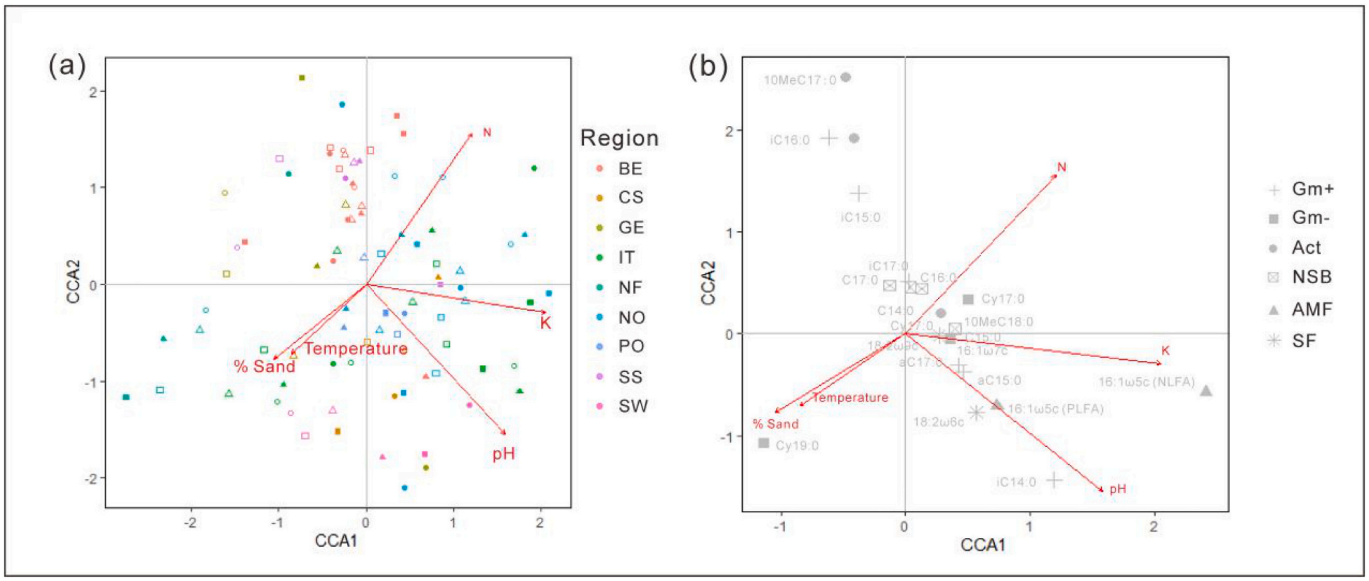

Fig. 5. The relationship between microbial community composition and microclimate soil temperature and soil properties based on canonical correspondence analysis (CCA). The first axis accounted for 20.15 % of the variability and the second axis accounted for 4.39 %. The significance levels of CCA1 and CCA2 were $p = 0.001$ and $p = 0.165$, respectively (permutation test). (a) The distribution of samples collected in different regions. (b) The distribution of single PLFA or NLFA biomarkers. Different symbols in this panel indicated the classified microbial groups. Gm+: Gram-positive bacteria; Gm−: Gram-negative bacteria; Act: Actinobacteria; NSB: non-specific bacteria; AMF: Arbuscular mycorrhizal fungi; SF: Saprotrophic fungi.

forests may also be associated with the higher functional diversity in the understorey due to more heterogeneous environmental conditions (Magura, 2017; De Pauw et al., 2021). Furthermore, AMF have been known to enhance the hosting plants tolerance to abiotic stresses, such as drought, salt, pollutants (Begum et al., 2019), and also benefit plants by increasing their disease resistance (Song et al., 2015). Thus, the higher AMF in forest edges revealed here may indicate the potential role of AMF in helping the hosting plant survive under complex and fluctuating environments in edges. In contrast, the microclimate in the forest interiors was more stable compared to the forest edges, since plant tissue can serve as a barrier that alleviates the forest interior from greater fluctuations in temperature, wind speeds, and moisture (Chen et al., 1995). Here, we found a significantly higher abundance of Gram-negative bacteria in forest interiors than edges (Table 1 & Fig. 2). Gram-negative bacteria are thought to be less resistant to stress and harsh conditions owing to their disability to sporulate, which makes them less competitively advantaged in an inhospitable condition (Huang and Hull, 2017). Thus, the less variable microclimate conditions such as found in forest interiors could provide a more favorable habitat than forest edges for Gram-negative bacteria to colonize and propagate.

