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Responses of soil microorganisms to land use in different soil types along the soil profiles

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Abstract: The objective of this study was to find out how land use affects the soil microbial attributes in different soil types and to which depth. The study was performed in Slovakia (Europe) in three areas differing in soil type (Chernozem, Stagnosol, Cambisol). Within each area, three localities with different land use (forest, grassland, cropland), representing a gradient with different intensity of management, were chosen. The soil samples were taken along a single soil profile up to a depth of 1 m with 10 cm increments at each locality. In the soil samples, the basic soil chemical properties and microbial attributes were determined. The effect of the land use on the microbial biomass and basal respiration was mainly observed in the Chernozem in the top 30 cm, while in the Stagnosol, no difference in the trend in the microbial biomass between the different ecosystems along the soil profile was found. The N-mineralisation reflected the different management practices especially in the Cambisol in the top 20 cm. The most distinct differences in the catalase activity between the soils differing in land use were found in the Cambisol along the whole profile. The richness and diversity of the functional groups did not differ significantly between the soils with the different land use and also no uniform responses of the functional groups composition to the land use were observed. The microbial biomass and activity were mainly affected by the amount of the soil organic matter; the intensity of the impact differed according to the soil type.

Keywords: cropland; forest; grassland; microbial community; soil types

Deforestation for agricultural use has been ongoing since human activity began and also persists recently. According to the FAO (Food and Agriculture Organization of the United Nations) in 2015, 129 million hectares of forest have been lost worldwide since 1990 due to forest land conversion to agriculture and other uses (FAO 2016). Many studies confirmed that forest clearing and the subsequent agricultural use lead to changes in the soil organic matter (SOM) dynamics and stocks, the concentration of the particulate organic matter as well as other soil

properties such as the total porosity, bulk density, pH (Lal 2002; Breuer et al. 2006; Keen et al. 2011). The conversion from forest to agriculture ecosystems can lead to a decrease of up to 50% in the soil organic carbon (Lal 2002). However, the different use of agricultural soils may also be reflected in the changes to the soil properties (Cade-Menun et al. 2017; Hebb et al. 2017).

Microorganisms represent a very important component of terrestrial ecosystems, as they play a key role in the decomposition and transformation of

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SOM and the nutrient cycling (Paul 2007). There are several factors that affect the soil microbial community. Soil properties such as the soil temperature and moisture, carbon and nitrogen content, soil reaction and nutrient content (Hofmann et al. 2016; Romanowicz et al. 2016) belong to the most important. However, the land use can distinctly modify the soil properties because of the vegetation cover and the anthropogenic disturbances and, consequently, indirectly to the living conditions for soil microbiota also (Ahmed et al. 2012; Caili et al. 2016).

A majority of the studies on the effect of the land use on the soil microbial characteristics are related to the topsoil (e.g., Wachendorf et al. 2017; Malik et al. 2018), while there is only limited information on the depth to which the microorganisms are affected by the different management schemes; moreover, they are restricted to one soil type (Liu et al. 2018). However, microbial processes also take place in deeper soil horizons (Paul 2007). As soil types differ in the physico-chemical properties and stratification, they could amplify or level the impact of the land use. Therefore, the objective of our study was to assess how the soil microbial attributes differ between the differently used soils, to which depth the differences occur, and whether and how they are influenced by the soil types. For this, we evaluated the impact of the different land use and associated management: the forests, grasslands and croplands represent the gradient starting with nearly no impact on the forest soil (evolved under relatively natural conditions), and ending up with the intensive management of the soil in the croplands (tilled, fertilised and often chemically treated to control pests). The sites were selected at three localities differing in soil types: Chernozem, Stagnosol and Cambisol, representing a natural gradient of the soil type sequence and wholly bracketing the range of climatological, soil and topography conditions for agriculture in Slovakia. The soil types differ in the SOM, pH, soil water content and differences in the soil temperature can be also expected because of the different altitudes. On the other hand, the soils exhibit similar textures. We hypothesise that the differences in the microbial attributes between the differently used soils will decrease with the depth and will be differently affected by the soil types due to the different soil properties. Moreover, the depth to which the impact is reflected may not be the same for all the microbial characteristics as they take part in the different processes and/or reflect a different physiological status.

