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Shifts in microbial diversity through land use intensity as drivers of carbon mineralization in soil

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ABSTRACT

Land use practices alter the biomass and structure of soil microbial communities. However, the impact of land management intensity on soil microbial diversity (*i.e.* richness and evenness) and consequences for functioning is still poorly understood. Here, we addressed this question by coupling molecular characterization of microbial diversity with measurements of carbon (C) mineralization in soils obtained from three locations across Europe, each representing a gradient of land management intensity under different soil and environmental conditions. Bacterial and fungal diversity were characterized by high throughput sequencing of ribosomal genes. Carbon cycling activities (*i.e.*, mineralization of autochthonous soil organic matter, mineralization of allochthonous plant residues) were measured by quantifying ^{12}C- and ^{13}C-CO_2 release after soils had been amended, or not, with ^{13}C-labelled wheat residues. Variation partitioning analysis was used to rank biological and physicochemical soil parameters according to their relative contribution to these activities. Across all three locations, microbial diversity was greatest at intermediate levels of land use intensity, indicating that optimal management of soil microbial diversity might not be achieved under the least intensive agriculture. Microbial richness was the best predictor of the C-cycling activities, with bacterial and fungal richness explaining 32.2 and 17% of the intensity of autochthonous soil organic matter mineralization; and fungal richness explaining 77% of the intensity of wheat residues mineralization. Altogether, our results provide evidence that there is scope for improvement in soil management to enhance microbial biodiversity and optimize C transformations mediated by microbial communities in soil.

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1. Introduction

In recent decades, human societies have adopted policies for land use intensification based on the conversion of complex natural ecosystems into simplified managed ecosystems, intensification of resource use through the mechanization of agricultural practices, and increased use of inputs such as fertilizers and pesticides (Tscharntke et al., 2005; Dallimer et al., 2009). This was originally motivated by the need to improve production to meet growing demands for food. However, it also led to profound alterations of the soil physicochemical properties, as well as of above-ground and below-ground biodiversity (Giller et al., 1997; Thiele-Bruhn et al.,

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2012; Bagella et al., 2014). For a long time, the development of intensive agriculture was not impeded by impairment of biodiversity, since the replacement of self-regulatory functions driven by soil organisms and their links with plants was considered by many to be offset by chemical and mechanical inputs. This viewpoint, however, is being challenged by an increasing awareness that the sustainability of agricultural systems, in terms of their capacity to maintain functions and ecosystem services, is compromised by the disruption of physicochemical and biological soil properties (Thiele-Bruhn et al., 2012; De Vries et al., 2013). This has evidenced the need to define new modes of land use management, which are adapted to the preservation and sustainable use of biodiversity to promote the driving of functions by biodiversity and reduce the use of chemical and mechanical inputs. To attain this objective, however, our ability to predict the effects of agricultural practices on soil biodiversity and functioning needs to be improved.

Microbial diversity, with its hundreds to thousands of taxa per gram of soil, dominates soil biodiversity (Torsvik and Øvreås, 2002) and contributes to key soil functions involved in the maintenance of soil fertility, and environmental and water quality. The impacts of increasing land use intensity on soil food webs have been documented (Giller et al., 1997; Bardgett and Cook, 1998; Thiele-Bruhn et al., 2012; De Vries et al., 2013), as have effects on the biomass, activity and structure of microbial and faunal communities (Meyer et al., 2013; Tsiafouli et al., 2015). However, effects of land use intensity on the diversity of soil microbial communities remain largely unknown. This question needs to be addressed, not only because of the intrinsic value of microbial diversity, in terms of a natural patrimony that needs to be preserved, but also because variations in the "amount" of soil diversity are likely to have significant repercussions in terms of soil nutrient cycling (Baumann et al., 2012; Philippot et al., 2013), pathogen management (Vivant et al., 2013), and stability of ecosystem services to environmental changes (Tardy et al., 2013). Recent studies based on estimates of the metrics of microbial diversity in terms of richness (number of species) and evenness (equality or distribution of individuals) in samples obtained over gradients of land use intensity suggest that microbial diversity may not follow a linear negative relationship to land management intensity, but instead a hump-backed relationship (Álvarez-Molina et al., 2012; Lai et al., 2014), with lower values at low and high intensity, and higher values at moderate intensity (Acosta-Martínez et al., 2008; Jangid et al., 2011; Shange et al., 2012). However, each of these studies focused only on the bacterial community in a single soil type, which limits the applicability of the conclusions. In addition they did not couple biodiversity measurements with estimates of soil functioning, and the functional significance of microbial diversity changes in response to land use remains an open question. Thus, new studies are needed to improve our knowledge of the patterns of microbial diversity and activity response to land management intensity.

The aim of this study was to investigate the impact on microbial (bacteria and fungi) diversity of changes in land management intensity in different farming systems, and to test how this links to transformations of soil organic matter (Seddaiu et al., 2013), a major function driven mostly by fungal and bacterial communities in soil (De Boer et al., 2005). For this, we sampled soils from three locations in different parts of Europe, each offering a gradient of land use intensity and covering a range of environmental conditions. The impact of land use on microbial diversity was assessed with a meta-barcoded pyrosequencing technique targeting ribosomal genes (Terrat et al., 2012). By generating several thousand sequences, this approach provides an accurate estimate of soil microbial diversity, including assessment of the richness and evenness of microbial communities. Changes in soil respiration patterns were measured by monitoring ^{12}C- and ^{13}C-CO_2 release after the soils had been amended or not with ^{13}C-labelled wheat residues, to study the response of microbial activity to the incorporation of an allochtonous carbon source in soil (Baumann et al., 2012; Lienhard et al., 2013). The resulting data obtained for microbial diversity, C mineralisation, and soil chemical and physical properties were analysed using variation partitioning to rank their relative contributions to C mineralization in soil.

2. Materials and methods

2.1. Experimental sites, soil sampling and analysis

Our study involved sampling soils from three locations across Europe, under Mediterranean to Temperate bioclimatic conditions, each with gradients of soil management intensity (low, medium and high). It is important to precise here that since the parameters determining the land use intensity level differed greatly between the three locations, intensity levels were not comparable among the locations. However, as presented below a gradient truly existed at each site. Consequently, in this study, the sampling strategy including these three contrasted locations was designed to identify general trends in terms of community response to land use intensity, and not to compare among the locations.

