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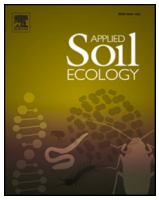

Interacting management effects on soil microbial alpha and beta diversity in Swiss agricultural grassland

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ABSTRACT

Agriculturally managed grasslands are a major land-use type and crucial for global food production. Yet, degradation of grassland soils endangers both soil microbial diversity and food security, as they harbor diverse microbial life integral to ecosystem functioning and therefore ultimately also human wellbeing. Despite its functional significance, the impact of different aspects of grassland management on the soil microbiome remains insufficiently elucidated and limits our ability to maintain this invaluable and insufficiently explored biological resource. This study examined the interacting impacts of grassland management intensity, harvest type (grazing or mowing predominate), and production system (organic vs. non-organic) on soil microbial alpha and beta diversity (community structure) in the context of the local environment using a metabarcoding approach of ribosomal markers across 86 permanent grasslands in Switzerland. The local environment including soil properties and topographical variables explained more of the variance in fungal and prokaryotic diversity than management, which was still significantly related to most microbial diversity measures. Soil prokaryotic and fungal communities were strongly driven by management intensity, and especially in the case of fungal communities, harvest type played an important role – for alpha diversity in the form of an interaction between management intensity and harvest type, for beta diversity in the form of a main effect. Organic farming had only little direct influence on soil microbial communities. Taxa enriched in intensively managed and fertilized grasslands were typically linked to coprophilous and nitrogen-cycling guilds. Grazed grasslands were characterized by high copiotroph to oligotroph ratios. Because the most diverse soil microbiomes in permanent grasslands appear to be driven by management intensity interacting with harvest types, grasslands of differing management regimes are needed to sustain and promote soil microbial diversity at the landscape level.

1. Introduction

Grasslands are highly important terrestrial ecosystems, covering 40 % of the terrestrial surface of the Earth (excluding Antarctica and Greenland) (White et al., 2000). They offer vital ecosystem services, contributing substantially to human wellbeing by providing feed for ruminants, regulating water cycles and the climate, and being of cultural value, among many others (Bengtsson et al., 2019). In temperate regions, many grasslands, and thus their ecosystem services, rely on human management like mowing or grazing by livestock to keep them free from shrubs and trees (Prangel et al., 2023). Grassland management influences soil microbial communities and thus the ecosystem processes mediated by these communities, such as plant growth, nutrient cycling, and decomposition (Bertola et al., 2021; Hartmann and Six, 2023).

In Europe, managed grasslands have experienced changes in contrasting directions: on the one hand abandonment and afforestation in more remote areas, and on the other hand management intensification in more favorable areas (Rutherford et al., 2008; Wesche et al., 2012).

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This has far-reaching consequences for grassland biodiversity and functioning, including significant effects on the soil microbiome (e.g., Fox et al., 2021, 2022). Although management practices were found to generally have smaller influence on soil microbial diversity when compared to edaphic and topographic properties (Degrune et al., 2019; Kaiser et al., 2016; Kuramae et al., 2012), edaphic properties such as pH, soil organic carbon, and nutrient contents are themselves strongly influenced by management (Leff et al., 2015; Mayel et al., 2021), leading to interrelated effects of management and environment on soil microbial communities. To understand grassland soil microbial diversity, it is thus crucial to understand how different grassland management practices influence soil microbial communities, while trying to account for soil and topographic factors.

Grassland management can be characterized by different aspects, which all potentially shape the soil microbiome and which in practice occur in combination (Fig. 1). This makes it challenging to disentangle their single effects on the soil microbiome and at the same time assess the effect when used in combination. The first management aspect addressed here is **management intensity**, which encompasses cutting frequency, grazing intensity, and fertilization intensity (Blüthgen et al., 2012), and which receives a lot of attention due to its strong impact on different aspects of the ecosystem, ranging from plant species composition to soil conditions, thus also impacting the soil microbiome (Mayel et al., 2021; Soussana et al., 2010). For example, intensive management has been found to increase soil prokaryotic and decrease soil fungal species richness (Bledsoe et al., 2020; Fox et al., 2021, 2022). Soil microbial taxa show varying responses to differences in soil properties between extensively and intensively managed grasslands, which can result in very distinct community structures in grasslands of varying management intensity (Fox et al., 2021; Leff et al., 2015).

Second, the mode of biomass removal, i.e., the **harvest type**, which can either be pasture (dominated by grazing) or meadow (dominated by mowing), is another management aspect with implications for soil microbes. Grazing animals browse selectively, thus altering plant composition compared to mown grasslands, and change soil properties with defecation and trampling activities (Mayel et al., 2021; Pauler et al., 2020). As opposed to nutrient addition, microbial species richness has been observed to be unchanged by mowing vs. grazing, while differences in microbial community structure between the harvest types have been observed (Qin et al., 2021; Randall et al., 2019; Wang et al., 2019).

Third, **organic farming** is of great significance for grassland management, as about two thirds of the area of certified organic agriculture globally consists of grasslands (Willer et al., 2023). In contrast to the afore-discussed management practices, organic farming is implemented on the whole farm but also affects field-scale grassland management. It is characterized by the absence of synthetic inputs such as pesticides and inorganic fertilizers (IFOAM, 2023). Yet, besides Yeates et al. (1997) who found no consistent effects of organic grassland farming on soil fungal and prokaryotic communities in Wales, UK, the effect of organic farming on grassland soil microbiomes has never been assessed in detail. Studies on arable croplands, though, are quite numerous, showing that organic as opposed to mineral fertilizer inputs enhanced especially prokaryotic diversity and played a large role in shaping soil microbial communities (Hartmann et al., 2015; Pan et al., 2020). As the use of mineral fertilizers and herbicides is lower in non-organic permanent grassland compared to arable management (Einarsson et al., 2021; Tamm et al., 2018), weaker effects of organic farming on the soil microbiome can be expected.

To better understand the single and interacting effects of grassland management intensity (extensive vs. intensive), harvest type (pasture vs. meadow), and production system (organic vs. non-organic) on soil microbial diversity and community structure, we comprehensively sampled 86 grassland parcels managed by farmers in Switzerland. We expected that: 1) grassland management will shape soil microbial diversity and community structure, and different management aspects will lead to distinct communities with characteristic taxa (i.e., indicator genera); 2) extensive management will increase fungal and decrease prokaryotic alpha-diversity compared to intensive management, and alter microbial community structure; 3) harvest type will not influence microbial alpha-diversity but significantly affect community structure; and 4) organic management will increase microbial alpha-diversity compared to non-organic farming and also alter microbial community

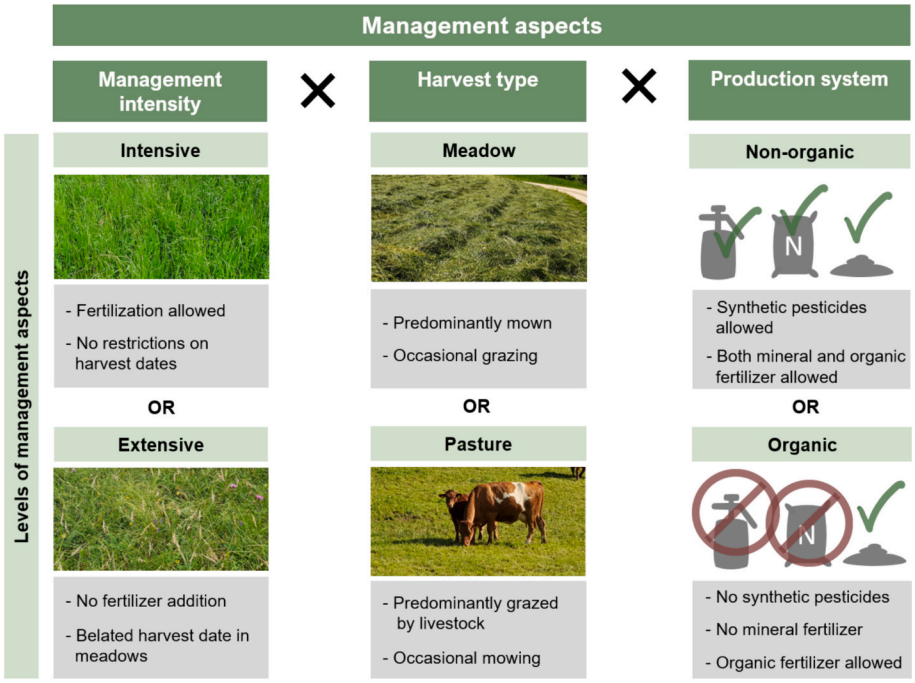

Fig. 1. Illustration of the three management aspects shaping the full-factorial sampling design used in this study. Grasslands were either managed intensively or extensively, the biomass utilized either predominantly by mowing (meadow) or grazing (pasture), and the production system was either organic or non-organic. Considering all possible combinations of the three management aspects resulted in eight distinct grassland management regimes that were included in this study.

structure. The results of this study will help to understand the management practices driving the soil microbiome of permanent grasslands and the mechanisms governing microbial soil diversity, contributing to an evidence-based decision-making for shaping future agricultural landscapes to maintain soil microbial diversities.