MATERIAL AND METHODS

Study sites and soil sampling. This study was performed at three sites (Figure S1 in the Electronic Supplementary Material (ESM)) differing in soil types and at each site in three localities with different land-use types including croplands, grasslands and forests. The following localities were selected for the study:

(i) Močenok, west Slovakia, an altitude of 138 to 173 m a.s.l., slope 0–3°; the Chernozem is developed from calcareous loess. The average temperature and annual precipitation for the years 1991–2016 represent 10.77°C and 594 mm, respectively. At the cropland, *Zea mays* L. was already harvested at the time of the soil sampling. The grassland is semi-natural, without any human intervention. *Fraxinus excelsior* L. and *Quercus petraea* L. dominate in the forest stand.

(ii) Trnĕ, central Slovakia, an altitude of 550 to 554 m a.s.l., slope 3–7°; the Cambisol is developed from volcanic agglomerates and epiclastic rocks. The average temperature and annual precipitation are 8.39°C and 775 mm, respectively. The soil at the cropland was sampled after a *Sorghum* harvest. The grassland had been mowed and grazed; unlike the Chernozem locality, more herbaceous species occur there. The mixed forest is formed of *Carpinus betulus* L., *Quercus robur* L., *Tilia cordata* Mill. and *Prunus avium* L.

(iii) Hanušovce nad Topľou, east Slovakia, an altitude of 258–308 m a.s.l.; the Stagnosol is developed from polygenetic loam. The average temperature and annual precipitation represent 8.61°C and 650 mm, respectively. At the cropland, wheat was grown and harvested before the sample collection. At this locality, the grassland had been mowed and was actively being grazed. The forest is mainly formed of *Carpinus betulus* L. and *Pinus sylvestris* L.

At each locality, a single soil profile (Figure S1 in ESM) was excavated in 2015 in October and described based on the morphological characteristics. The soil samples were collected along the soil profiles up to a depth of 1 m (except the Cambisol, where sample collection was possible only to the depth of 0.8–0.9 m). The depth increment for the sampling was 10 cm. At each depth, the soil samples were taken from the entire width of the profile, mixed and homogenised. The samples were immediately transported to the laboratory; the subsamples intended for the determination of the microbial attributes were stored at 4°C until the analyses were performed. The soils were not sieved to preserve the natural conditions for the microorganisms. All visible root and fresh litter material, as well as rocks, were removed.

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Soil analyses. The soil physico-chemical properties are shown in Tables S1–S3 in the ESM and were already evaluated and published (Barančíková et al. 2019). The concentrations of the total SOC (soil organic carbon) and nitrogen (N_T) were determined by a dry combustion analysis using a Euro EA 3000 Elemental analyser in the CN configuration (Kobza et al. 2011). The labile carbon (C_L) and nitrogen (N_L) were determined by $KMnO_4$ oxidation (Stanford & Smith 1978; Loginov et al. 1987). The humic substances (HS) content was determined according to the Kononova-Belchikova method (Kobza et al. 2011). The soil pH was measured potentiometrically in a supernatant suspension of a 1 : 2.5 soil to liquid mixture (aqua, 1 M KCl). The cation exchange capacity (CEC) and base cations (BC) were estimated according to the method of Kappen (Kobza et al. 2011).

The microbial biomass carbon (C_{mic}) was determined using the microwave-irradiation procedure described by Islam and Weil (1998). The N-mineralization (N_{min}) was determined using the laboratory anaerobic incubation procedure following Kandeler (1993). The basal respiration (Resp) was measured by estimating the amount of CO_2 released from the fresh soil after a 24 h incubation period and absorbed in 0.05 M NaOH (Alef 1991). Among a large group of soil enzymes, the catalase activity was chosen, since previous studies showed that the minimum effects of seasonal changes, a relative spatial congruence, and distinct temporal (inter-annual) trends qualify this characteristic to be an indicator of the long-term changes (Gömöryová et al. 2006). The catalase activity (Catal) was assessed on the basis of the discharged oxygen volume from 10 g of the fresh soil sample 10 min after the addition of 20 ml 3% H_2O_2 (Khazijev 1976). All the results were expressed on the dry mass of the soil determined gravimetrically by drying the fresh soil at 105°C for 24 h.