The Veluwe chronosequence is located on a 30 × 50 km area with post-glacial loamy sand in central Netherlands and is composed of abandoned ex-agricultural fields, which have been abandoned and reverted into semi-natural grasslands (Kardol et al., 2006; Van der Wal et al., 2006; Holtkamp et al., 2011). The gradient of management intensity is based on three individual, long-term abandoned fields (abandoned for 26–29 years, *Ve-low*), three distinct medium term abandoned fields (16–23 years, *Ve-med*) and three distinct short term abandoned fields (6–9 years, *Ve-high*). The vegetation at this site consisted of seminatural grass-forb vegetation with *Festuca rubra*, *Agrostis capillaris*, *Jacobaea vulgaris* and *Plantago lanceolata* as dominant grasses and forbs (Kardol et al., 2005). Interestingly, compared to the other two locations this gradient integrates a strong temporal aspect, with the intensity being determined more by the time since abandonment (referring to a high management intensity at the moment of the abandonment) rather than by the actual management intensity. All abandoned fields are subject to extensive natural grazing by wild horses, deer, wild boar, and small mammals in order to prevent forest development.

The Berchidda site is located in the northern hills of Sardinia, Italy, and characterized by an agro-forest ecosystem under same soil and similar topography (Bagella et al., 2014). The low intensity treatment (*Be-low*) is a semi-natural grassland not manured nor tilled since at least 80 years emerging from the selective mechanical cutting of the understory of a cork oak forest to get access for the cork harvest. The medium intensity treatment (*Be-med*) is a wooded grassland (25–50% tree cover of cork oaks) grazed by sheep and periodically cultivated (5–10 years) to grow annual forage crops (Rossetti et al., 2015). The high intensity treatment (*Be-high*) consists of intensively managed permanent grassland, grazed and periodically cultivated (1–5 years) to grow annual forage crops (Bagella et al., 2013). The vegetation at this site was represented by cork oak woods of the Violo dehnhardtii-Quercetum suberis association. Therophytes (67%) were much more abundant than perennials, mainly represented by hemicriptophytes. Unpalatable species were the most numerous, whilst the only excellent forage species were *Lolium rigidum*, *Trifolium subterraneum*, *T. incarnatum* and *T. michelianum* (Bagella et al., 2013).

In England, a series of mesotrophic grasslands in the Yorkshire Dales National Park, on the same soils and of similar topography were sampled in October 2011. Soils were sampled from grasslands

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representing a gradient of management intensity, ranging from intensively managed species poor grassland (*Yo-high*) (grazed and receiving >100 kg fertiliser N year), to intermediate intensity management (*Yo-med*) (grazed and receiving 50–100 kg fertiliser N year), to traditionally managed (*Yo-low*) (unfertilised, extensively grazed and cut), species-rich haymeadow of high conservation value (Bardgett and McAlister, 1999; De Vries et al., 2012a). At this site, plant communities of intensively managed grasslands (*Yo-high*) were *Lolium perenne-Cynosurus cristatus* grassland, according to the UK National Vegetation Classification of Rodwell (1992), whereas intermediate intensity (*Yo-med*) and traditionally managed grasslands (*Yo-low*) were sub categories of *Anthoxanthum odoratum-Geranium sylvaticum* grassland.

For all locations and management intensity treatments, three spatially independent soil samples were taken. Each sample consisted of a composite of five soil cores 5 cm diameter taken to a depth of 20 cm during autumn 2011. For more details on the sampling procedure and soil processing, see https://www.youtube.com/watch?v=_k7BEInBXEc. Soil samples were sieved to 4 mm. One portion of the soil was then stored at 4 °C before being incubated, and another portion was air dried for analysis of physico-chemical parameters, and lyophilized for analysis of biological parameters. Particle size distribution (clay, fine silt, coarse silt, fine sand, coarse sand), pH, soil organic carbon (SOC), soil total nitrogen (total N), soil C/N ratio and Cation Exchange Capacity (CEC) were determined by the Soil Analysis Laboratory of INRA (ARRAS, France, http://www.lille.inra.fr/las). In Berchidda, Veluwe, and Yorkshire Dales, soil types were respectively Haplic Cambisol; Anthrosol, and Luvisol according to the WRB classification. At all locations, topsoil was more than 20 cm depth, so there was no mixing with subsoil.

2.2. Soil microcosms

Microcosms were set up by placing 30 g of equivalent dry soil in 150-ml hermetically sealed plasma flasks. These soil microcosms were supplemented with sterile water to attain 60% soil water-holding capacity. After 3 weeks pre-incubation at 20 °C, the microcosms were then either amended with ^{13}C-residues of wheat (5 mg g^{-1} of dry weight soil), which had been finely ground in a bead beater to obtain a powder (C:N ratio of wheat residues = 77.7, and ^{13}C labelling = 7.01%), or were not amended (control). Wheat residues were used as "model" C-input to assess the response of microbial activity to addition of a given quality of plant material in all soils. Although they were not amended with wheat, control microcosms were mechanically disturbed as amended microcosms. In total our experimental design yielded 162 microcosms corresponding to the 3 locations × 3 levels of intensity × 3 plots/level × 2 treatments (amended or control) × 3 replicates/treatment. Microcosms were incubated in the dark for 105 days under controlled temperature (20 °C) and moisture conditions.

2.3. DNA extraction and molecular microbial biomass determination

At T0 (*i.e.* after the pre-incubation), microbial DNA was extracted from 1 g of soil from each triplicate microcosm of each intensity level from each location using the ISO-10063 procedure (Petric et al., 2011) which had been slightly modified (Plassart et al., 2012) to include a mechanical lysis step, using fastPrep®-24 instead of the recommended mini bead-beater cell disruptor. DNA concentrations of crude extracts were determined by electrophoresis in a 1% agarose gel using a calf thymus DNA standard curve, and used as estimates of microbial molecular biomass (Dequiedt et al., 2011). After quantification, DNA was purified using a MinElute gel extraction kit (Qiagen, Courtaboeuf, France).

2.4. Pyrosequencing of 16S and 18S rRNA gene sequences

Bacterial and fungal diversities were determined at T0 for the three levels of land use intensity for each location (triplicates/level of location) by 454 pyrosequencing of ribosomal genes. For bacteria, a 16S rRNA gene fragment with sequence variability and the appropriate size (about 450 bases) for 454 pyrosequencing was amplified by PCR using the primers F479 and R888. For fungi, an 18S rRNA gene fragment of about 350 bases was amplified using the primers FR1 and FF390. Primers and PCR conditions were as described previously (Tardy et al., 2014). The PCR products were purified using a MinElute gel extraction kit (Qiagen, Courtaboeuf, France) and quantified using the PicoGreen staining Kit (Molecular Probes, Paris, France). A second PCR of 9 cycles was then conducted under similar PCR conditions with purified PCR products and ten base pair multiplex identifiers added to the primers at 5′ position to specifically identify each sample and avoid PCR biases. Finally, the PCR products were purified and quantified as previously described. Pyrosequencing was then carried out on a GS FLX Titanium (Roche 454 Sequencing System).