2. Methods

2.1. Study area, management practices, and sites

The permanent grasslands included in this study were located in the Swiss Canton of Solothurn. Grassland plots were located throughout the Canton and selected as described in **Supplementary material S1.1**, resulting in a set of 86 grassland parcels, belonging to 36 farms (18 organic and 18 non-organic). The plots were managed either extensively or intensively and either as pastures or meadows, resulting in a full-factorial design with eight distinct management regimes, with plots spanning an elevational gradient from 435 to 1145 m a.s.l. (Fig. 1). All of these grasslands had been permanent grasslands for at least 15 years, without being included in a crop rotation. Some grasslands might have been occasionally overseeded with grassland seed-mixtures and could potentially also be renewed using ploughing. Yet, grassland renewal employing ploughing is generally rarely practiced in Switzerland and no such frequently (re-)sown grasslands were included in the study. The number of replicates for organic and non-organic intensive meadows was 14 each, for organic and non-organic intensive pastures 12 each, for organic and non-organic extensive meadows 11 each, and for organic and non-organic extensive pastures 6 each. Extensively managed meadows may not be fertilized and are allowed to be mown only starting from a pre-defined date (usually mid-June in lowland areas). Extensively managed pastures may not be fertilized, but there are no restrictions on the timing of grazing and the grazing intensity. Since extensive meadows and pastures are usually long-term unfertilized and supplementary feeding on extensive pastures is not allowed, the annual number of cuts and the stocking density are therefore determined by the natural growth potential of a site. This can also vary from year to year depending on weather conditions. For intensive meadows and intensive pastures, no regulations are in place concerning cutting dates, and fertilization up to 135 (organic) or 162 (non-organic) kg available N is allowed (BioSuisse, 2023). Organically managed grasslands in Switzerland receive no inorganic fertilizers or synthetic pesticides, among other regulations, but intensive organic fertilization is allowed, though lower than in the non-organic system (BioSuisse, 2023). This differentiation follows the official typology for Swiss grasslands and was confirmed by farmer interviews (Supplementary material, **Table S2.1**).

2.2. Data collection

In June 2020, 20 soil samples were taken to a depth of 20 cm on each plot along two orthogonal transects of 18 m each, mixed, cooled and sieved to 2 mm to remove plant parts and stones. These samples were used to measure soil texture, soil organic carbon content, plant available phosphorus (P), calcium (Ca), magnesium (Mg) and potassium (K), and pH, as described in detail in **Supplementary material S1.2**. Subsequently frozen (−20 °C) soil from this sampling campaign was used for microbial analyses. Microbial laboratory analyses and bioinformatic processing of sequence data were largely carried out as described in Longepierre et al. (2021), and are described in detail in **Supplementary material S1.3.** Briefly, DNA was extracted, and markers were amplified using the primers ITS3ngs and ITS4ngs targeting the fungal internal transcribed spacer region ITS2 (Tedersoo and Lindahl, 2016), and the primers 341F and 806R targeting the prokaryotic V3-V4 region of the 16S rRNA gene (Frey et al., 2016). Amplicons were sent for sequencing to the Functional Genomics Center Zurich (FGCZ) on an Illumina MiSeq platform with the PE300 read mode. Bioinformatic analyses including delineation and taxonomic classification of amplicon sequence variants (ASVs) were largely based on VSEARCH (Rognes et al., 2016) with some customization as described previously (Longepierre et al., 2021, see **Supplementary material S1.3** for details). The samples for the grassland soil microbial communities were taken at only one timepoint across all the plots for reasons of cost and effort as well as based on other research from similar regions in Switzerland showing little temporal variation of soil microbial communities compared to agricultural influences (Fox et al., 2022).

Total soil nitrogen (N) and organic carbon concentration (C_{org}), to calculate C:N ratio, was measured from samples collected in August/September 2020, taking three soil samples per plot in 0–5 and 5–10 cm depth, pooled per depth level, sieved, and dried at 60 °C. Details are provided in **Supplementary material S1.2**. The elevation of the plots was derived from a Digital Elevation Model (DEM) of the Copernicus Land Monitoring Service of the European Environment Agency (European European Union, 2018) at a resolution of 25 m. Using a compass, the exposition of the plot was assessed and subsequently, northness, representing the orientation of the raster cell to the north, with +1 indicating north, and − 1 south, was calculated. In QGIS.org (2020), aspect of the land in radians, and subsequently the cosine of this grid was computed to provide the northness. The inclination of each plot was assessed using the cell phone application Clinometer plaincode™.

To acquire detailed information on grassland management in 2020 and 2021, we conducted oral interviews with farmers managing the plots. Because grassland management intensity often varies between years, interviews were conducted for both years to gain robust average data. The questions concerned grazing dates, number, age, and type of animals, as well as timing, amounts and nature of fertilizer applications. We used the grazing information to calculate the average livestock unit days ha^{-1} $year^{-1}$ for each plot over the two years. We calculated the total plant-available fertilizer N ha^{-1} $year^{-1}$, with the help of the information about amount and type of fertilizer, and based on information of Richner et al. (2017) about available N contents of the different organic fertilizers. We assumed the availability of mineral fertilizer to be 100 %. The interviews also included questions about weed control measures (pesticide or mechanical; **Supplementary material, Table S2.1**). Overall land use intensity was calculated according to Blüthgen et al. (2012) from available N from fertilizers (kg ha^{-1} $year^{-1}$), number of cuts $year^{-1}$, and grazing intensity (livestock unit days ha^{-1} $year^{-1}$) averaged over both years.

In May and June 2021, vegetation surveys were carried out on all the plots. To this end, in two 2 m × 2 m plots, 20 m apart from each other, all vascular plant species were recorded and their %-cover estimated. The cover mean values from the two plots were used for further analysis of similarities in community composition. For plant species richness, the cumulative number of species from both plots was used.

2.3. Data analysis

Prokaryotic and fungal data were analyzed separately. Iterative subsampling (100 iterations), performed with the *rrarefy* function from *vegan 2.6–2* (Oksanen et al., 2020), was used to normalize the number of reads across samples (Schloss, 2023). For every iteration, observed ASV richness, Shannon Diversity Index, and Bray-Curtis dissimilarities were computed, and the median was used for further analysis. Linear models were used to calculate the relationship between microbial ASV richness and land use intensity as well as plant species richness.

To assess the effects of the eight grassland management regimes (dummy coded) on fungal and prokaryotic alpha diversity and community structure, univariate and multivariate permutational analysis of variance capable of dealing with unbalanced designs (PERMANOVA, Anderson, 2001) was carried out with the *adonis2* function in *vegan 2.6–2*, using 999 permutations. Number of ASVs converted to Euclidean distances or the Bray-Curtis dissimilarity matrix were the response variables, and management intensity, harvest type (pasture or meadow) and production type (organic or non-organic) were explanatory

variables, including all interactions. PERMANOVA was also used to investigate the effect of topography and soil variables on fungal and prokaryotic alpha diversity and community structure. Again, number of ASVs converted to Euclidean distances or the Bray-Curtis dissimilarity matrix were the response variables, and elevation, northness, inclination, pH, clay content, C_{org}, C:N, Ca, K, Mg, and P content were explanatory variables. The marginal effects of the terms were calculated. For variation partitioning, the same models were used for distance-based redundancy analysis (dbRDA, Legendre and Anderson, 1999) using the function *capscale* in *vegan 2.6–2*. Models were subsequently reduced using a stepwise forward selection with the *ordistep* function in *vegan 2.6–2*, using 999 permutations. This model reduction for the environmental variables was necessary, as there were several variables explaining little variance, and too many variables can cause artefacts in variation partitioning. These models were then used within the function *varpart* to perform variation partitioning of fungal and prokaryotic ASV richness and community structure with two groups each. The differences in community structure between the grassland management regimes were assessed with constrained ordination via canonical analysis of principal coordinates (CAP) (Anderson and Willis, 2003), using the *CAPdiscrim* function in *BiodiversityR 2.14–2* (Kindt and Coe, 2005). Multivariate homogeneity of groups dispersion (Anderson, 2006) was evaluated for different grassland management regimes with the *betadisper* and *permutest* functions in *vegan 2.6–2*.