The physiological profiles of the microbial communities were determined using BIOLOG® EcoPlates (Insam & Goberna 2004). The inocula were prepared by resuspending the fresh soil in 0.85% NaCl, centrifuging it (1000 rpm for 5 min), the supernatant was diluted from 1 : 10 000 to 1 : 1000 depending on the microbial biomass carbon. 150 µl of the extract were incubated in microtitration plates at 27°C for 5 days. The absorbance at 590 nm was recorded using a Sunrise Microplate reader (Tecan, Salzburg, Austria). The measured data were corrected against the initial readings at time zero. The data were expressed as individual optical well densities. The

richness (Richn) of the soil microbial community was assessed as the number of different substrates used by the microbial community. For the estimation of the diversity, Hill's diversity index (Diver), encompassing both the substrate richness and evenness, was calculated (Hill 1973) (Eq. (1)):

$$Diver = 1/\sum p_i^2 \quad (1)$$

where:

p_i – the ratio of the activity on a particular substrate to the sum of the activities on all the substrates

Data evaluation. The data were analysed using the statistical package SAS/STAT® (Ver. 6.03, 2010). The effects of the land use, soil type (both categorical fixed-effect factors) and depth (continuous covariate) were analysed by the analysis of covariance. In the case of the respiration in the Chernozem, the data from the depth of 40–100 cm were excluded from the analysis because of their over-estimation due to the presence of carbonates. Duncan's test was used to test the pairwise differences between the means. Pearson's correlation coefficients were calculated to assess the correlations among the microbial attributes and the soil chemical properties.

To identify the effects of the land use and soil type on the microbial community composition, we performed a redundancy analysis (RDA). The optical density for each carbon source of the BIOLOG assay was taken as a measure of the abundance of microbial group able to metabolise the respective substrate. CANOCO 5 for the Windows package (ter Braak & Šmilauer 2002) was used for running the analyses.

RESULTS

The soil microbial attributes in relation to the soil type, land use and soil depth. A significant effect of the soil type was observed for most of the microbial attributes except for Catal and Diver (Table 1, Table S4 in ESM), while the land use and soil depth were not found to be significant in the Richn and Diver of the functional groups. Most of the soil type × depth and land use × depth interactions were also significant.

The microbial characteristics generally reached the highest values in the Chernozem (Table 2), only N-min was significantly lower there. The pattern of the microbial characteristics between the Cambisol and Stagnosol is generally not clear. Surprisingly, the highest Richn and Diver were found in the Stagnosols,

Table 1. The analysis of covariance of the microbial characteristics (the significance of the *F*-tests)

	df	Cmic	Nmin	Catal	Richn	Diver	df	Resp
Soil type	2	***	***	ns	**	ns	1	***
Land use	2	***	**	**	ns	ns	2	***
Depth	1	***	***	***	ns	ns	1	***
Soil type × depth	2	***	**	**	ns	*	1	**
Land use × depth	2	*	*	ns	ns	ns	2	*
Error	68						44	

****P* < 0.001; ***P* = 0.001–0.01; **P* = 0.01–0.05; ns – non-significant; Cmic – microbial biomass C; Nmin – N-mineralisation; Catal – catalase activity; Richn – richness of the microbial functional groups; Diver – diversity of the microbial functional groups; Resp – basal respiration; df – degree of freedom

the lowest in the Cambisol. Among the microbial attributes, only Cmic differed significantly between all the soil types. Regarding the land use, a high biomass and activity were observed in the forest soils. The differences between the grassland and the cropland were mostly non-significant.

The microbial biomass decreased down the soil profiles; the trend in the decline differed among the soil types (Figure 1). The most pronounced gradual changes were observed in the Chernozem. The differences in the Cmic between the forest and the agricultural soils were observable especially in the top 30 cm of the soil. In the Cambisol, the differences between the differently used soils were considerably lower than in the Chernozem. In the Stagnosol, no trend in the Cmic between the different ecosystems was observed.

The microbial activity generally decreased with the depth also (Figure 1). N-min was high in the top 10 cm and then significantly dropped. No clear trend was identified for Catal. The impact of the different land use on the N-min was observed only in the top 10 cm, while the Catal differed between the soils with the different land use up to the depth of 80 cm. However, the magnitude of the differences between the plots depended on the soil type. The most distinct differences in Resp were observed in the Chernozem and were quite consistent among all the measured depths; in the Cambisol and the Stagnosol, the differences were generally small, except for the top 10 cm of the Cambisol.

The Richn and Diver did not differ significantly between the soils with the different land use and no pattern was found down the soil profile (Figure S2 in ESM).

Among the microbial groups metabolising the BIOLOG substrates, quite a lot varied significantly

among the soil types. However, the land use affected the abundance of only three groups (Table S5 ESM).