2.5. Bioinformatics analysis of 16S and 18S rRNA gene sequences

Bioinformatic analyses were done using the GnS-PIPE developed by the GenoSol platform (INRA, Dijon, France) and initially described by Terrat et al. (2012). First, all reads were sorted according to the chosen identifiers sequences. The raw reads were then filtered and deleted based on their: (a) length, (b) number of ambiguities (Ns), and (c) primer(s) sequence(s). We then applied PERL programs to obtain strict dereplication, alignment of reads using infernal alignments (Cole et al., 2009) and clustered at 95% sequence similarity into operational taxonomic units (OTU) that cluster rare reads with abundant ones, and do not count differences in homopolymer lengths. Another homemade filtering step was then applied to eliminate potential sources of errors (e.g., PCR chimeras, sequencing errors, OTU overestimation). In order to efficiently compare the datasets and avoid biased community comparisons, the samples reads were reduced by random selection closed to the lowest datasets (5000 and 12,000 reads for 16S and 18S rRNA gene sequences respectively). The retained high-quality reads were used for: (*i*) taxonomy-independent analyses, to determine 1/Simpson, Shannon and richness diversity indices using the defined OTU composition, and (*ii*) taxonomy-based analysis using similarity approaches against dedicated reference databases from SILVA. The 1/Simpson index measures the probability that two individuals randomly selected from a sample will belong to the same species (*i.e* same OTU in our study). For this diversity index, the higher the value is, the greater the diversity. Simpson's Index gives more weight to the more abundant species in a sample. The addition of rare species to a sample causes only small changes in the value of D, contrary to the Shannon index. The raw data sets are available on the EBI database system under project accession number [PRJEB6118].

2.6. Total and ^{13}C-CO_2 measurements

Respired CO_2 (total and ^{13}C-CO_2) was measured after 0, 3, 7, 14, 21, 28, 44, 60, 80, 105 days of incubation on triplicates of the amended and control microcosms. At each sampling date, the gaseous phase (headspace in microcosms) was sampled in 10 ml airtight flasks to measure the CO_2 concentration and in 12 ml airtight flasks to determine the carbon isotope abundances. Since the microcosms were hermetically sealed and aerated by flushing with air at each sampling date, the measured concentrations corresponded to the CO_2 accumulated in the microcosm headspace

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between two sampling dates. The concentration of CO_2 in headspace gas was measured using an Agilent 7890 GC system equipped with a thermal conductivity detector coupled to an automatic sampler (Agilent G1888 Headspace), as described previously (Pascault et al., 2013). For isotopic CO_2, a pure bottle (CO_2 >99.999%, N48, Air Liquide, France), previously calibrated against a certified isotopic standard ($\delta^{13}C = -25.5 \pm 0.2$‰ vs. PDB, ISO-TOP, Air Liquide), was selected as internal standard. Gas samples were injected into the trace gas with an air gas syringe.^{13}C labelling of the plant residues allowed separation of the soil C (R_s) and plant residue (R_r) respiration (μg C-CO_2 g^{-1} soil) using the following mass balance equations:

$$R_s + R_r = R_t \text{ and } R_s \times {A_s}^{13} + R_r \times {A_r}^{13} = R_t \times {A_t}^{13}$$

where ${A_s}^{13}$ is the ^{13}C abundance regardless of soil carbon, ${A_r}^{13}$ the ^{13}C abundance of plant residue, R_t the total CO_2 emitted by soil with plant residue and ${A_t}^{13}$ its ^{13}C abundance.

The priming effect (PE) induced by the addition of plant residue was calculated as:

$$PE = (R_s \text{ soil with plant residue}) - (R_s \text{ control soil})$$

where R_s control soil is the CO_2 emitted by the soil in non-amended microcosms (*i.e.* basal respiration).

2.7. Statistical analysis

Differences in soil microbial communities structure between land use systems within a given location and between the locations were characterized using UniFrac distances (Lozupone and Knight, 2005). Non Metric Multidimensional Scaling (NMDS) was then used to graphically depict differences between soil microbial communities. The significance of the observed clustering of samples on the ordination plot was assessed by an Analysis OF SIMilarity (ANOSIM, 999 permutations).

C-mineralization activities and diversity indices (Richness and 1/Simpson) were compared between land use management strategies in the different locations with a two-way ANOVA (location and management treatment as factors) and the differences between them by Fisher test ($P < 0.05$). Physicochemical parameters were compared between the levels of management intensity for each location with the non parametric Kruskal–Wallis test. All these analyses were carried out using *XLSTAT* software (Addinsoft®).

Multiple linear regressions were used to determine the abiotic and biotic properties significantly affecting the respiration parameters measured in the different locations. In total, 10 soil physicochemical properties (Clay, fine silt, coarse silt, fine sand, coarse sand, pH, organic carbon, total N, C/N and CEC; Table 1) and 9 biotic variables (microbial biomass, fungal and bacterial diversity indices including richness, evenness, Shannon and 1/Simpson) were selected. The respiration parameters (Rt, Rr, PE and Rs control) were obtained from the log10-transformed areas under the cumulated CO_2 emission kinetics curves up until 105 days of incubation. All the explanatory (biotic and abiotic) variables were checked for collinearity (Supplementary Fig. 1) since this can inflate the variance of the regression coefficients in the models, leading to reduced precision in predicting the response variables (Ramette, 2007). When explanatory variables were strongly correlated, the ones to be kept in the multiple regression model were selected on the basis of *a priori* knowledge of the experimental system. All quantitative explanatory variables were transformed by applying Box–Cox transformation prior to the analyses (Cook and Weisberg, 1999). The significant explanatory variables for each respiration parameter were chosen by backward model selection and by minimizing the Akaike Information Criterion (AIC). Statistical significance was assessed by 1999 permutations of the reduced model. All these analyses were performed with the R free software (http://www.r-project.org/).

3. Results

3.1. Diversity and composition of bacterial and fungal communities

Pyrosequencing yielded a total of 527,017 and 659,091 sequences of 16S and 18S rDNA with an average of 19,519 and 24,410 sequences per sample, respectively. The rarefaction curves of bacterial OTUs confirmed that our sequencing effort allowed an accurate description of the bacterial diversity in each soil sample (*data not shown*).