PERMANOVA (Anderson, 2001) was used to calculate the differences in topographical and soil variables between the different grassland management regimes. The functions *betadisper* and *permutest* in *vegan 2.6–2* were used to test whether any of the environmental variables differed in their variability between the grassland management regimes. *Pairwise.adonis2* (Marzinez Arbizu, 2017) was used to test for pairwise differences in community structure of the four grassland management regimes (extensive meadow, extensive pasture, intensive meadow, intensive pasture). Mantel tests using the *mantel* function in *vegan 2.6–6* were used to investigate the correlation between the microbial dissimilarity matrices and the plant dissimilarity matrices, using Bray-Curtis dissimilarities for plant- and microbial dissimilarity matrices and 9999 permutations.

We used the mean number of rRNA gene copies of detected prokaryotic taxa as an indicator for prokaryotic life history strategy, as copiotrophic, faster-growing taxa have been found to possess higher copy numbers as oligotrophic, slower-growing taxa (Klappenbach et al., 2000; Roller et al., 2016). We used the rrnDB database documenting variation in ribosomal RNA operons in Bacteria and Archaea (Stoddard et al., 2015) version 5.7 to obtain estimated rRNA gene copy numbers per taxon as described in Lori et al. (2023). If the mean rRNA copy number of a taxon was lower than 5, it was assumed to be oligotrophic, otherwise copiotrophic (Bledsoe et al., 2020). Effects of management on the ratio of abundance of copiotrophs vs. abundance of oligotrophs were tested for significance with *adonis2* using Euclidean distances. Linear models were used to test the influence of the management aspects grazing intensity and fertilization on the copiotroph:oligotroph ratio. To make inferences about the potential ecological roles of the taxa, Faprotax v.1.2.5 (Louca et al., 2016) and FUNGuild v.1.1 (Nguyen et al., 2016) were used for prokaryotes and fungi alongside a literature search.

For indicator species analysis, fungal and prokaryotic ASVs were aggregated at the genus level and then indicator analysis was carried out with *multipatt* from the *indicspecies 1.7.14* package (De Caceres and Legendre, 2009) using the group-equalized point-biserial correlation coefficient. This coefficient corrects for unequal group sizes, as was the case in this study (De Caceres and Legendre, 2009). Combinations of groups (management aspects) were also taken into account (De Cáceres et al., 2010). Benjamini-Hochberg correction was used to correct *p*-values for multiple testing using the *p.adjust* function. A tree matrix was generated from the taxonomy table of the statistically significant indicator species with *taxa2dist* from *vegan*, and clustered using the *as.phylo* function from the *ape 5.0* package (Paradis and Schliep, 2019). The resulting tree was visualized using iToL v.6 (Letunic and Bork, 2019).

3. Results

3.1. Environmental variables differed between grassland management regimes

Elevation and inclination differed between management regimes, with extensive pastures showing higher elevation than other management regimes. Grasslands used as pastures and all extensively managed grasslands showed higher inclination than meadows and all intensively managed grasslands (**Supplementary material, Tables S2.1 and S2.2**). All soil variables except Ca and Mg content were significantly influenced by grassland management regime (**Supplementary material, Tables S2.1 and S2.2).**

3.2. Microbial alpha diversity

Variation partitioning showed the eight grassland management regimes alone to only explain around 1 % of the variance in fungal richness, while management regimes and environment (topography and soil, northness, P content, and clay) jointly explained 7 %, and environment alone 23 % (**Supplementary material, Fig. S2.1**). Note that topography and soil factors can also be partly influenced by and related to current or former grassland management. Fungal richness was positively related to high clay content and decreased with increasing P and Ca content (Table 1). Grassland plots facing north had marginally higher fungal richness. For prokaryotic richness, grassland management regimes did not explain any variance alone. Jointly with environment (soil pH, Ca, C:N, and clay) grassland management regimes explained 11 %, while environment alone explained 24 % of the variance (**Supplementary material, Fig. S2.1**). Prokaryotic richness increased at higher levels of soil pH and decreased with increasing C:N ratios (Table 1).

The effect of management intensity on microbial alpha diversity differed between meadows and pastures. Fungal ASV richness was significantly higher in extensively managed pastures, however not in meadows ($F = 5.15$, $p = 0.027$, Fig. 2a, Table 1). Prokaryotic ASV richness was significantly reduced by extensive management ($F = 10.62$, $p = 0.003$, Fig. 2a, Table 1). There was also an interaction between management intensity and harvest type in the case of prokaryotes, however only marginally significant ($F = 3.08$, $p = 0.085$, Table 1), with prokaryotic richness being more strongly reduced by extensive management in meadows compared to pastures. Production type had a marginally significant positive trend on fungal ASV richness ($F = 3.28$, $p = 0.076$) but none on bacterial richness.

Like ASV richness, Shannon index decreased for prokaryotes under extensive management, while there was a marginally slight increase for fungi in extensive pastures in the form of a marginally significant interaction between harvest type and management intensity (**Fig. 2b**, $F = 14.92$, $p = 0.001$ for prokaryotes and $F = 4.15$, $p = 0.051$ for fungi). In line with the positive impact of extensive management on fungal and the negative on prokaryotic richness, the continuous compound index for land-use intensity, taking into account grazing, mowing, and fertilization, significantly increased prokaryotic and decreased fungal richness (Fig. 2c). Yet, the effect of management intensity on fungi is primarily found in pastures and that on prokaryotes in meadows. There was a positive relationship between fungal and plant species richness, whereas there was no significant relationship between prokaryotic and plant species richness (Fig. 2d).

3.3. Microbial community structure (beta diversity)

The eight grassland management regimes alone explained 4 % of the variance in fungal community structure, management regimes and environment (elevation, northness, soil pH, clay, C:N, Ca, C_{org}, K, P content) together explained also 4 %, and environment alone explained

Table 1
Permutational analyses of variance (PERMANOVA) on the effect of the three grassland management aspects and topography/soil on ASV richness (above) and community structure (below) of fungi (left) and prokaryotes (right). The direction of change of ASV richness is denoted with arrows. For the models explaining ASV richness, Euclidean distances and for community structure, Bray-Curtis dissimilarity matrices from the normalized ASV abundance data were used. The pseudo–F and R^2 values are provided for the respective variables. Factors with $p \leq 0.05$ in bold. The same models were used as the basis for variation partitioning following model reduction, see **Fig. S1 in** Supplementary material 2. Note that some soil variables might be changed by management such as fertilization intensity (i.e., indirect management effects).