The sample scores of the first two RDA axes relying on the abundances of the microbial functional groups (BIOLOG assay) sorted according to the land use and depth for the individual soil types are shown in Figure 2. The soil types seem to be well separated. On the other hand, there is no uniform response of the community-level physiological profiles to the land use. The groups of points representing the different land-use types overlap completely in the Stagnosol, and there are also substantial overlaps in the Chernozem and the Cambisol. However, the RDA scores are generally correlated to the depth, although the correlations are not consistent among the soil types and land uses.

The microbial response to the soil physico-chemical properties. The microbial biomass was

Table 2. Duncan's pairwise tests of the differences of the means between the soil types and the land uses

	Cmic	Nmin	Catal	Richn	Diver	Resp
Soil type						
Chernozem	190 ^a	0.10 ^b	1.45 ^a	22.2 ^a	9.8 ^b	0.29 ^a
Cambisol	140 ^b	0.27 ^a	1.44 ^a	20.3 ^b	9.6 ^b	0.07 ^b
Stagnosol	89 ^c	0.23 ^a	0.81 ^b	22.4 ^a	11.4 ^a	0.08 ^b
Soil use						
Forest	171 ^a	0.26 ^a	1.40 ^a	21.8 ^a	10.4 ^a	0.08 ^b
Grassland	124 ^b	0.17 ^a	1.31 ^a	21.4 ^a	9.9 ^a	0.15 ^a
Cropland	126 ^b	0.17 ^a	0.96 ^b	22.0 ^a	10.6 ^a	0.12 ^{ab}

Cmic – microbial biomass C; Nmin – N-mineralisation; Catal – catalase activity; Richn – richness of the microbial functional groups; Diver – diversity of the microbial functional groups; Resp – basal respiration; the means with the same capital letters do not differ significantly

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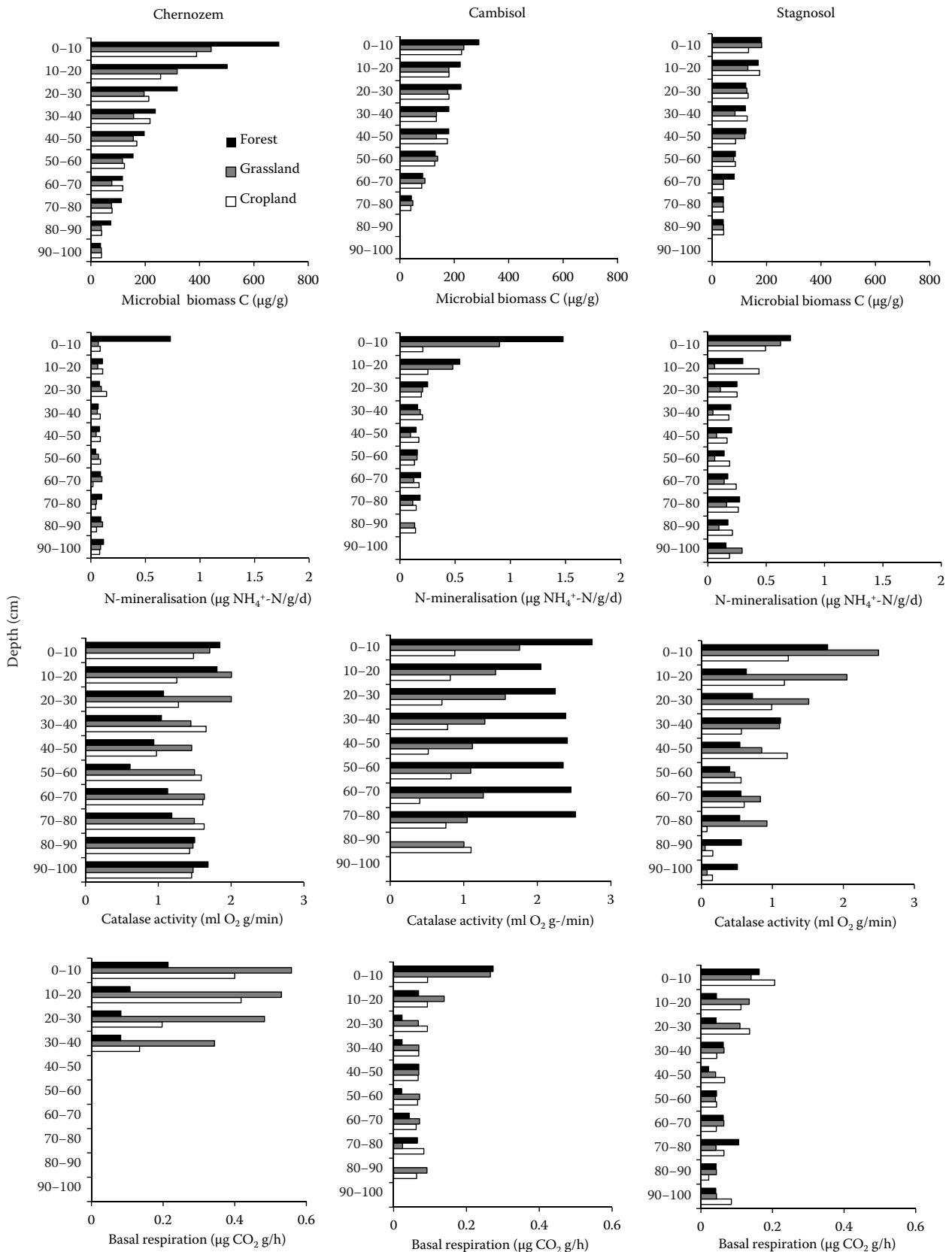