4.2. *Forest density effect*

In contrast, forest density did not exhibit a significant impact on microbial abundance and community composition (Table 1 and Fig. 4). Compared with clear-cutting, thinning (selective harvesting) has been

acknowledged as an alternative way in forest management practice due to the benefits in maintaining mature forest functioning as well as the above- and below-ground biodiversity (Gundersen et al., 2006; Lohmus, 2011; Muscolo et al., 2021). As an example, Cheng et al. (2018) studied the change of microbial community after a long-term thinning practice (18 years) and found no significant differences in the overall soil microbial composition among different treatments. Besides, the soil microbial community might recover from the disturbances even faster than we expect under reasonably moderate management. For example, Shao et al. (2016) evaluated the effects of plant removal practices on the soil biotic community in a bamboo forest and found that microbial community composition only changed in the first year after the plant removal and quickly recovered in the second year. Therefore, it is reasonable to infer that the microbial communities in open forests (recently thinned) and intermediate forests (thinned) were less affected by the management, or soon recovered to the original (dense forests) composition at the moment of our sampling. Moreover, the soil microbial community is expected to change in response to environmental properties including pH, soil texture, nutrient levels, and water content (Richter et al., 2018). However, most of these factors in the present study did not significantly differ between forests with different densities (Table S1), indicating that the soil responses appear to be insensitive to forest thinning under current operational prescriptions.

4.3. Interactive effect of distance-to-edge and forest density

We found no evidence of interactive effects of forest density and distance to the edge on any microbial response variable. The lack of interaction suggested that PLFA community level responses of these two factors operate independently of each other. This contradicts our hypothesis from our previous work on plants (Govaert et al., 2020), i.e., the most contrasting edge effects of plant richness would be found in forest with most open canopy. It has been proved that the well-developed plant structure in dense forests can play a protective role on the microclimatic changes between forest edge and interior, and help to preserve the original microclimate in the forest interior (Matlack, 1993; Meeussen et al., 2020). In the open forests, there was more solar radiation entering the forest floor, which can somewhat level off the contrasting microclimate between forest edge and interior compared to those in dense forests (Wright et al., 2010). While in thinned forests, the plant structure was under development, and the relatively open edges may result in a steep edge-to-interior gradient, which potentially enlarges the contrasting microclimate conditions between edges and interiors compared to those in dense forests. In this study, although we found the most significant effect size of several microbial groups (such as AMF and Gram-negative bacteria) in intermediate forests (Fig. 3), the results of the belowground community were weak compared with previous experimental evidence from plant communities, which revealed strong evidence of plant community composition along edge-to-interior gradients responding differently according to forest density (Govaert et al., 2020). Ultimately, our results agreed with previous studies, in which ecological theory developed for aboveground communities differs in the degree of applicability to those belowground communities living in the soil matrix (Deyn and Putten, 2005; Wardle, 2010).

4.4. Conclusions

Our results demonstrated, over a large geographic gradient, that the overall forest structure (forest density) did not affect soil microbial community composition but the distance-to-edge did, suggesting an environmental selection for microbial communities along the edge-to-interior gradients. Notably, AMF and Gram-negative bacteria were the two microbial groups most affected by the edge effects. Considering the warmer microclimate and higher soil nutrient availability in edges, more plant generalists occur there, which can facilitate the enrichment of AMF in edges. Besides, the symbiosis of AMF and plant species would also lead to a change in nutrient cycling and forest ecosystem functioning in turn. We also found that the overall microbial composition is closely related to the soil pH, N, K concentration, % sand and temperature, which should be explicitly considered in affecting the soil microbial composition in European deciduous forests. Overall, this study provided a profound basis of forest belowground community responses to distance to the edge and forest density. Further investigations are still required to expand our observations to other forest types and also dive deep to their impact on forest functioning.

CRediT authorship contribution statement

J.Y., H.B., P.D.F., and K.V. conceived the ideas and designed methodology; all authors collected data; J.Y. performed statistical analyses; J.Y., with contributions from H.B., P.D.F., and K.V. wrote the paper; all authors discussed the results and commented on the manuscript drafts.

Data availability

Data related to this manuscript are available on Figshare: https://figshare.com/s/9b6b0518ff1f6df96b82.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2022.104586.

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