Microbial diversity indices (richness (R) and 1/Simpson (1/D) indices) differed significantly with land use intensity at each location (Fig. 1). At Veluwe, both bacterial and fungal diversity were greater in *Ve-med* (bacterial R = 1359 ± 213; 1/D = 105.2 ± 22.9; fungal R = 1011 ± 130), with *Ve-med* > *Ve-high* = *Ve-low*. Likewise, in the Yorkshire Dales, fungal diversity was greatest in the *Yo-med* sites, whereas bacterial diversity increased along the gradient of increasing management intensity. At Berchidda, fungal diversity

Table 1
Top soil (0–10 cm layer) physicochemical parameters according to land use management of location. Q3

ID sample[b]	Clay (<2 μm)	Fine silt (2/20 μm)	Coarse silt (20/50 μm)	Fine sand (50/200 μm)	Coarse sand (200/2000 μm)	pH	Organic carbon (C)	Total N	C/N	CEC
	g/kg	g/kg	p/kg	g/kg	g/kg	–	g/Kg	g/Kg	–	cmol+/Kg
Ve-low	44 ± 14 [a]	24 ± 13 [a]	33 ± 27 [a]	242 ± 83 [a]	657 ± 133 [a]	4.8 ± 0.8 [a]	26.4 ± 6.9 [a]	1.47 ± 0.25 [a]	17.9 ± 1.6 [ab]	2.5 ± 1.4 [a]
Ve-med	84 ± 4 [b]	36 ± 3 [a]	16 ± 8 [a]	148 ± 87 [a]	716 ± 90 [a]	5.1 ± 0.5 [a]	23.3 ± 4.1 [a]	1.49 ± 0.32 [a]	15.7 ± 0.7 [a]	3.9 ± 1.0 [a]
Ve-high	77 ± 7 [ab]	37 ± 10 [a]	37 ± 12 [a]	172 ± 111 [a]	678 ± 92 [a]	5.6 ± 0.3 [a]	39.2 ± 10.8 [a]	1.71 ± 0.47 [a]	23.0 ± 2.3 [b]	3.7 ± 1.3 [a]
Be-low	151 ± 14 [a]	153 ± 14 [a]	63 ± 3 [a]	121 ± 4 [a]	511 ± 26 [a]	6.2 ± 0.2 [b]	27.0 ± 7.3 [a]	1.68 ± 0.50 [a]	16.2 ± 0.4 [b]	8.5 ± 3.0 [a]
Be-med	125 ± 17 [a]	110 ± 11 [a]	65 ± 17 [a]	131 ± 18 [a]	570 ± 62 [a]	5.7 ± 0.1 [ab]	19.8 ± 1.5 [a]	1.43 ± 0.13 [a]	13.9 ± 0.7 [ab]	8.1 ± 1.4 [a]
Be-high	163 ± 21 [a]	129 ± 11 [a]	82 ± 4 [a]	156 ± 12 [a]	471 ± 42 [a]	5.2 ± 0.1 [a]	21.2 ± 1.8 [a]	1.65 ± 0.13 [a]	12.8 ± 0.1 [a]	4.5 ± 0.7 [a]
Yo-low	336 ± 15 [ab]	160 ± 5 [a]	129 ± 12 [a]	314 ± 30 [a]	61 ± 8 [a]	5.4 ± 0.3 [a]	82.4 ± 9.5 [a]	7.69 ± 1.16 [a]	10.8 ± 0.5 [a]	17.0 ± 3.4 [a]
Yo-med	381 ± 36 [b]	208 ± 32 [a]	124 ± 15 [a]	219 ± 41 [a]	68 ± 6 [a]	5.3 ± 0.2 [a]	61.8 ± 1.8 [a]	6.46 ± 0.10 [a]	9.5 ± 0.1 [a]	21.3 ± 5.3 [a]
Yo-high	308 ± 9 [a]	211 ± 7 [a]	161 ± 8 [a]	241 ± 9 [a]	79 ± 10 [a]	5.4 ± 0.1 [a]	60.4 ± 7.5 [a]	5.16 ± 0.21 [a]	11.7 ± 1.6 [a]	17.7 ± 0.8 [a]

[a] Values are means (n = 3) ± standard errors.
[b] For ID sample, the samples from Veluwe location are represented by *Ve-low* (long term abandoned grassland: 26–29 years), *Ve-med* (medium term abandoned grassland: 16–23 years) and *Ve-high* (short term abandoned grassland: 6–9 years). The samples from Berchidda location are represented by *Be-low* (Woodland), *Be-med* (Wooded pasture grazed and periodically (5–10 years) cultivated to grow annual forage crops) and *Be-high* (Intensive grassland grazed and periodically (1–5 years) cultivated to grow annual forage crops). The samples from Yorkshire Dales location are represented by *Yo-low* (natural grassland grazed), *Yo-med* (natural grassland grazed and fertilized) and *Yo-high* (cultivated grassland (tillage + seeding), grazed and fertilized). For each parameter, the values with different letters differ significantly ($P < 0.05$).

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did not vary significantly between the three intensity levels, whereas bacterial diversity, estimated using the 1/Simpson index, was greatest in *Be-med*. This response was not related to a greater bacterial richness, but a higher evenness of the bacterial community (data not shown).

NMDS analysis of the full bacterial- and fungal-sequences datasets enabled the structures of the bacterial and fungal communities to be discriminated according to location and management intensity (Fig. 2). The main parameter discriminating both bacterial and fungal communities was the "location effect", with distinct structures observed between the three locations confirmed by ANOSIM test ($R = 0.721$, $P = 0.001$ for bacteria; and $R = 0.569$, $P = 0.001$ for fungi). The same dominant bacterial and fungal phyla were detected in all three locations, but the distribution of these groups in terms of relative abundance varied according to the location: *Actinobacteria*, *Firmicutes* and *Basidiomycota* were more frequent at the Berchidda location; *Proteobacteria*, *Ascomycota*, and *Glomeromycota* were more abundant at the Veluwe location; and *Bacteroidetes*, *Planctomycetes*, *Gemmatimonadetes*, *Nitrospirae*, *Glomeromycota* and *Chytridiomycota* were more abundant in the Yorkshire Dales (Fig. 2).

Land use intensity also significantly impacted the structure of bacterial and fungal communities at each site ($R = 0.77$, $P = 0.001$ for bacteria; and $R = 0.678$, $P = 0.001$ for fungi) (Fig. 2). We identified the bacterial and fungal phyla explaining this discrimination by analysing taxonomic composition at the three intensification levels for each location (Fig. 3; Supplementary Table 1). At Veluwe, discrimination across the gradient of management intensity was mainly explained by an increase in the relative abundance of *Actinobacteria* (from 11.2 ± 1.3 to 17.2 ± 2.7%), and a decrease in the relative abundance of *Planctomycetes* (from 4.2 ± 0.1 to 3.4 ± 0.5%) and *Proteobacteria*. At Berchidda, the relative importance of *Actinobacteria*, *Firmicutes*, *Nitrospirae* and *Ascomycota* increased significantly with increasing land management intensity, whereas that of *Bacteroidetes*, *Proteobacteria*, *Verrumicrobia* and *Basidiomycota* decreased. In the Yorkshire Dales, the relative abundance of *Actinobacteria* and *Bacteroidetes* groups was greatest at intermediate levels of management intensity.