			Fungi				Prokaryotes			
Response	Category	**Variables**	**Pseudo F**	**R^2**	***p***		**Pseudo F**	**R^2**	***p***	
ASV richness	Grassland management aspects	Production System (organic vs. non-organic)	3.28	0.035	▪	↑	0.55	0.006		
		Harvest Type (pasture vs. meadow)	1.66	0.018			2.35	0.025		
		Management Intensity (extensive vs. intensive)	3.42	0.037	▪	↑	**10.62**	**0.111**	**	↓
		Production System × Harvest Type	0.18	0.002			0.034	<0.001		
		Production System × Management Intensity	0.49	0.005			0.01	<0.001		
		Harvest Type × Management Intensity	**5.15**	**0.056**	*	↑	3.08	0.032	▪	↓
		Three-way interaction: P. S × H. T. × M. I.	0.73	0.008			0.96	0.010		
	Topography and soil	Elevation	0.25	0.002			0.05	<0.001		
		Northness	3.46	0.028	▪	↑	0.46	0.003		
		Inclination	0.38	0.003			1.67	0.010		
		pH	1.89	0.015			**47.76**	**0.028**	***	↑
		Clay	**8.81**	**0.071**	**	↑	0.39	0.002		
		C_{org}	1.38	0.011			0.31	0.002		
		C:N	0.83	0.007			**4.77**	**0.028**	*	↓
		Ca	**6.52**	**0.053**	*	↓	2.13	0.013		
		K	1.45	0.012			2.97	0.017	▪	↑
		Mg	0.09	0.001			1.48	0.009		
		P	**4.24**	**0.035**	*	↓	3.58	0.021	▪	↑
Community structure	Grassland management aspects	Production System (organic vs. non-organic)	1.18	0.013			0.69	0.008		
		Harvest Type (pasture vs. meadow)	**2.76**	**0.030**	***		1.65	0.019	▪	
		Management Intensity (extensive vs. intensive)	**6.12**	**0.066**	***		**3.95**	**0.045**	**	
		Production System × Harvest Type	0.85	0.009			0.58	0.007		
		Production System × Management Intensity	1.05	0.011			1.05	0.012		
		Harvest Type × Management Intensity	1.44	0.016	▪		1.37	0.015		
		P. S × H. T. × M. I.	0.99	0.011			1.32	0.015		
	Topography and soil	Elevation	**2.79**	**0.026**	***		**2.90**	**0.020**	**	
		Northness	**2.29**	**0.021**	***		1.86	0.013	▪	
		Inclination	1.35	0.012	▪		1.42	0.009		
		pH	**3.40**	**0.031**	***		**7.10**	**0.049**	***	
		Clay	**2.69**	**0.025**	**		**5.15**	**0.036**	***	
		Corg	**1.53**	**0.014**	*		2.17	0.015	▪	
		C:N	**1.88**	**0.017**	*		1.64	0.011		
		Ca	**1.74**	**0.016**	*		**4.34**	**0.030**	***	
		K	**1.56**	**0.014**	*		1.73	0.012	▪	
		Mg	1.39	0.013	▪		1.38	0.010		
		P	1.47	0.014	▪		1.44	0.010		

▪ Significant at the 0.1 probability level.
* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.

17 % of variance. For prokaryotes, grassland management regimes alone explained 3 %, management regimes and environment (elevation, northness, soil pH, clay, Ca, K, C_{org}, C:N) together 1.5 %, and environment alone 38 % of the variance (**Supplementary material, Fig. S2.1**). Fungal community structure was significantly influenced by elevation, northness, pH, clay content, C_{org}, C:N ratio, Ca, and P content. Prokaryotic community structure was influenced significantly by elevation, pH, clay, C:N, and Ca content (Table 1).

The fungal community structure was strongly affected by management intensity and harvest type ($F = 6.12$, $p < 0.001$ and $F = 2.76$, $p < 0.001$, Table 1). There was also a marginally significant interaction between these two management aspects. In the case of prokaryotes, there was a strong effect of management intensity ($F = 3.95$, $p = 0.003$) and a weak (marginal) effect of harvest type ($F = 1.65$, $p = 0.010$). As organic farming had no significant effect on microbial community structure, organic and non-organic grasslands were pooled for CAP, resulting in four combinations of the levels of management intensity (extensive vs. intensive) and harvest type (pasture vs. meadow). Here, fungi showed a slightly higher reclassification success rates than prokaryotes (76.7 % vs. 73.3 %) and were in general more clearly separated into the four remaining grassland management regimes than prokaryotes (Fig. 3). This visual assessment was confirmed by pairwise PERMANOVA, in which all four grassland management regimes differed from each other in their community structure in the case of fungi, while no significant difference was observed between extensive pastures and meadows for prokaryotes (**Supplementary material, Table S2.3**). There was also no significant difference between intensive meadows and pastures, in line with the only marginal influence of pasture in Table 1.

The fungal community of extensively managed grassland plots showed a higher variability in community structure than those of intensive grassland plots, as observed in the analysis of multivariate homogeneity of groups dispersion (**Supplementary material,**

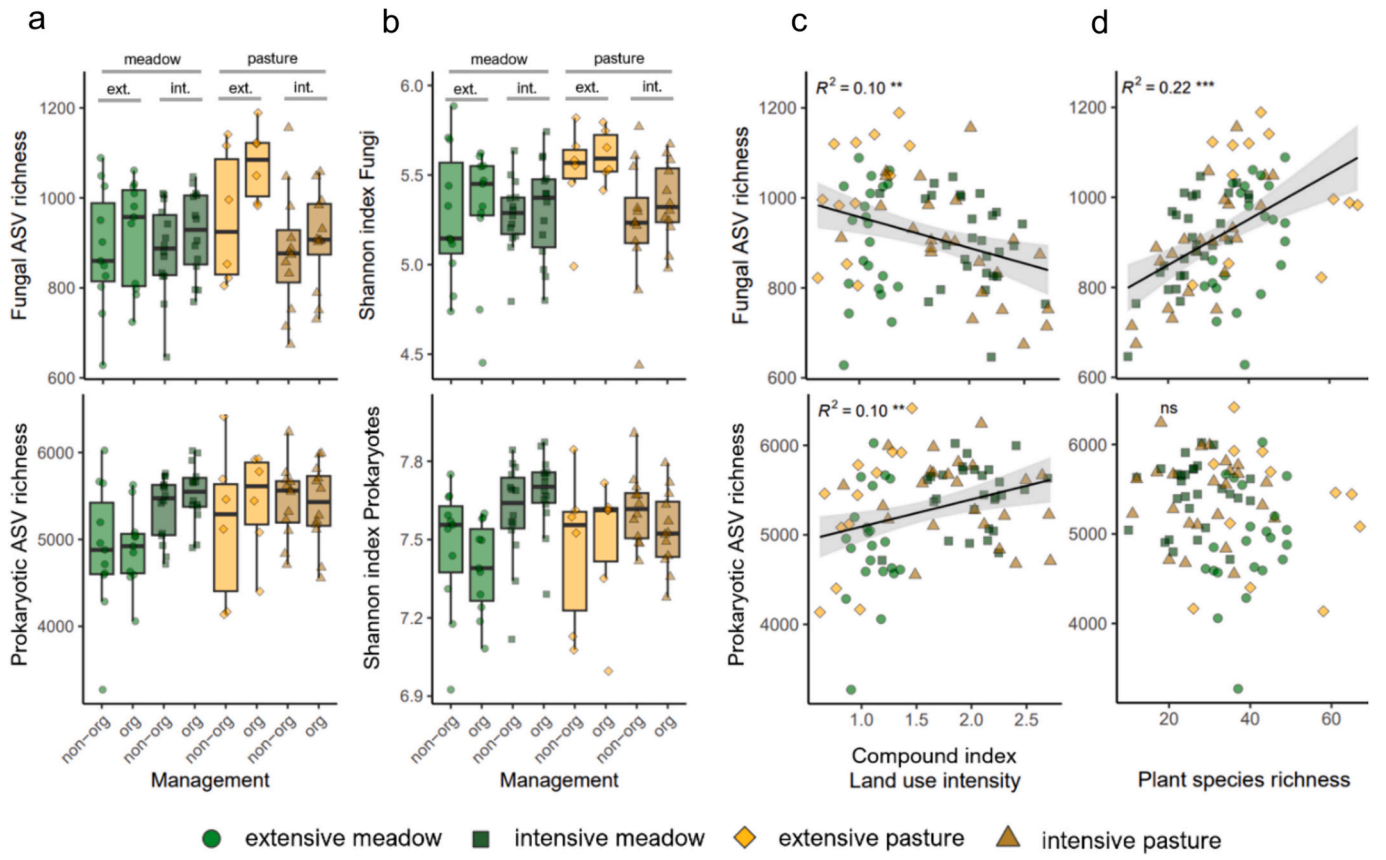

Fig. 2. Fungal (above) and prokaryotic (below) observed richness (a) and Shannon Diversity (b) across the eight different grassland management regimes (Fig. 1). Relationships between observed richness and the compound index for land use intensity taking grazing, mowing, and fertilization into account (Blüthgen et al., 2012) (c) as well as plant diversity (d) are shown including linear regression fits with the associated R^2 values. Significance levels of Regression: 0.1 ≥ "." > 0.05 ≥ "*" > 0.01 ≥ "**" > 0.001 ≥ "***".

