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Soil bacterial and fungal communities show within field heterogeneity that varies by land management and distance metric

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ABSTRACT

Increasing interest in the use of microbial metrics to evaluate soil health raises the issue of how fine-scale heterogeneity can affect microbial community measurements. Here we analyse bacterial and fungal communities of over 100 soil samples across 17 pasture farms and evaluate beta diversity at different scales. We find large variation in microbial communities between different points in the same field, and if Aitchison distance is used we find that within-field variation is as high as between-farm variation. However, if Bray-Curtis or Jaccard distance are used this variation is partially explained by differences in soil pH and vegetation and is higher under mob grazing for fungi. Hence, field scale variation in microbial communities can impact the evaluation of soil health.

There is increasing pressure to manage agriculture sustainably for both food production and environmental health (Tilman et al., 2011; Amundson et al., 2015). Microbial community structure and activity are often suggested to be key determinants of soil health (Stone et al., 2016; Bünemann et al., 2018), yet our understanding of how to use microbial data to guide farm management is still lacking (Fierer et al., 2021). A major issue in using microbial data within soil health metrics is the variability of soil microbial communities over space and time. It is known that soil properties such as soil pH, organic matter and nutrient content can all show fine scale spatial variation across agricultural landscapes (Ball and Williams, 1968; Lark et al., 2004; Kariuki et al., 2009). Therefore, it might be expected that microbial communities show similar levels of variation. Here we compare the levels of within-field variation in microbial communities to variation between fields and farms in order to evaluate the impacts of fine-scale variation upon microbial communities and to assess effects of land management, plant and soil properties.

In summer 2019, 17 pasture farms from across Great Britain within the Pasture Fed Livestock Association were surveyed for soil and vegetation properties. On each farm at least two fields undergoing differing land management practices were surveyed and within each field three sites were sampled for vegetation plus soil microbiological analysis and pH in water. In total, 110 samples of soil and vegetation were taken over 38 fields. Soil physicochemical properties were measured on bulked auger samples taken across each field in a W pattern. Land management within each field was categorised into ley, mob grazing, rotational grazing and set stocking based on farmer interviews. Bacterial and fungal communities were analysed through DNA sequencing of the 16S and ITS2 regions respectively. For a full description of the methods see Seaton et al. (2022). DNA sequences are publicly available in the European Nucleotide Archive under primary accession code PRJEB46195, sample accession codes ERS7103117 to ERS7103228. All statistical analysis was performed in R using the vegan and nlme packages (Oksanen et al., 2020; R Core Team, 2020; Pinheiro et al., 2021).

Comparison of the differences between microbial communities within fields indicated that while on average there was a gradient of increasing dissimilarity from within-field to within-farm to between-farm comparisons, within many fields the bacterial and fungal communities at different locations were as different to each other as they were to communities from different farms (Fig. 1). Across both bacteria and fungi at least 80% of comparisons within field communities were within the 5–95% range of between field/within farm distances, and at least 40% of those within field comparisons were within the 5–95% range of between farm comparisons. Using a community dissimilarity metric that is suggested to be particularly effective at finding biological differences, i.e. Aitchison distance (Martino et al., 2019), microbial

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communities within the same field were on average as dissimilar as communities from different farms (Fig. 1, bottom). In contrast, use of the Bray-Curtis or Jaccard metrics indicated that communities were more dissimilar between farms and fields than within fields. Overall, Bray-Curtis and Jaccard distances were significantly similar to each other (Mantel $r = 0.96$ (bacteria) and 0.71 (fungi), $p < 0.001$), while Bray-Curtis distance showed no relationship with Aitchison distance (Mantel $r = 0.07$ (bacteria) and 0.04 (fungi), $p > 0.1$). Jaccard distance was significantly associated with Aitchison distance for fungi ($r = 0.36$, $p < 0.001$) but not bacteria ($r = -0.08$, $p > 0.1$). It is worth noting that the Aitchison distance involves weighting change in low abundance species equally to change in high abundance taxa while Bray-Curtis distance more strongly weights change in high abundance taxa and Jaccard distance ignores abundance. In this context abundance is based upon standardised read count, which is not necessarily related to biomass (Knight et al., 2018). The importance of rare taxa in determining ecosystem function is a much debated topic (Jousset et al., 2017). Our results show how conclusions can vary drastically depending