3.2. Impact of land use management on carbon mineralization

Each of the four activities (i.e. basal respiration in control microcosms; total mineralization in wheat amended microcosms; wheat residue mineralization; priming effect) was expressed as the areas under the cumulated CO_2 emission (Fig. 4). Results showed that impact of land use intensity on different C cycling activities was dependent on the location (Fig. 4). At Veluwe, basal respiration, and total and wheat residue mineralization were significantly greater in *Ve-med* than in *Ve-low*, with intermediate values in *Ve-high*. In contrast, the intensity of the priming effect increased with increasing land management intensity, ranging from 5.0 ± 1.0 in *Ve-low* to 7.7 ± 0.8 mg CO_2 g^{-1} dry soil in *Ve-high*. At Berchidda, the four C-cycling activities measured were always significantly lower in *Be-med* than in *Be-low* and *Be-high*. Similar values for wheat residue mineralization and priming effect were observed in *Be-low* and *Be-high*, whereas the highest values for basal- and total

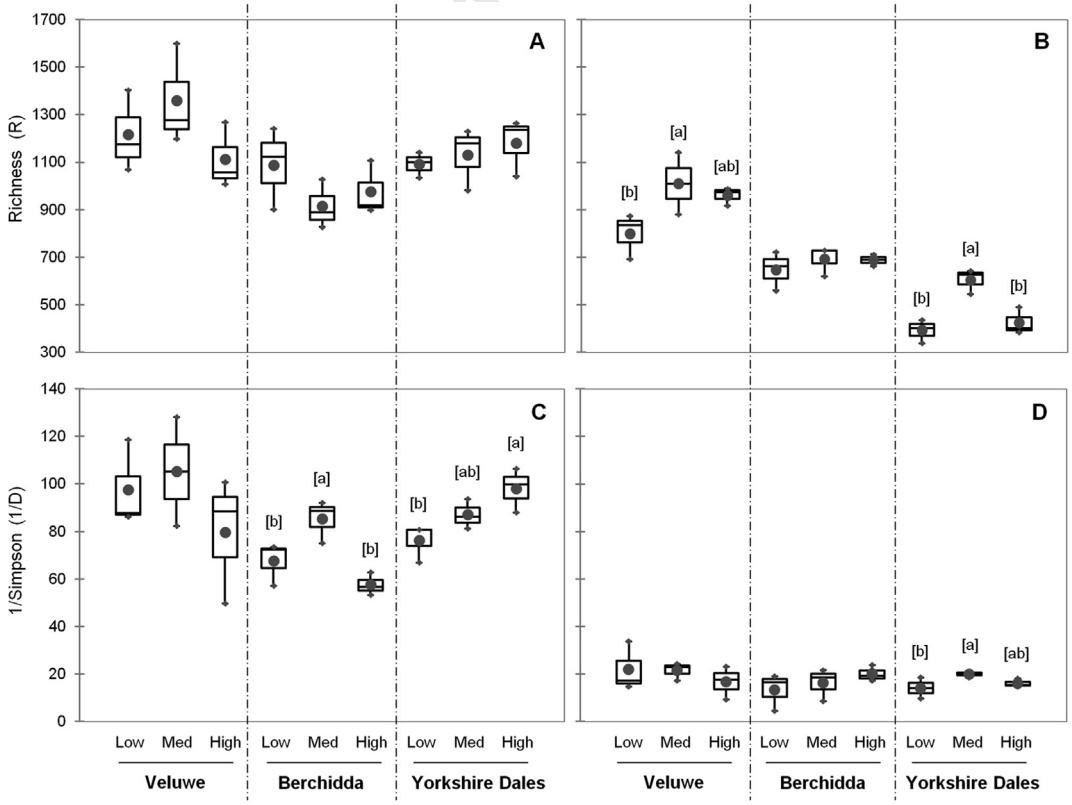

Fig. 1. Variation of diversity indices represented by bacterial (**A**) and fungal (**B**) richness (R) and 1/Simpson indices (1/D) for bacterial (**C**) and fungal communities (**D**) for each level of land use management (low, medium and high) for the three locations (Veluwe, Berchidda and Yorkshire Dales). The richness index represents the number of OTUs defined at the genus level. The 1/Simpson index measures the probability that two individuals randomly selected from a sample will belong to the same species (*i.e* same OTU in our study). In the whisker box representation, the first (Q1), median, and third (Q3) quartiles are indicated by the bottom, the central, and the top line of the box respectively. The bottom whisker extends to the lowest value of the data set, while the top whisker extends to the highest one. Letters in brackets indicate significant differences between land use for each location, according to the *Fisher* test ($P < 0.05$).

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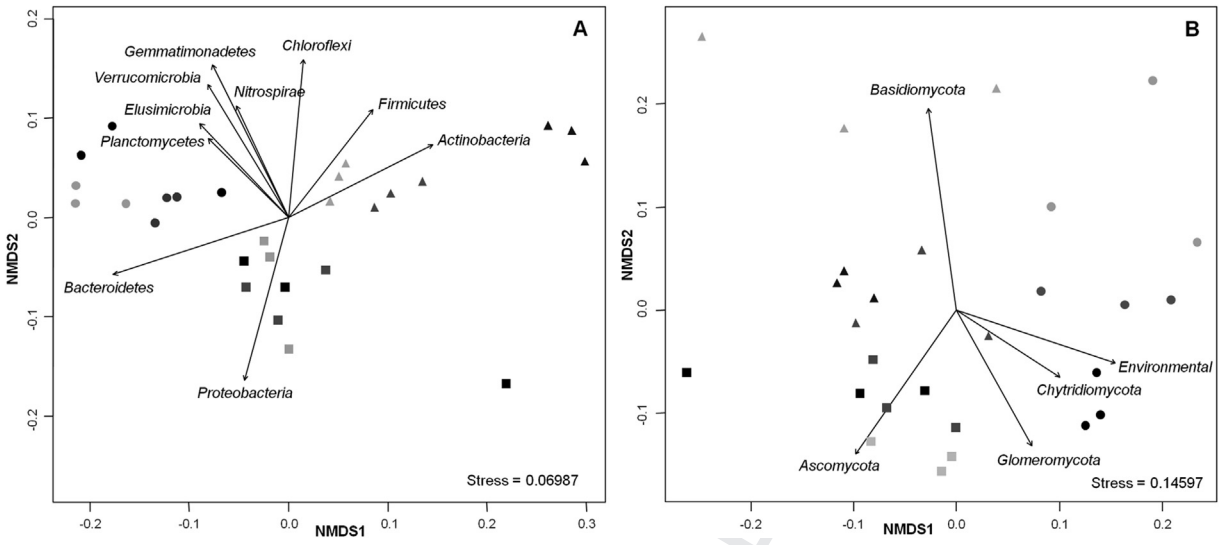

Fig. 2. Non-metric multi-dimensional scaling (NMDS) ordination plot derived from weighted pairwise UniFrac distances of (**A**) bacterial and (**B**) fungal communities for the location of Veluwe (□), Berchidda (Δ) and Yorkshire Dales (○) with each level of intensification corresponding to low (light grey), medium (dark grey) and high (black). The stress values for all plots were <0.2 which indicates that these data were well-represented by the two dimensional representation. Vectors in the bi-plot overlay were constructed from a matrix containing the relative abundances of each microbial *phylum*. Only correlations ≤0.05 were included. The angle and length of the vector indicate the direction and strength of the variable.

mineralization were recorded in *Be-low*. At the Yorkshire Dales, both basal and total mineralization decreased with increasing land use intensity. In contrast, wheat residue mineralization increased with increasing land use intensity, ranging from 50.8 ± 1.9 to 57.7 ± 1.3 mg CO_2 g^{-1} dry soil. PE intensity did not differ between the three land use intensities.