Figure 1. The microbial biomass C, N-mineralisation, catalase activity and basal respiration along a soil profile in three soil types (Chernozem, Stagnosol and Cambisol) in the areas with the different land use (forest, grassland, cropland)

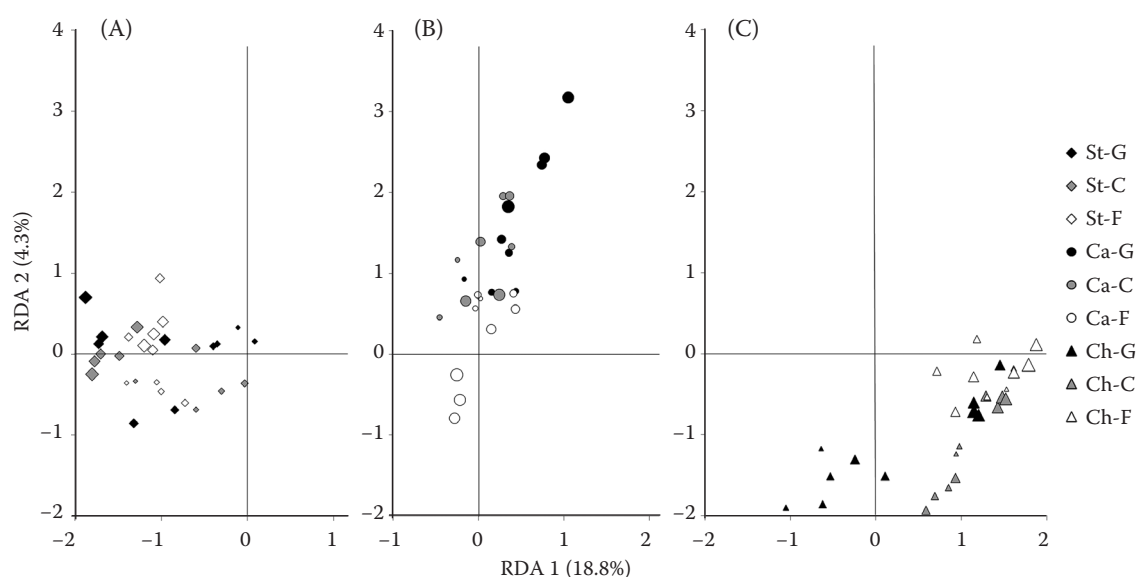


Figure 2. The redundancy analysis (RDA) of the soil microbial data: the sample positions in the Stagnosol (A), Cambisol (B), Chernozem (C)

St – Stagnosol; Ca – Cambisol; Ch – Chernozem; G – grassland; C – cropland; F – forest; the different symbol sizes correspond to the soil depth, (bigger depth – larger symbol)

Table 3. The correlations between the microbial community attributes and the soil characteristics for the different soil types