Fig. S2.2a), in other words, the fungal communities of extensively managed grassland plot were more different from each other (more heterogenous) than the intensively managed grassland plots. Prokaryotic community structure differed most among extensive meadow plots, while intensive meadows, extensive and intensive pastures showed a similar homogeneity (**Supplementary material, Fig. S2.2b**).

A potential driver of community structure is the variability of environmental factors within grassland management regimes as expressed through inter-plot variability. Intensive grasslands had higher variability in the soil nutrient contents of K and P ($F = 8.02$, $p = 0.007$; $F = 9.71$, $p = 0.001$), respectively, whereas extensive grasslands had higher variability in soil pH than intensive grasslands ($F = 8.20$, $p = 0.008$) as revealed by analysis of multivariate homogeneity of groups dispersions. Extensive pastures had higher variability in soil C_{org} than intensive meadows ($F = 2.80$, $p = 0.044$), and extensive meadows showed higher variability in northness than extensive pastures, intensive meadows, and intensive pastures ($F = 3.19$, $p = 0.025$). Intra-plot variability is potentially also an important driver of community structure (Carini et al., 2020) but could not be assessed with the present sampling design. The plant community was more closely correlated with the fungal community (Mantel statistic $r = 0.492$, $p < 0.001$) than with the prokaryotic community (Mantel statistic $r = 0.283$, $p < 0.001$).

3.4. Indicator analysis

In total 39 fungal and 155 prokaryotic indicator genera were found to be indicative of one (or more) of the four grassland management regimes (organic and non-organic pooled). For both fungi and prokaryotes, indicator genera for the management regimes were broadly distributed across the phyla (Fig. 4). The strong influence of management intensity on indicator genera was reflected in the fact that both for fungi and prokaryotes, many indicator genera were indicators for both intensive meadows and intensive pastures (18 % and 38 % of indicator genera for fungi and prokaryotes, respectively). Comparatively less indicator genera were found for extensive grasslands, both extensive meadows and extensive pastures (8 % and 7 % of indicator genera, respectively). Harvest type also led to distinct indicator taxa, although less so than management intensity, with 5 % of the indicator genera being indicative for pastures (i.e., both extensive and intensive pastures). Interestingly, only one indicator genus was found indicating both intensive and extensive meadows, i.e., the fungal genus *Psychroglaciecola*. While many indicator genera were specific for one management regime, interactions between management intensity and harvest type were also relevant, as some indicator genera were indicative only for one out of the four management regimes. Intensive meadows had the highest proportion of indicator genera, both for fungi and prokaryotes (51 % and 72 %, respectively), while extensive meadows had the lowest proportion of indicator genera (15 % and 11 %, respectively).

For fungi, the most prevalent trophic mode among the indicator genera was saprophytic (Fig. 4a), and the most prevalent fungal guilds were plant pathogens, endophytes, and wood and dung saprotrophs. Fungal genera indicative of extensive meadows were *Claviceps* and *Pezicula*, whereas *Truncatella* and *Absidia* were indicative of extensive pastures. *Clavaria*, *Pyrenochaeta*, and *Ilyonectria* were enriched in both extensive meadows and pastures. All indicator genera from *Microascaceae (Acaulium, Kernia, Microascus, Scopulariopsis)* and *Sordariales (Ramophialophora, Remersonia, Cercophora)* were indicative of intensive meadows, along with, among others, the basidiomycetes *Ustilago* and

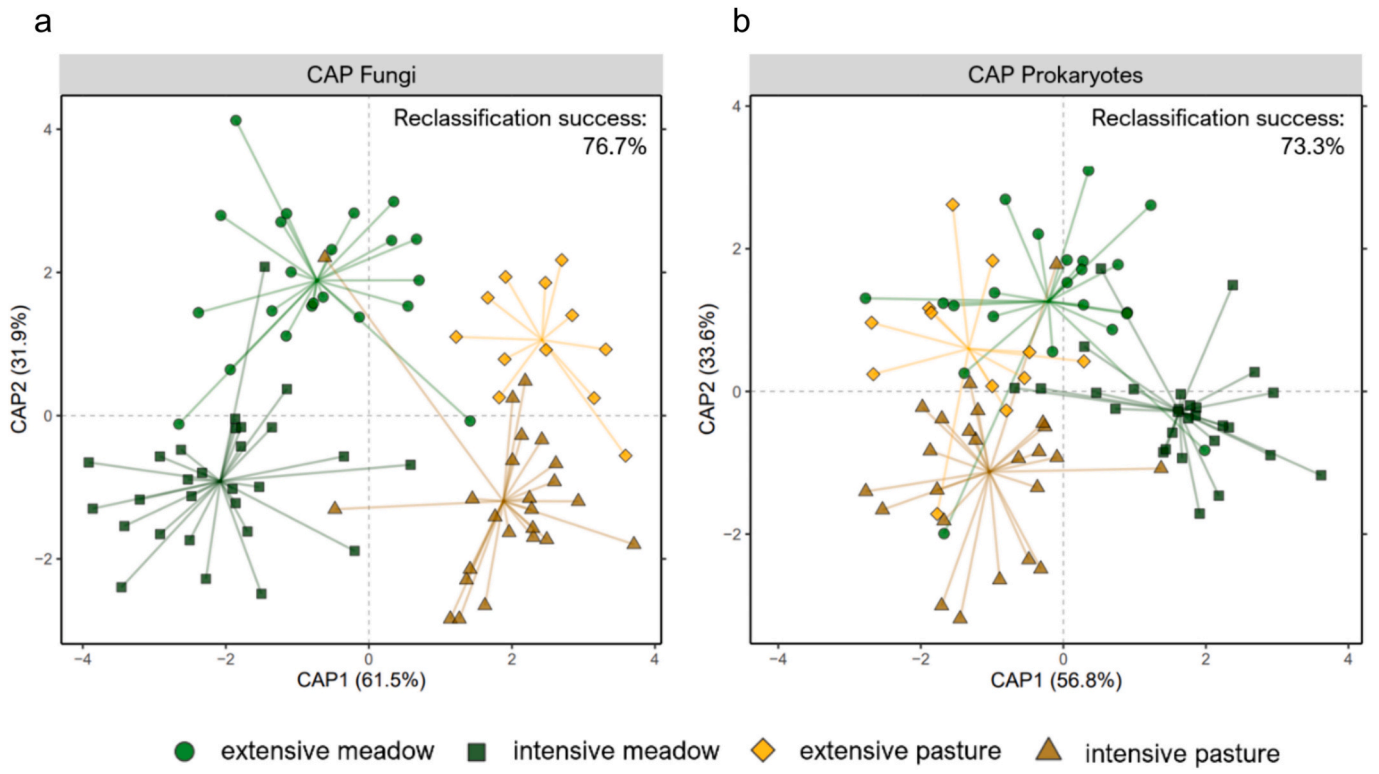

Fig. 3. Canonical analysis of principal coordinates (CAP) based on Bray-Curtis dissimilarities of normalized ASV counts, visualizing differences in fungal (a) and prokaryotic (b) community structure attributable to the four different grassland management regimes (i.e., extensive meadow, intensive meadow, extensive pasture, intensive pasture, with organic and non-organic plots being pooled). Symbols are connected to the overall group centroids, and reclassification success (as a degree of the overall discrimination of the groups) is indicated in the top-right corner of the graph. Percentages in axis titles refer to the percent between-group variation represented by each canonical axis.

Psathyrella, whereas *Pycenochaetopsis* and *Acremonium* were indicators for intensive pastures. *Plectosphaerella* and *Holtermaniella* were strong indicators for both intensive pastures and meadows. *Microdochium* and *Testudomyces* were jointly enriched in extensive and intensive pastures.

In the case of prokaryotes, a high percentage of the indicator genera identified for pastures (30 % for extensive and 32 % for intensive) had a putative copiotrophic lifestyle, with a similar proportion for intensive meadows (28 %), but a very low proportion in extensive meadows (6 %; Fig. 4b). The overall copiotroph:oligotroph ratio computed for the whole prokaryotic community was higher in pastures compared to meadows ($F = 31.5$, $p = 0.001$) and higher in intensively compared to extensively managed grasslands ($F = 4.9$, $p = 0.029$; Fig. 5a). Grazing intensity ($R^2 = 0.21$, $p < 0.001$) better explained the copiotroph:oligotroph ratio than fertilization ($R^2 = 0.04$, $p = 0.043$; Fig. 5b).