3.3. Ranking the influence of biotic and abiotic variables on C-cycling activities

Eight out of 20 variables, selected on the basis of their low cross-correlation (Supplementary Fig. 1), were included in the multiple regression models. These 8 variables represented abiotic (physicochemical properties of soil: pH, soil C/N ratio, SOC and fine sand) and biological variables (richness and the 1/D index for both fungal and bacterial communities). The multiple regression model with selected variables was able to explain very large proportions of the variance in intensity for each of the four C-cycling activities, ranging from 62 for PE to 91% for wheat residue mineralization (Table 2).

Biological variables were the strongest predictors for three of the measured activities, explaining 42, 50, and 80% of the observed variance for total, basal, and wheat residue-mineralization, respectively. In contrast, PE was better predicted by abiotic (56%)

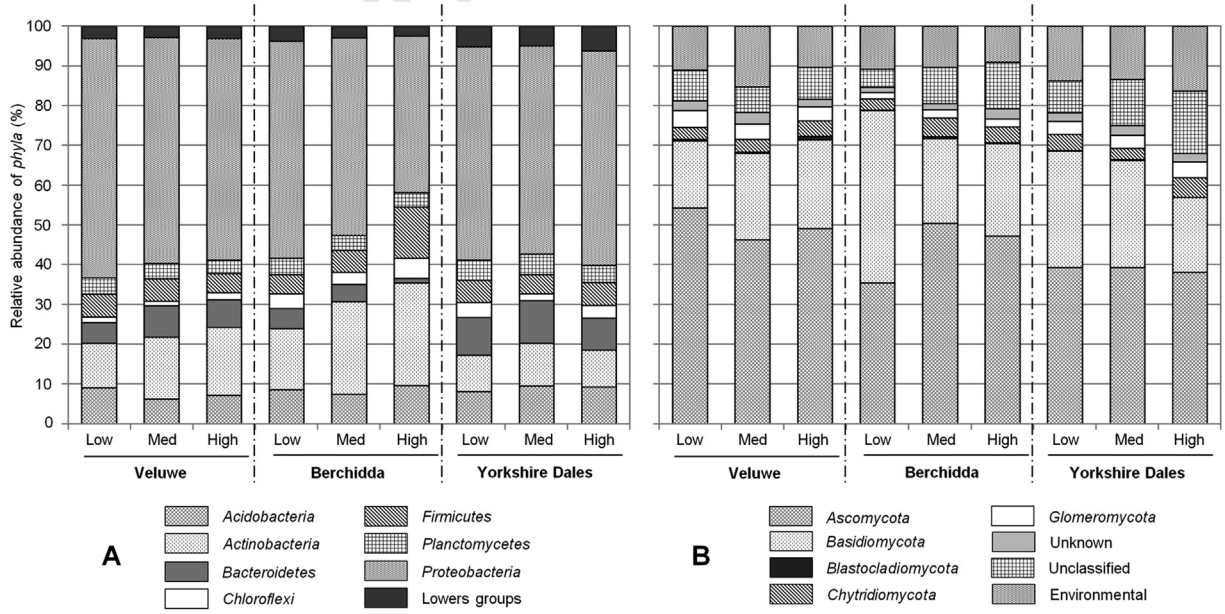

Fig. 3. Relative abundance of both (**A**) bacterial and (**B**) fungal phyla in microbial composition according to locations (Veluwe, Berchidda and Yorkshire Dales) and level of intensification of land use management (low, med (medium) and high). Lower groups represent the phylogenetic groups (phyla) with a relative abundance <1%.

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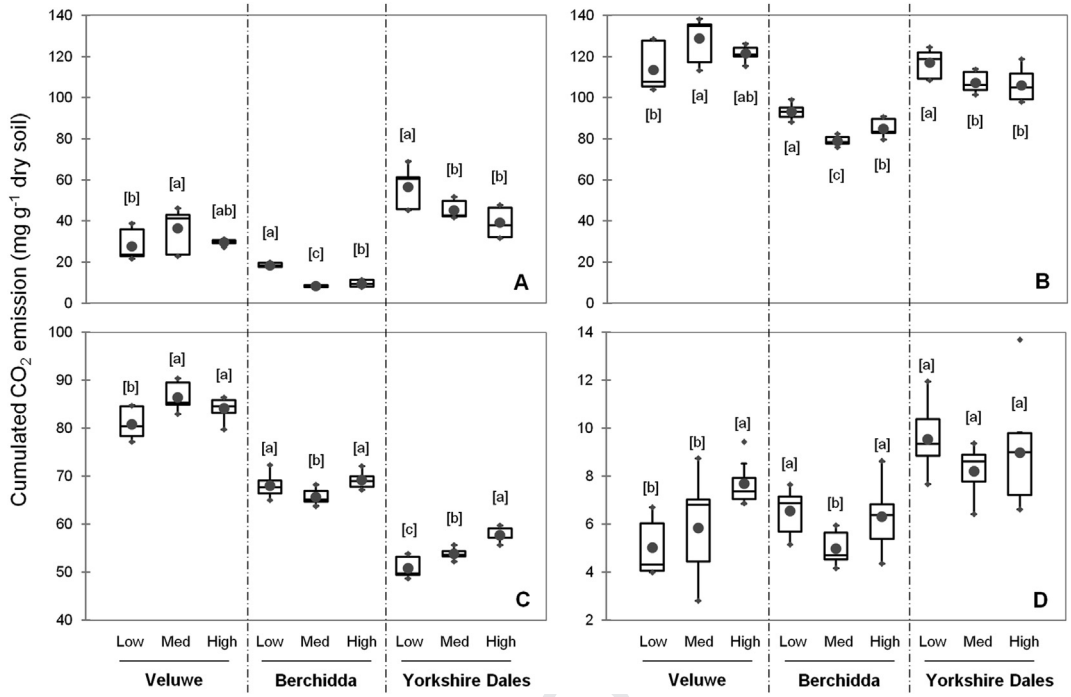

Fig. 4. Variation of areas (mg g^{-1} dry soil) under the cumulated CO_2 emission of different C-cycling activities measured according to land use management (low, medium and high) for the three locations (Veluwe, Berchidda and Yorkshire Dales) with (**A)** basal mineralization (R_s control soil), (**B**) total mineralization (R_t), (**C**) wheat residues mineralization and (**D**) Priming Effect. In the whisker box representation, the first (Q1), median, and third (Q3) quartiles are indicated by the bottom, the central, and the top line of the box, respectively. The bottom whisker extends to the lowest value of the data set, while the top whisker extends to the highest one. Letters in brackets indicate significant differences between land use for each location, according to the *Fisher* test ($P < 0.05$).