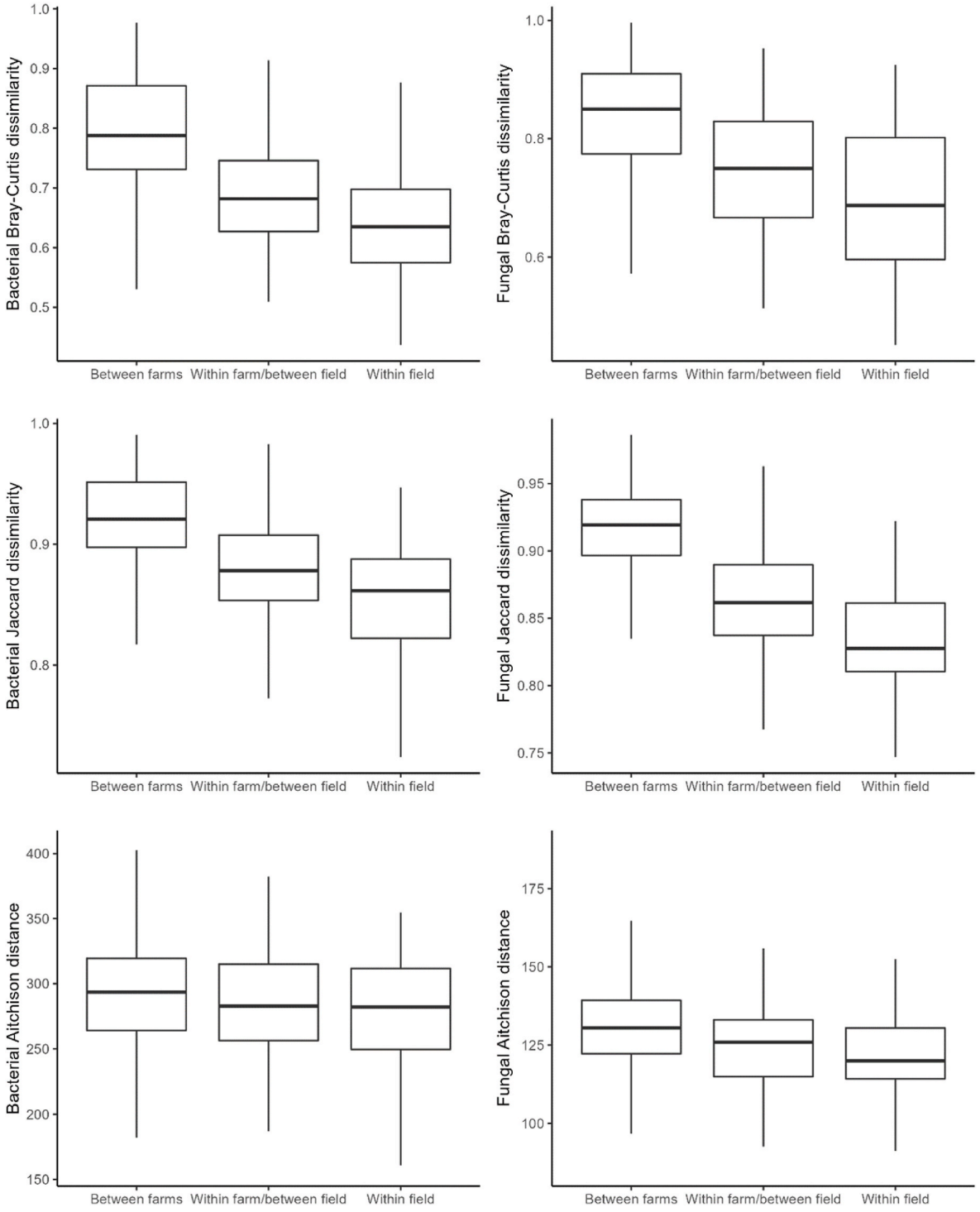

Fig. 1. The community dissimilarity between farms, between different fields of the same farm, and between different points in the same field for bacteria (left) and fungi (right) as measured by Bray-Curtis distance (top), Jaccard distance (centre) and Aitchison distance (bottom).

on how strongly the rarer members of the community are weighted in the analysis.