Examples of prokaryotic indicator genera for extensive meadows included *Rudaea* and *Jatrophihabitans*, for extensive pastures *Nostoc* and *Coxiella*. *Luedemaniella* and especially Frankia were strong indicators for both extensive pastures and meadows. *Methanosarcina* and *Cellvibrio* were strong indicators for intensive meadows, and all indicator genera belonging to the *Thermoactinomycetaceae* (*Laceyella*, *Novibacillus*, *Planiflum*, *Thermoactinomyces*, *Thermoflavimicrobium*) and *Oscillospiraceae* (*Hungateiclostridium*, *Pseudobacteroides*, *Acetivibrio*, *UCG 012*, *HNHF0106*) were indicative of intensive meadows. Intensive pastures were, for instance, enriched in *Mumia* and *Arthrobacter*. *Gaiella*, *Aeromicrobium*, *Turicibacter*, *Rhodococcus*, *Pedosphaera* and *Nitrospira* were some of the strongest indicators for intensive meadows and pastures. Extensive and intensive pastures were enriched in *Bacillus*, *Lysinibacter*, *Clostridium*, *Streptosporangium* and *Anaerolinea*.

4. Discussion

4.1. Environmental variables and management drive soil microbial diversity in grasslands

Soil microbial diversity in the studied grasslands was more strongly affected by environment than by management, corroborating our hypothesis. In general, the proportion of variance in microbial alpha and beta diversity that could be explained by all studied drivers of management and environment was between 25 % and 40 % (**Supplementary material, Fig. S2.1)**, which is comparable with other studies (Chen et al., 2017; Labouyrie et al., 2023). Prokaryotes showed a higher proportion of explained variance than fungi both for richness and community structure, as also observed by Labouyrie et al. (2023), mainly driven by the very strong influence of the measured soil variables on prokaryotic diversity, especially soil pH. The variance in microbial diversity shared by environment and management can be due to many reasons. Soil conditions, such as nutrients and pH, are partly influenced by management, but also by farmer's choices and preferences to manage naturally poorer or shallower soils extensively (Kampmann et al., 2008; Peter et al., 2008), and even soil microbial activities themselves, that can shape soil conditions such as soil carbon (Buckeridge et al., 2020; De Vries et al., 2015; Schimel and Schaeffer, 2012). In addition, plant species diversity played a major role in shaping soil microbial communities, especially for fungi, as fungal richness was positively influenced by plant species richness and the fungal community was correlated with the plant community more strongly than the bacterial community, as observed in other studies (Cassman et al., 2016; Wang et al., 2022). Thus, plant diversity emerges as a third crucial driver of fungal diversity besides environmental variables and grassland management, however being itself also influenced by soil conditions and management and

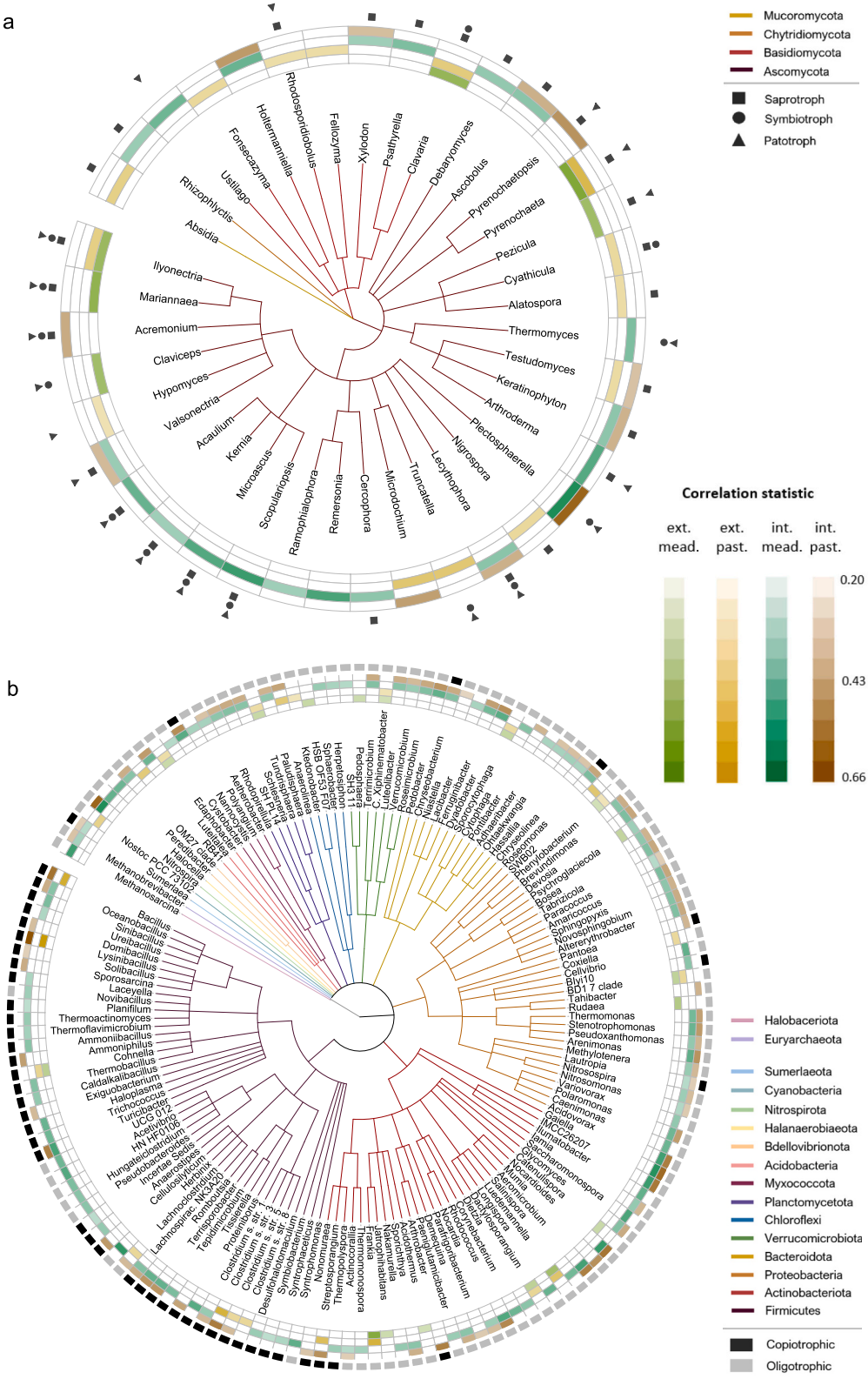

Fig. 4. Fungal (a) and prokaryotic (b) genera indicative for one or more of the four grassland management regimes (i.e., extensive meadow, extensive pasture, intensive meadow, and intensive pasture, with organic and non-organic plots being pooled). Only genera that responded significantly ($p < 0.05$) after Benjamini-Hochberg correction are displayed. Light green, yellow, dark green and brown fields denote indicator genera for extensive meadow, extensive pasture, intensive meadow, and intensive pasture, respectively, with the saturation of the field indicating the strength of the correlation. For fungi, symbols represent trophic modes as extracted from FUNGuild (lack of symbols denotes missing data); for prokaryotes, the outer ring denotes genera with putative oligotrophic (grey) or copiotrophic (black) lifestyle based on rRNA gene copy number estimation.