Table 2
Partitioning of the functional variation of different C-cycling activities measured as a function of biotic and abiotic parameters.

	df[a]	Sum of square	F[b]	Significance[c]	Variance explained (%)	Relation[d]
Basal mineralization (R_s control soil)						
Bacterial richness	1	0.6955	39.511	***	32.23	+
Fungal richness	1	0.3820	21.703	***	17.71	−
Fungal 1/Simpson	1	0.0006	0.034	ns	0.03	
Fine sand	1	0.3042	17.279	***	14.10	+
SOC	1	0.4057	23.048	***	18.80	+
Residuals	21	0.3697				
Total mineralization (R_t)						
Bacterial richness	1	0.0583	28.493	***	41.92	+
Fungal richness	1	0.0000	0.015	ns	0.02	
Fungal 1/Simpson	1	0.0013	0.624	ns	0.92	
Fine sand	1	0.0196	9.558	**	14.06	+
SOC	1	0.0170	8.284	**	12.19	+
Residuals	21	0.0430				
Wheat residues mineralization (R_r)						
Fungal richness	1	0.1334	187.618	***	76.99	+
Bacterial 1/Simpson	1	0.0011	1.617	ns	0.66	
Fungal 1/Simpson	1	0.0048	6.714	*	2.76	+
pH	1	0.0012	1.652	ns	0.68	
Soil C/N ratio	1	0.0156	21.912	***	8.99	+
SOC	1	0.0030	4.184	◦	1.72	−
Residuals	20	0.0142				
Priming effect (PE)						
Fungal 1/Simpson	1	0.0219	3.532	◦	5.83	−
Fine sand	1	0.1874	30.270	***	49.97	+
Soil C/N ratio	1	0.0234	3.772	◦	6.23	−
Residuals	23	0.1424				

[a] Degrees of freedom.
[b] Fisher test.
[c] Significance was determined by 1000 permutations with ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ◦$P < 0.1$ and ns (not significant), $P \geq 0.1$.
[d] Relationship was determined from the linear regression between area and significant variable, with a positive relationship (+) when the area of respiration increased with an increase of the variable, and a negative relationship (−) when the area of respiration decreased with an increase of the variable.

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than by biotic variables (6%). All variables were always positively correlated with the measured activities, except fungal richness that was negatively correlated with basal respiration.

The identity and/or rank of the most predictive variables varied according to the activity. More precisely, bacterial richness was the best predictor of basal and total C mineralization. However, fungal richness explained 17.7% of basal respiration (negatively correlated), but was not a significant driver of total C mineralization. Among the abiotic variables, fine sand and soil organic C content were both good predictors of basal and total C mineralization. In contrast to the two above-mentioned activities, bacterial diversity was not a significant driver of wheat residue mineralization and PE, which were instead driven by fungal diversity. Thus, fungal richness accounted very strongly (77%) for wheat residue mineralization, and fungal diversity explained a small but significant part of the variance in PE (5.8%). Soil C/N ratio, an indicator of organic matter quality, but not soil organic C content, was also a predictor of wheat residue mineralization and PE. A very significant proportion of the variance in PE was explained by fine sand soil content.

Negative correlations were observed for SOC and wheat residues mineralization, as well as for fungal 1/Simpson, soil C/N and PE. However, these negative correlations were weakly significant ($P < 0.1$), indicating that in our study these parameters were not strong predictors of the activities measured. In the case of Rr, our results suggested that the quality of soil organic matter (C/N; $P < 0.001$) rather than the quantity (SOC, $P < 0.1$) may be determinant for wheat residues decomposition. For priming effect, result suggested that PE may be increased for lower values of (C/N = less recalcitrant organic matter), which makes sense since energy needed to re-activate organic matter decomposition may be lower for low values of C/N.

4. Discussion

Microbial diversity and composition differed more between the three contrasting locations across Europe than between the three treatments within each location. Microbial diversity was not expected to be similar at all 3 locations but results showed that the "site effect" was more important than the "land use effect" in modifying the diversity of the communities. The large differences in soil physicochemical characteristics, plant cover and climate between the three locations is likely to have largely accounted for the discrimination of microbial communities in terms of richness and composition (Fierer and Jackson, 2006; Dequiedt et al., 2011; De Vries et al., 2012b; Kuramae et al., 2012) (Table 1). Microbial composition provided indications about the environmental filters that may have driven the microbial diversity in each location. For instance, the greater abundance of *Actinobacteria* and *Firmicutes* at Berchidda suggests that the microbial diversity signature may have been influenced by the Mediterranean climate at this location. Indeed, both groups share the ability to produce endospores, which has been shown to increase their ability to survive stressful climatic conditions, such as warming and desiccation, over other phyla (Hayden et al., 2012; Sharmin et al., 2013). In addition, plant cover, and especially the presence of oaks, might also explain the greater overall contribution of *Basidiomycota* to the fungal composition at this location, in agreement with Orgiazzi et al. (2013). This fungal group is indeed widely represented in forest soils since it possesses improved metabolic capacities for decomposing lignocellulose, a major component of organic C in tree-wood debris (De Boer et al., 2005; Baldrian, 2008; Voříšková and Baldrian, 2013). The Veluwe and Yorkshire Dales sites were dominated by *Proteobacteria* and *Bacteroidetes*, two groups described as fast growing copiotrophs stimulated by C-rich environments (Fierer et al., 2007; Pascault et al., 2013), which is in agreement with the higher overall C content measured at these two sites than at Berchidda.