	SWC	TOC	C _L	N _T	N _L	C/N	HS	pH-H ₂ O	pH-KCl	BC	CEC	BS
Chernozem												
Cmic	0.757***	0.958***	0.938***	0.952***	0.864***	–	–	–0.622***	–0.583***	–0.538**	–0.483**	–0.634***
Resp												
Nmin	0.601***	0.718***	0.780***	0.764***	0.508**	–	–	–	–		–	–0.393*
Catal	–	–	–	–	–	–	–0.786*	0.369*	0.392*		0.368*	–
Richn	–	–	–	–	–	–	–	–	–		–	–
Diver	0.368*	0.374*		0.363*	0.378*					–0.377*	–0.365*	–
Cambisol												
Cmic	0.551**	0.771***	0.719***	0.720***	0.717***	–	–0.669*	–0.625***	–0.540**		–	–0.591**
Resp	0.437*	0.810***	0.815***	0.517***	0.694***	–	–	–0.406*	–		–	–0.500**
Nmin	0.479*	0.922***	0.949***	0.717***	0.694***	–	–	–	–		–	–
Catal	–	–	–	0.430*	–	–	–0.857**	–	–	0.787***	0.844***	–
Richn	–	–	–	–	–	–	–	–	–	–0.421*	–	–
Diver	–	–	–	–	–	–	–	–	–		–0.493	
Stagnosol												
Cmic	0.539***	0.708***	0.659***	0.708***	0.735***	0.520**	–	0.430*	0.584***		–0.425*	
Resp	0.712***	0.758***	0.766***	0.782***	0.751***	0.432*	–	0.643***	0.683***		–	
Nmin	0.686***	0.791***	0.825***	0.813***	0.582***	–	–	–	–		–	
Catal	0.597***	0.753***	0.730***	0.763***	0.645***	0.472**		0.509**	0.613***		–	
Richn	–	–	–	–	–	–	–	–	–		–	
Diver	–	–	–	–	–	–	–	–	–		–	

Significance labels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns – non-significant; SWC – soil water content; TOC – total organic carbon; C_L – labile carbon; N_T – total nitrogen; N_L – labile nitrogen; BC – base-cations content; CEC – cation exchange capacity; BS – base-cations saturation; Cmic – microbial biomass C; Resp – basal respiration; Nmin – N-mineralisation; Catal – catalase activity; Richn – richness of the microbial functional groups; Diver – diversity of the microbial functional groups

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significantly correlated to almost all the soil properties (Table 3). Especially the amount and availability of the SOM determined a high C_{mic} in all the soil types. The relationships were very strong in the Chernozems. Although significant relationships were also found with the other soil characteristics, their intensity differed according to the soil type and was less strong in comparison to the SOM characteristics.

For Resp, the intensity of the relationships was only tested in the Cambisols and Stagnosols. The highest Resp was associated with a high C and N content. While in the Stagnosols, the strength of the correlation with the C and N contents was similar, in the Cambisols, a more intensive relationship was found with the C content (TOC, C_T). On the other hand, Resp correlated more with the soil moisture and the pH in the Stagnosols than in the Cambisols.

N-min seems to be affected by the C and N content, but not by the pH or the CEC. Especially strong relationships were found in the Cambisols. Slightly weaker correlations were found in the Stagnosols and followed by the Chernozems.

Unlike the previous microbial attributes, the effect of the physico-chemical properties on the Catal was not so distinct and differed significantly according to the soil type. While in the Chernozems, the Catal showed a similar association with the pH and the CEC, in the Cambisols, it was closely related to the CEC and the BC. Surprisingly, a significant influence of C and N was only observed in the Stagnosols.

Richn and Diver generally did not show strong relationships with the soil physico-chemical properties. Only Diver in the Chernozems was slightly associated with the soil moisture, the N content and the CEC.

DISCUSSION

Our study showed that the effect of the soil type on the microbial attributes was more pronounced than the effect of the land use which is in accordance with the findings of Zhao et al. (2016). It is not surprising as the soil types differ in physico-chemical properties reflecting the different climatic conditions and parent materials. The differences in the microbial characteristics between the soils with the different land use were, in general, not as distinct as expected. Many studies (Islam & Weil 1998; Celik 2005) showed that extensive agriculture practices lead to changes in the soil physico-chemical properties and, consequently, to the serious degradation, destruction and fertility depletion of soils. Changes in the soil properties

mean also changing the living conditions for the soil microbiota, and several studies have confirmed the impact of the land use on them (Ye et al. 2009; Zhang et al. 2016). In our study, some differences in the microbial biomass and activity associated with the land use can be observed, however, no general pattern was identified; the depth and trend of the changes differ depending on the microbial attribute and soil type. For instance, while the C_{mic} differed distinctly between the differently managed soil in the upper 30 cm of the Chernozem, the N-min and catalase activity differed especially in the Cambisol (Nmin in the top 20 cm, Catal even up to 80 cm).