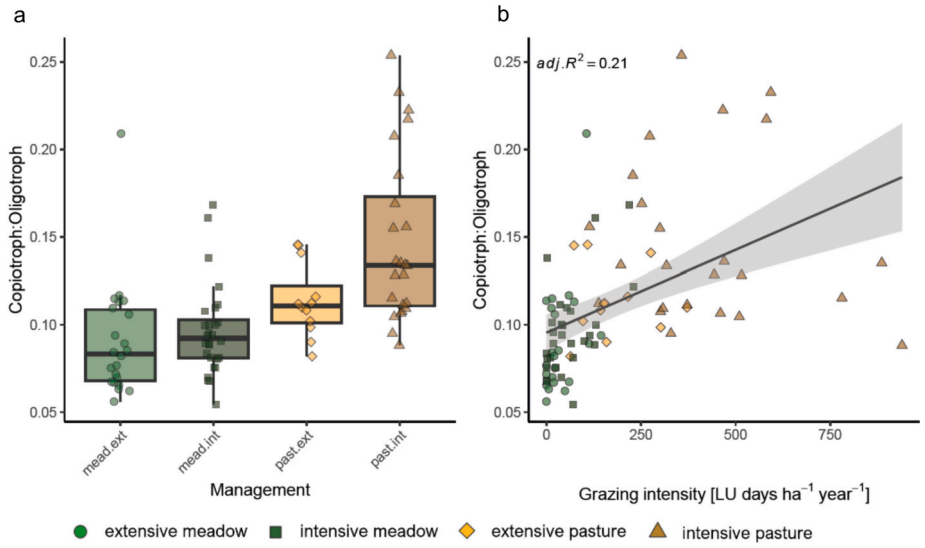

Fig. 5. Ratio of relative abundance of copiotrophic to oligotrophic bacterial taxa for the four different grassland management regimes, (a), and fit of a regression of the relationship between grazing intensity and the copiotroph:oligotroph ratio (b). Note that for this analysis organic and non-organic plots were pooled. Thus, the four management regimes are mead.ext. = extensive meadow, mead.int = intensive meadow, past.ext. = extensive pasture, and past.int = intensive pasture.

potentially also by soil microbial communities. In our experimental design conducted on managed farms in a real-world landscape setting, it was not possible to fully disentangle all these potential interactions of management and environment. Instead, we gained insights into conditions in a realistic agricultural landscape, in which grassland management regimes are not randomly placed but according to the local environmental settings (Klaus et al., 2023). Yet, we did find that management, especially management intensity, harvest type (pasture vs. meadow), and their combination had relevant effects on microbial diversity, which is discussed in the following.

4.2. Management intensity shapes fungal and prokaryotic alpha and beta diversity

Of the three grassland management aspects investigated here, management intensity had the greatest impact on soil microbial diversity, often in interaction with harvest type. Prokaryotic richness was higher in intensive grasslands, while intensive management decreased fungal richness in the case of pastures (Fig. 2, Table 1). This positive response for prokaryotes and negative response for fungi (though in this case only in the case of pastures), is in line with our expectations and other studies investigating grasslands (Labouyrie et al., 2023; Fox et al., 2021, 2022). Management intensity was also the management aspect that most strongly explained shifts in soil fungal and prokaryotic community structure, in agreement with previous studies (e.g., Leff et al., 2015; Fox et al., 2021). Additionally, the fungal and prokaryotic compositions of extensive plots showed higher heterogeneity than the microbial compositions of the intensive plots (**Supplementary material, Fig. S2.2).** This trend to higher heterogeneity in soil microbial community structure between extensively managed sites with nutrient-poor conditions is a phenomenon similar to the reduced stochasticity that has been observed to occur in long-term fertilized grassland soils, possibly due to a homogenization effect of fertilization on the nutrient conditions or decreasing cumulative deterministic linkages due to unidirectional selection (Liang et al., 2020). The authors of the latter study, too, found the dispersion to be larger in the unfertilized compared to the long-term fertilized grasslands. Similarly, Hartmann et al. (2015) observed a reduced dispersion in crops receiving manure compared to unfertilized systems. Another explanation could be that environmental conditions were more heterogeneous in the extensive grasslands. Testing for differences in inter-plot variances in the eleven environmental variables between the management regimes revealed that, while extensive grasslands did tend to have higher variability in soil pH and extensive pastures higher variability in organic carbon content, intensive grasslands had higher variability in K and P supply. As pH was found in this study to be the environmental variable most strongly explaining fungal and prokaryotic community structure, as well as having been shown to strongly influence soil microbial composition in numerous other studies (e.g., Zhalnina et al., 2015; Widdig et al., 2020), the higher variability in pH among extensive grasslands compared to intensive grasslands could also well be part of the explanation for higher heterogeneity of extensive grassland microbial communities. Future studies with a sampling design allowing for an assessment of intra-plot variability in addition to inter-plot variability could be helpful to better understand the influence of environmental variability across different scales on microbial diversity.

The strong influence of grassland management intensity on soil prokaryotic diversity compared to the harvest type and production system was also reflected in the indicator analysis. A great number of taxa identified as indicator genera either were indicators for both extensive meadows and extensive pastures or for both intensive meadows and intensive pastures. Microbial indicator genera for intensive grasslands were for a large part coprophilous taxa such as *Terrisporobacter, Rhodococcus, Paracoccus*, which were enriched in both intensive management regimes (Kelly et al., 2006; Mitchell et al., 2023; Rowbotham and Cross, 1977). In the case of fungi, there were relatively few taxa indicating either both extensive meadows and pastures or intensive meadows and pastures. However, those taxa that were enriched in both intensive meadows and pastures tended to be known coprophilic taxa as well, such as *Ascobolus, Kernia*, and *Microascus* (Kirk et al., 2001; Su et al., 2020). This could be explained by the higher availability of substrates in the form of dung, manure, and slurry under intensive management. Also likely related to these substrates, and their origins, many fungal and prokaryotic taxa indicating intensive grasslands were associated with animal digestion, such as the fungal genera *Acremonium* (for intensive pastures), *Valsonectria* (for both intensive pastures and meadows), and *Scopulariopsis* and *Microascus* (for intensive meadows), that have been found to play an important role in the gastrointestinal tract of sheep (Yin et al., 2022), or the prokaryotic taxa *Romboutsia,* which can be found in the hindgut of cattle (Zhong et al., 2020), and *Methanobrevibacter*, an important genus of methanogens in the rumen (Morgavi et al., 2010). High slurry application rates and nutrient availability in intensive grasslands likely promoted taxa with

the ability to degrade urease, such as *Roseomonas, Thermomonas, Verrucomicrobium* (enriched in intensive meadows and pastures) and *Ureibacillus* (enriched in intensive meadows) (Denner et al., 2015; Fortina et al., 2001; Hedlund, 2010; Rai et al., 2021). Quite a number of indicator genera for intensive grasslands were taxa involved in N cycling (other than N_2-fixation), which is not surprising due to the larger inputs of organic (and in some cases mineral) fertilizers containing N, and thus also higher availability of readily accessible N. Examples for these N cycling taxa typical for intensive management include members of *Stenotrophomonas* and *Rhodococcus*, that can reduce nitrate (Deng et al., 2022; Goodfellow, 2012; Heylen et al., 2007), *Nitrospira,* which is involved in nitrite oxidation, and some strains performing complete nitrification (Daims et al., 2015), *Nitrosospira* and *Nitrosomonas,* important genera of ammonium oxidizing bacteria (AOB) (Prosser et al., 2014), and *Paracoccus*, containing species capable of nitrate denitrification (Kelly et al., 2006).

Fungal indicators for extensive grasslands on the other hand included rare and in some cases endangered macrofungal species with conservation value related to nutrient poor grassland habitats, from the genus *Clavaria* and *Geoglossum* (Senn-Irlet et al., 2007; Griffith et al., 2013; Dämmrich et al., 2016, the latter was a marginally significant indicator after Benjaimi-Hochberg correction, $p = 0.06$). This highlights the value of extensive grasslands not only for animal and plant species conservation, but also for fungal taxa (Fox et al., 2022; Griffith et al., 2013). Recent studies in Switzerland and throughout Europe also found *Clavariaceae* to be a taxon indicative of extensive grasslands and more coprophilous taxa to be indicative of intensive grasslands (Fox et al., 2021, 2022). Prokaryotic indicators for extensive grasslands included potential N_2-fixing taxa such as *Frankia* and *Nostoc* (Mus and Wu, 2023; Tamagnini et al., 1997), along with a slightly higher abundance-weighted proportion of prokaryotic N_2-fixers as intensive grasslands as identified by FAPROTAX. On this topic, considerable discrepancy between different studies exists with respect to the response of N_2-fixing taxa to grassland management intensification or nutrient addition. In some cases, N_2-fixing taxa or genes are found to decrease under nutrient addition (Labouyrie et al., 2023; Liao et al., 2021), and in others, to increase (Chen et al., 2020; Meyer et al., 2013; C. Zhang et al., 2019). Some studies observe that N only additions decrease, while joint N and P additions increase N_2-fixing activity, as on the one hand an over-supply of N could reduce the advantage of N_2-fixation and on the other hand enough P could enable the ATP-intensive process of N_2-fixation (Schleuss et al., 2021; Zhang et al., 2013). Thus, in this study, P could perhaps have been a limiting factor in the intensive grasslands.