Land use intensity had a significant impact on the diversity and composition of bacterial and fungal communities in each location. This shows that even though the soil's ability to host microbial diversity may be highly constrained by pedoclimatic properties, land use may serve as a proximal "control lever" to modify microbial diversity. This is in agreement with other studies conducted at the field scale (Acosta-Martínez et al., 2008; Lienhard et al., 2013) or regional scale (Drenovsky et al., 2010). However, our study of three contrasting locations representing different gradients of land use intensity made it possible to link land use intensity with microbial diversity in contrasting pedoclimatic contexts. Interestingly, no simple decrease in soil microbial diversity (*i.e.* richness and 1/D) with increasing land use intensity was observed, whatever the location. Instead, the general trend observed for both bacterial and fungal communities, in all three locations, was an increase in diversity (*i.e.* richness and 1/D) under medium land use intensity, as compared to low- and high-intensities. In agreement with other recent works (Acosta-Martínez et al., 2008; Jangid et al., 2011; Shange et al., 2012), this finding suggests that the hump-back model, describing the response of a community to stress (Giller et al., 1998), may also be applied to the microbial response to perturbations associated with land management intensity. According to this model, a decrease in apparent diversity may occur (i) in highly stressed environment due to dominance of particularly competitive species through competitive exclusion, and (ii) in highly unstressed environment due to the dominance of particularly adapted species through selection. Contrastingly, moderate stress may increase apparent diversity by lowering the likehood of competitive exclusion and the selection mechanism. In our study, this suggests that increasing land management intensity in agrosystems may not necessarily have a negative, linear impact on soil microbial diversity, but may instead enable an optimum (*i.e.* climax of soil microbial genetic resources) to be attained. Interestingly, this optimum was reached for both bacteria and fungi at medium intensity land use at Berchidda and Veluwe. In the Yorkshire Dales however, the same pattern was observed for fungi, but not for bacteria; bacterial diversity showed a linear increase with increasing land use intensity. This discrepancy may be ascribed to the fact that at this location tillage was only applied in the high-intensity plots. Soil mechanical disturbance, particularly tillage, has recently been demonstrated to increase bacterial diversity and reduce fungal diversity (Lienhard et al., 2013; Pastorelli et al., 2013), probably due to the greater sensitivity of the fungal hyphal network to physical disruption (Helgason et al., 1998; Van der Wal et al., 2006).

Similar to the biotic and abiotic soil parameters, patterns of C-mineralization activity differed between the locations, but also along the gradient of intensification within each location (Fig. 4). Partitioning of the functional variation, using the set of biotic and abiotic soils parameters, revealed that 62–91% of the variance in intensity of C-cycling activities could be explained (Table 1). Among the parameters selected in our model, a significant proportion of this variance was explained by soil organic matter status (*i.e.* SOC, soil C/N). This positive effect of soil organic matter quantity and quality on the intensity of CO_2 fluxes is well established (Henriksen and Breland, 1999; Nicolardot et al., 2001). Indeed, the degradability and the amount of C-resources are known to be two key factors controlling soil microbial biomass and activity (supported by our results showing a correlation between molecular biomass and SOC, Supplementary Fig. 1). As such, these are the parameters included in most of the current models of C-dynamics in soil (Fang et al., 2005). However, our results also showed that microbial diversity parameters were the best predictors of all the activities measured (except priming effect). This finding highlights the

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significant role of microbial diversity in determining C-dynamics in soil, which may be at least as important as microbial biomass and soil chemical and physical properties. These results also confirm the positive relationship between microbial diversity and carbon mineralization observed in the context of other studies involving experimental erosion of microbial diversity (Bell et al., 2005; Baumann et al., 2012; Tardy et al., 2013).

Focusing on the effect of each biological variable, microbial richness was the best predictor of all the activities measured, except PE. Interestingly, the relative importance of bacterial *vs*. fungal diversity varied between the activities measured, suggesting that the relative involvement of these two microbial groups is dependent on the quality of the C-sources (De Boer et al., 2005). Bacterial, and to a lesser extent fungal, richness were good predictors of soil basal respiration (explaining 32.2 and 17.7% of the variance, respectively). However, the relationship between microbial diversity and basal respiration was positive for bacteria and negative for fungi, suggesting a major role of bacteria. This result may be related to our particular soil selection, which essentially included agricultural and grassland soils. In forest soils, it is likely that involvement of fungal communities in soil processes would have been increased (Voříšková and Baldrian, 2013). Indeed, soil fungal biomass has been demonstrated to be more affected by soil management practices and grassland intensification than bacterial biomass (Bardgett and Leemans, 1996; Bardgett and McAlister, 1999; Frey et al., 1999; De Vries et al., 2012b), hence reducing the relative involvement of fungi in ecosystem processes under intensively managed agricultural land (Van der Wal et al., 2006). This major involvement of bacteria was also observed for total mineralization, measured after wheat residue incorporation, with bacterial richness alone explaining 41.9% of the variance of this activity whereas the fungal diversity parameters were not significant explanatory variables. In contrast, fungal richness, but not bacterial diversity, explained an impressive proportion of the intensity of wheat mineralization (77.0%). This is in agreement with the general assumption that fungi are the primary decomposers of dead plant biomass in terrestrial ecosystems (Voříšková and Baldrian, 2013). In other respects, the strength of the relationship between fungal richness and residue decomposition was likely to be further enhanced by the high recalcitrance to decomposition of the wheat straw residues used, (C/N ratio of 77.7). Fungi, through their ability to produce a wide range of extracellular enzymes and to perforate plant cell walls, are assumed to be better decomposers of recalcitrant organic matter than bacteria (De Boer et al., 2005).

Addition of wheat straw residues to the soil induced a PE in all locations, whatever the land use intensity, highlighting the widespread occurrence of this process in soil. PE was the only one of the four C-activities, for which the variance was more explained by soil physical properties (soil fine sand content and C/N ratio, together accounting for 56.2% of the variance) than by the microbial diversity parameters taken into account in our variance partitioning model. This was not in agreement with recent studies showing that PE may depend on interactions between different guilds of bacteria (Pascault et al., 2013) and fungi (Fontaine et al., 2011), and consequently on microbial diversity. However, this discrepancy may be due to the fact that these particular processes may depend more on the composition (*i.e*. presence of particular microbial populations/groups, referred to as r-, and k-strategists (Pascault et al., 2013)) than on the quantitative estimates of diversity taken into account in our model.

5. Conclusions

In conclusion, by using three gradients of land management intensity in three different European countries, we were able to demonstrate that increasing land management intensity in agrosystems may not necessarily have a negative, linear impact on soil microbial diversity, but may instead enable an optimum (*i.e*. climax of soil microbial genetic resources) to be attained. This result has important implications since it suggests that it may be possible to improve soil genetic resources by applying appropriate land management practices. Another important output of this study is that, for the first time, it has been possible to rank the soil chemical, physical and microbiological diversity properties contributing to C-transformations in soil. Thus, our results indicate that microbial diversity may be at least as good a predictor of the transformations involved in the C-cycling in soil, as soil chemistry or structure, explaining up to 80% of the variance in intensity of the activities measured. Altogether, this study provides evidence, in different farming systems across Europe, that changes in soil microbial diversity in response to land use practices link to soil functioning through modulations of carbon mineralization in soil.

Conflict of interest

The authors declare no conflict of interest.

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Lienhard et al., 2014. Q4

Acknowledgements

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2015.08.010.

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