Land management and plant community structure explained some of the differences between fungal communities at sampling locations on the same field and farm, but less so for bacterial communities. Mob and rotational grazing, which result in variable stocking levels across a field over time, resulted in somewhat higher variation in fungi than either set stocking or leys, but not in bacteria (Fig. 2). Both the bacterial and fungal communities were strongly affected by the physicochemical soil variables, with soil pH and calcite explaining the first axis of variation and aggregate stability being roughly orthogonal (Table 1, Figs. S1–2). The pH of the microbial sample showed a stronger relationship with community composition than the field average pH, showing the importance of including fine-scale edaphic information when evaluating responses of soil microbial communities to larger-scale drivers. Fungal communities showed greater associations with the plant community composition at each site, with a clear relationship with grass species richness (Table 1). The greater impacts of farm management and plant community composition upon fungi relative to bacteria is in agreement with previous studies of the soil microbial communities in British pasture (Seaton et al., 2022) and the known greater sensitivity of fungi to farm management techniques (Maharning et al., 2009).

Our results show that field-scale variability in soil microbial communities is widespread even in relatively homogenous land uses. We found higher levels of microbial heterogeneity at fine spatial scales than that found by previous studies (De Gruyter et al., 2019), although previous studies have shown that soil microbial heterogeneity is scale-specific, with the greatest heterogeneity and negative spatial autocorrelation at the 10s–100 s m scale (Meyer et al., 2018; Zinger et al., 2019). The standard approach to deal with high levels of within field variability when evaluating soil condition is to take several samples and then bulk them together (Kariuki et al., 2009). However, not only does the very small amount of soil used within standard DNA metabarcoding methods mean that a bulking approach will be unlikely to yield a true average of the field microbial community but also the compositional nature of DNA analyses means that the microbial community will not be exhaustively surveyed (Gloor et al., 2017). Therefore, the microbial community obtained within any one analysis is more likely to be either from an extreme environment relative to averaged soil properties and/or composed of multiple sections of communities that are in fact not co-located in reality. Our results also demonstrate that the patterns of variation are dependent on current land management and how we choose to evaluate them, i.e. which taxa are of interest, with mob grazing and rarer taxa showing greater variation at finer spatial scales. In summary, our results illustrate important considerations in the development and use of soil microbiome based characterisations of soil condition and show the importance of accounting for fine-scale variation within farm-level soil health assessment through survey design and inclusion of fine-scale soils information.