The microbial biomass differed significantly between the forest and agriculture soils, reflecting the depth of the tillage. The most distinct effect in the Chernozem can be associated with the high SOM content and warm conditions leading to suitable living conditions for the microbiota and, consequently, an increase in the C_{mic} , compared to the other soil types. However, suitable conditions together with intensive agricultural management lead to the rapid decomposition of plant residues and C-mineralisation, and, consequently, to high losses of SOM leading to a lower C_{mic} in the agricultural soils. Although the microbial activity generally reflected the SOM content well, based on our results, we suppose that the amount and composition of the plant residues coming into the soil can affect the microbial process in different ways. The high rates of N-min in the top-soil indicate an association with the incorporation of fresh plant residues and root exudates which could serve as more easily utilisable nutrient sources. On the other hand, high rates of catalase activity were found along the whole profile. Catalase belongs to the oxidative enzymes, activities of which exhibit a different depth distribution compared to the hydrolytic enzymes and can indicate the degradation of the recalcitrant C compounds in the subsoil horizons (Herold et al. 2014).

The biomass and activity of the soil microorganisms usually drops along the soil profile because of a decreased amount and availability of carbon sources and prey (Paul 2007; Marinari & Antisari 2010). The correlation analysis showed that, in all the soil types, the distribution of C and N along the soil profile determined most of the microbial attributes more strongly than the soil reaction or the properties of the sorption complex. On the other hand, the effect of the SOM quality on the microbial attributes is not so pronounced and unambiguous. It seems that in

the Stagnosol, i.e., a soil with a lower average TOC and worse physical properties, the C/N ratio plays a more important role for the microorganisms than in the other soils; on the other hand, the amount of the stable humic substances influenced some microbial attributes distinctly in the Chernozems and the Cambisols.

Many studies have shown that the microbial community structure changes with the land use (van Leeuwen et al. 2017; Seuradge et al. 2017). Van Leeuwen et al. (2017) observed a differentiation in the microbial community structure between the land use types and along the soil profile. While in the topsoil, the microbial structure differed significantly between the land uses, in the C horizon, it was similar. However, as demonstrated by Cao et al. (2017), the changes need not to be necessary qualitative, but they can be more quantitative. They found that the dominant phyla and genera were almost the same among the land-use types, but their relative abundances differed significantly. In our study, the changes with the land use were not so pronounced as between the soil types which is in agreement, e.g., with the studies of Girvan et al. (2003) or Zhao et al. (2016). Lauber et al. (2008) found that the bacterial-to-fungal ratios did not differ distinctly across the land-uses, and distinct land-use types did not necessarily exhibit distinct microbial communities. Thus, changes in the microbial community structure across a landscape can be better predicted by the specific changes in the edaphic properties, not necessarily by the land-use type itself. Moreover, the lack of a consistent land-use effect on the soil attributes can be also due to the variability in the land management practices within a given land-use. Although we attempted to choose similar sites as possible, the vegetation cover and management history differed within the land-use types among the sites. The different quality of the organic residues entering the soil and small-scale variability in the bedrock properties across the landscape may have partially obscured the effects of the land-use on the microbial communities.

CONCLUSION

Our study demonstrates that the effect of the soil type on the microbial community is more pronounced in comparison to the land use effect. However, the depth at which the land use effects are still observable, as well as the trend of the changes along the soil profiles, differ depending on the microbial char-

acteristic and soil type, and no general pattern was observed. The depth to which the land use impact was reflected was the smallest in the case of the N-mineralisation, followed by the respiration, and the biggest was found in the catalase activity, involved in the degradation of the more stable C compounds. While the Chernozem, rich in the SOM and located in warmer areas, was sensitive to changes in the microbial biomass and respiration due to the different land use, the Cambisol reflected changes throughout the soil profile, especially in the oxidative enzymes. The results in the context of other studies showed that the effect of the land use on the soil microorganisms may vary distinctly and more knowledge is needed to better understand the relationships in such ecosystems for sustainable land management. Nevertheless, they also indicate that although the most distinct impact of land use can be observed in the rooted zone, the deeper horizons should not be neglected when studying, e.g., the nutrient cycling and carbon sequestration. However, there is a need to take the soil types into account because they strongly influence the magnitude of the land use impact.

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