4.3. Harvest type shaped fungi stronger than prokaryotes

Management intensity played a crucial role in shaping soil microbial alpha and beta diversity, both for fungi and prokaryotes. In the case of fungi harvest type (meadow vs. pasture) was also an important factor: ASV richness (alpha diversity) was influenced by an interaction between harvest type and management intensity, and beta diversity was influenced by both factors as well, in this case however the interaction was not significant (Table 1). Specifically, fungal richness of extensive grasslands was increased by grazing compared to the other management regimes (Fig. 2 **a and b**), a finding that is in agreement with a recent global meta-analysis that observed an increase in soil microbial diversity at moderate levels of grazing (Wang and Tang, 2019). This could partially be attributed to a higher spatial heterogeneity in vegetation and nutrient contents due to urine and dung patches in grazed sites, which might create more niches for microbes (Millard and Singh, 2010), especially in nutrient-poor soils with low water holding capacity.

Grassland harvest type significantly influenced fungal community structure, as expected, but only marginally influenced prokaryotic community structure. We can only speculate on the reasons for this. Perhaps it is due to the fungal community potentially being more sensitive to differences in plant community between extensive meadows and pastures brought about by selective grazing of livestock, as soil fungal diversity has, in this study as well as in other studies, been shown to be more strongly correlated with plant diversity than prokaryotic diversity – either due to fungi being directly influenced by plants or vice versa, or due to similar reactions to environmental conditions (Cassman et al., 2016; Wang et al., 2022). Or, perhaps, fungi are more sensitive to the small differences in nutrient supply between extensive meadows and pastures than prokaryotes are. While both are unfertilized, extensive meadows are likely to deplete in soil nutrients on the long run due to the compete removal of the aboveground biomass, while in extensive pastures the majority of consumed plant biomass is returned via animal dung.

Pastures, and especially intensive pastures, had a higher ratio of copiotrophic to oligotrophic prokaryotes (Fig. 5). This result is interesting, as increases in the copitroph:oligotroph ratio in grasslands have mainly been observed with elevated nutrient supply, often with additions of synthetic fertilizer or grazing compared to no grazing in the absence of fertilization (Fierer et al., 2012; Leff et al., 2015; Xun et al., 2018). In our study, intensively managed meadows received as much N, applied via organic and mineral fertilizers plus minor inputs from grazing animals, as intensively managed pastures, and still pastures had a significantly higher copiotroph:oligotroph ratio. Especially striking in this sense is the fact that even extensively managed pastures, that did not receive fertilization except excrements from grazing animals, and in which supplementary feeding is prohibited, had a higher copiotroph: oligotroph ratio than intensive meadows. Additionally, the copiotroph: oligotroh ratio was better explained via grazing intensity than with fertilization (Fig. 5). These results suggest that grazing could favor copiotrophs mainly via fresh dung being distributed in a patchier way, which creates different conditions compared to slurry and manure, which are distributed in a more even way after storage in tanks, further exhibiting a lower C:N ratio than fresh dung.

The indicator analysis revealed a specific set of indicator taxa for pastures vs. meadows, but it was difficult to identify patterns as to the differing functions of these taxa. In the case of fungi, *Microdochium* and *Testudomyces* were enriched in both extensive and intensive pastures, the former presenting a widely feared plant pathogen in grasslands, and the latter a dung and plant saprotroph (Domsch et al., 2007). The prokaryotic genera enriched in both intensive and extensive pastures tended to be anaerobic or facultatively anaerobic taxa (such as *Anaerolinea*, *Bacillus*, *Clostridium*, *Lachnoclostridium*, *Lysinibacillus* (Kayath et al., 2018; Yamada and Sekiguchi, 2018; Yutin and Galperin, 2013). In the case of *Streptosporangium*, it is found in rumen (Song et al., 2023), which can perhaps be attributed to the frequent presence of animals on pastures and putative origins of these prokaryotes from their gastrointestinal tracts. Regarding indicator genera for intensive meadows specifically, many genera were able of performing xylanolysis and/or cellulolysis, such as *Halocella, Cytophaga, Thermobacillus* and *Saccharomonospora,* some of which are consequently often found in compost (Goodfellow, 2012; McBride et al., 2014; Oren, 2014; Touzel and Prensier, 2015).

4.4. No significant effects of organic management on plot-level grassland microbial diversity

Organic grassland management impacted plot-level soil microbial diversity only marginally, potentially also because soil and topographical factors were separately included in the models. Fungal and prokaryotic community structure as well as prokaryotic richness were not affected, only fungal richness was marginally increased by organic management. This weak effect on fungi contrasts many studies from croplands that found clear increases in richness and differences in microbial community structure (e.g., Hartmann et al., 2015; Degrune et al., 2019). However, in contrast to croplands, grasslands show usually less severe differences in management between organic and non-organic systems. Use of pesticides was low even in non-organic intensively

managed grasslands studied, with only about 30 % receiving pesticide applications, and, with only one exception, spraying was restricted to individual plants or small groups of plants instead of the whole area (**Supplementary material, Table S2.1**). This is in line with national average grassland management in Switzerland, where grasslands receive very low amounts of pesticides compared to croplands (Tamm et al., 2018). The other main aspect of organic farming, the absence of inorganic fertilizers, can also influence microbial communities and many studies have shown organic and inorganic fertilizers to differently affect microbial diversity, which is often linked to a beneficial effect of higher organic matter content under organic fertilization (Pan et al., 2020; X. Zhang et al., 2013). However, the non-organic intensive grasslands studied here received on average only about 20 kg mineral N per ha and year, on top of much higher inputs of organic fertilizers (**Table S2.1**). Apparently, this small amount of mineral fertilizer was not sufficient to measurably influence the soil microbial community, apart from a trend to lower fungal richness that is also related to slightly lower soil P content in organic versus non-organic intensive grasslands. Thus, since we separately assessed the effects of soil P as well as topography on soil microbial communities, in our study respective differences between organic and conventional grasslands, as observed by Klaus et al. (2024), do not appear as an effect of organic farming but are mainly classified as environment. However, in more intense grassland systems receiving higher amounts of mineral fertilizers, such as in the Netherlands or Belgium (Einarsson et al., 2021), the impact of organic farming on grassland soil microbial communities is likely larger.

5. Conclusions

Besides the strong effects of management intensity, harvest type and the interaction of both also affected the microbial diversity of grassland soils, especially fungal diversity. Organic management, on the other hand, had only a marginal effect on soil microbial diversity at the plot level in our study within the Swiss farming system, in which organic and non-organic management are not extremely different. The strong interacting effects of management intensity and harvest type indicate that it is crucial to maintain grasslands with different management intensities, in combination with a range of differently grazed and mowed sites throughout the landscape to conserve and promote soil microbial diversity. Future research should further assess the mechanisms that determine the interactions between environment, management beyond the aspects studied here, and the soil microbiome to enable informed management decisions. Such research should ideally investigate soil microbial diversity at different timepoints to include seasonality as a driver and separate it from the other drivers. Another important factor to consider is land-use history and respective changes or legacy effects on soil microbial diversity, which could not be investigated in this study design. More real-world landscape surveys such as ours are required to identify combinations of practices that optimally promote and conserve belowground biodiversity as a crucial resource for developing sustainable agricultural systems. As we have learned from this study, sustainable agricultural systems will have to include differently managed permanent grasslands that show a high level of complementarity in promoting and conserving both prokaryotic and fungal diversities.

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CRediT authorship contribution statement

Franziska J. Richter: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Rafaela Feola Conz:** Writing – review & editing, Methodology, Investigation. **Andreas Lüscher:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Nina Buchmann:** Writing – review & editing, Supervision. **Valentin H. Klaus:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Martin Hartmann:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Valentin H. Klaus reports financial support was provided by Mercator Foundation Switzerland. Valentin H. Klaus reports financial support was provided by Pancivis Foundation. Valentin H. Klaus reports financial support was provided by Fondation Sur-la-Croix. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Soil, environmental and management data is available in zenodo (https://doi.org/10.5281/zenodo.13831563). Raw sequences were deposited in the European Nucleotide Archive under the accession number PRJEB72428.

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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.2024.105650.

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