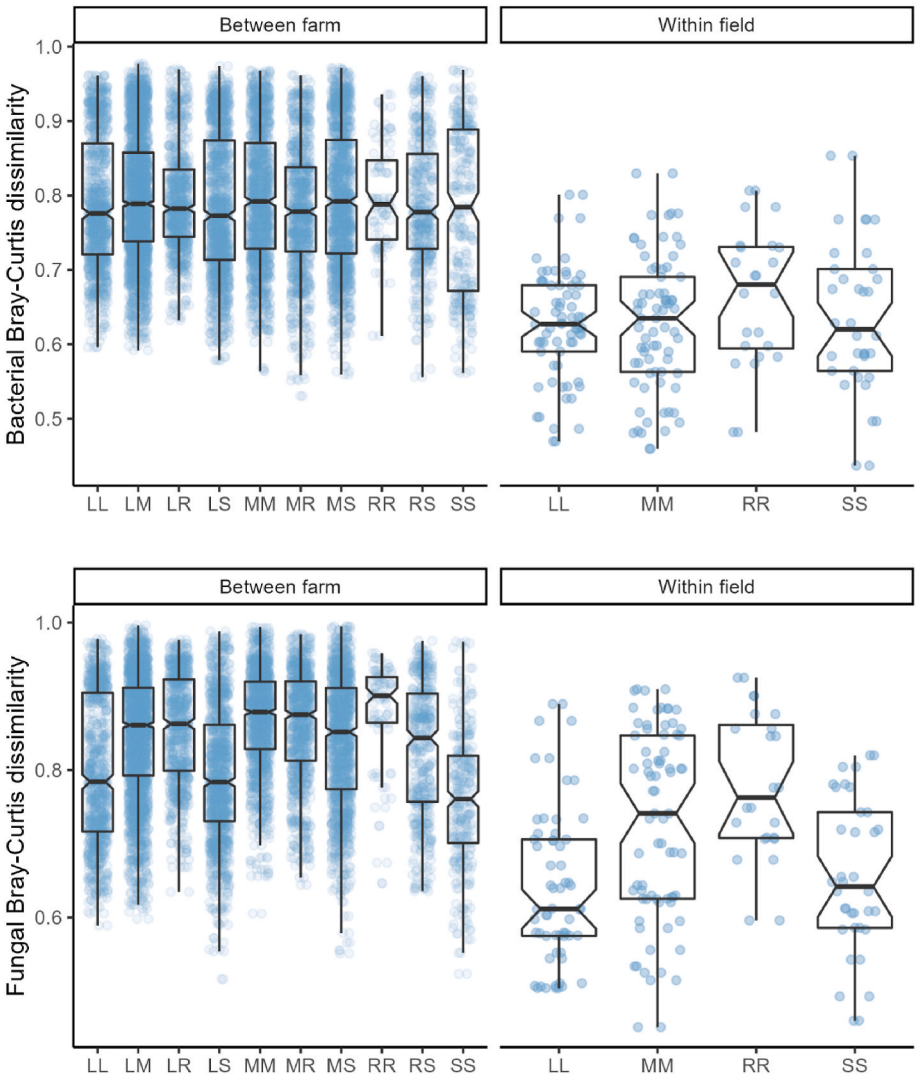

Fig. 2. The Bray Curtis dissimilarity between farms and between different points in the same field, by land management technique for bacteria (top) and fungi (bottom). L indicates ley, M indicates mob grazing, R indicates rotational grazing and S indicates set stocking. Two of the same letter indicate a comparison between areas of the same land management, and two different letters indicate a comparison between the two land management types, e.g. LM indicates a comparison between ley and mob grazing.

Table 1
The variation in bacterial and fungal communities explained by the different plant and soil properties. Values are from fitting environmental data to NMDS ordinations of bacterial and fungal communities based on Bray-Curtis, binary Jaccard or Aitchison distance, information on the ordinations given in Figs. S1–2. Soil pH is given for both the bulked samples across the field which were measured in $CaCl_2$ and the pH in water for the microbial sample after freezing. Note that once the farm and field structure was accounted for there were no significant differences between the physicochemical or plant variables between land use types (all FDR-corrected p-values >0.1). P values are not included as the soil variables are represented by one bulked sample measurement per field leading to inflated type I error (i.e. increased false significant effects). The plant ordination (PCoA) results are shown in Fig. S3.

Variable	Depth (cm)	Bacteria R^2			Fungi R^2		
		Bray-Curtis	Jaccard	Aitch.	Bray-Curtis	Jaccard	Aitch.
pH (micr. sample)	–	0.856	0.861	0.443	0.728	0.721	0.545
pH (CaCl2)	0–5	0.602	0.672	0.498	0.508	0.526	0.335
	5–15	0.716	0.764	0.548	0.571	0.582	0.424
Electrical conductivity	0–5	0.299	0.515	0.453	0.293	0.301	0.248
	5–15	0.572	0.688	0.527	0.500	0.525	0.456
Loss On Ignition (%)	0–5	0.181	0.312	0.201	0.263	0.309	0.298
	5–15	0.272	0.336	0.248	0.252	0.301	0.262
Calcite	0–5	0.323	0.370	0.375	0.248	0.275	0.438
	5–15	0.310	0.365	0.344	0.248	0.278	0.439
Clay	0–5	0.278	0.305	0.143	0.102	0.143	0.130
	5–15	0.365	0.396	0.200	0.181	0.233	0.176
Silt	0–5	0.057	0.097	0.068	0.110	0.115	0.066
	5–15	0.031	0.061	0.055	0.057	0.064	0.063
Sand	0–5	0.067	0.080	0.040	0.061	0.060	0.056
	5–15	0.070	0.086	0.055	0.185	0.041	0.077
Aggregate stability	0–5	0.140	0.175	0.286	0.132	0.135	0.086
	5–15	0.189	0.215	0.088	0.173	0.199	0.131
Forb richness	–	0.104	0.158	0.100	0.034	0.020	0.239
Grass richness	–	0.101	0.147	0.137	0.403	0.370	0.250
Plant PCoA 1	–	0.037	0.064	0.103	0.180	0.160	0.184
Plant PCoA 2	–	0.172	0.182	0.213	0.098	0.101	0.094
Plant PCoA 3	–	0.067	0.064	0.029	0.195	0.194	0.092
Plant PCoA 4	–	0.128	0.141	0.043	0.135	0.146	0.257

Declaration of competing interest

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

Data availability

DNA sequences have been made available on the European Nucleotide Archive under primary accession code PRJEB46195, sample accession codes ERS7103117 to ERS7103228.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108920.

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