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Comparison of metrics to reveal the role of soil fauna in soil health assessment in peat meadow restoration

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Abstract

Understanding the nuances of soil health is more important than ever to improve the quality and sustainability of agroecosystems. However, it is poorly understood how the variety of metrics currently in use to evaluate soil health relate to each other, and in what situations their use is not sensitive enough to indicate environmental changes. The use of faunal co-occurrence networks is a novel, potentially valuable tool that has hitherto received little attention in the context of soil health. Here, we used a meadow land-use intensity gradient to compare the response of a number of soil community metrics, including chemical and ecological indicators as well as faunal co-occurrence network parameters. Our findings indicate that the examined metrics displayed distinct, often contrasting patterns to one another, and that network analysis detected patterns that strongly aligned with the land-use effects. This pattern was qualitatively different from patterns arising from traditionally used metrics. The soils with conventional farming, that is, the least regenerative land-use, generally scored well in traditionally used metrics, including C:N ratio, faunal abundance and the ratio of Acari to Collembola. Regenerative farming was comparable with conventional farming in all conventional metrics—however, network analysis revealed that the soil faunal communities under regenerative farming had the highest species connectivity out of all research areas potentially due to grazing increasing the connectivity of faunal networks. Overall, these results suggest that network analyses are best suited to capture subtle land-use intensity differences while traditional metrics performed well in big changes. While more research is needed to better interpret soil faunal co-occurrence networks, our findings imply that it could be a useful method to provide further insight in aspects of soil health.

KEYWORDS

agroecosystems, land-use intensity, networks, peat meadow, soil health, soil invertebrates

1 | INTRODUCTION

There is an urgent need to move towards greater agricultural soil quality and sustainability via a change from conventional to regenerative land-use practices (Foley et al., 2005; Rockström et al., 2009). To aid a transition from conventional to regenerative farming, appropriate soil health assessment methods are needed. Soil health encompasses three interlinked parts: physical, chemical and biotic components (Lehmann et al., 2020). Traditionally, soil health has mostly been evaluated based on physical properties and chemical composition, with a strong focus on soil organic matter (SOM) content (Moebius-Clune et al., 2016) and various stoichiometric measures. SOM is generally considered one of the key abiotic indicators of soil health as it is tightly linked to a number of biotic and abiotic soil processes: it serves as an important food source for soil biota, and it enhances aggregate stability and porosity, creating a favourable environment for soil organisms (Cotrufo & Lavallee, 2022). Another chemical indicator, the ratio of carbon to nitrogen (C:N ratio) is often used as an important parameter indicative of SOM quality and the rate of nutrient cycling within the soil food web (Berg & Bengtsson, 2007; De Vries et al., 2006). Soil ecosystems with bacterially dominated food webs are generally associated with a low C:N ratio, and high C, N and P losses as run-off. Fungal-based food webs, on the contrary, are associated with a high C:N ratio and high levels of nutrient immobilization (De Vries et al., 2006; Morriën et al., 2017; Rousk & Frey, 2015). A C:N ratio between 20:1 and 30:1 is typically deemed the most conducive for a healthy soil (Biswas & Micallef, 2019).

While the abovementioned abiotic metrics can serve as indicators of overall soil health and are critical in shaping an environment that is conducive to soil organisms (Cotrufo & Lavallee, 2022), direct measurements on soil faunal communities likely provide more straightforward insights into the state of soil ecosystems and their functioning. In general, biotic measurements (e.g. abundance, biomass, richness and species composition of soil communities) respond faster to land-use change compared with relatively slowly changing parameters such as SOM content and have therefore been proposed as a more sensitive method of assessment of short-term changes in soil management (Yan et al., 2011). To evaluate how soil communities react to change, the focus has been on these classical indices, but the ecological significance and comparability of these metrics between studies have repeatedly been called into question (Hurlbert, 1971; Jost, 2009; Kirkpatrick et al., 2018; van Horne, 1983). In addition, abundance of specific bioindicator taxa have been used as metrics with a more easily discernible ecological meaning. A notable example is the

> **Highlights**
> - Soil health evaluation is crucial when restoring degraded agricultural land.
> - We evaluated soil chemical and biological metrics in their ability to differentiate between land-use intensities.
> - Traditional metrics separated more extreme land-use types well but failed to differentiate between agricultural practices.
> - Network analyses performed well separating between agricultural practices making them good indicator for recovery.

ratio of Acari to Collembola, used as a gauge for the level of agricultural pressure on soils due to the disparaging levels of tolerance to this type of disturbance in both groups (Menta & Remelli, 2020). However, these taxonomic groups are also equally sensitive to other forms of disturbance (Santamaria et al., 2012), making the merit of such indices limited.

Recently, co-occurrence networks have been proposed as a tool to map species interactions (Freilich et al., 2018; Ochoa-Hueso et al., 2021) and can serve as a proxy for ecosystem functioning. Changes in network structure have been suggested to function as early warning signal for species and functional loss (Valiente-Banuet et al., 2014). As it explicitly includes the spatial arrangement of species assemblages, it has been hypothesized to be a powerful method to evaluate impacts of land-use change and has been used for such purposes in recent years (Creamer et al., 2016). As such, it might prove a promising candidate to evaluate soil health based on soil fauna, a key group in many soil processes. Yet, research comparing network analytics with more traditional indicators is currently lacking. Over the last decade, the overwhelming majority of studies utilizing a network approach have focused on the soil microbiome due to the increasing availability of high-throughput sequencing (see review by Goberna & Verdú, 2021). Higher trophic levels consisting of meso- and macrofauna are comparatively understudied, though they are crucial to many soil ecosystem functions (Briones, 2018), and are highly sensitive to changes from bacterial- to fungal-based food webs (Bardgett & Wardle, 2010). While network analysis holds great potential in capturing intricate developments in simple network level metrics, it is not yet understood how network-based measures compare with other soil indicators. Moreover, it is also not well understood how they relate to internal ecosystem dynamics. This study therefore aims to examine how multiple

different metrics (chemical, biological, network analysis) perform in assessing the effects of land-use practices on soil communities. To this end, we sampled a meadow land-use gradient, from conventional farming with high inputs and high mowing frequency to regenerative farming with almost no current human-disturbance, across three closely situated polders and compared the performance of each of the metrics to better understand how they relate to each other, and how they inform on the relation between soil quality and land-use intensity.

2 | METHODS

This study focused on a gradient of agricultural practices on three closely located meadows in the peatland district in the western part of the Netherlands (Figure 1). These were the Noord Vrouwe Vennepolder (NVV; 52°11′29.1″ N 4°33′11.4″ E), Boterhuispolder (BHP;52°11′20.2″ N 4°32′11.2″ E) and the Lakerpolder (LP; 52°12′10.6″ N 4°32′10.5″ E), all located in the province of South Holland, The Netherlands. The soil in the top layer from which the samples were taken (0–15 cm) in all meadows consists of approximately 11% SOM (SD 1.23; see Figure 1a), 11% clay (SD 2.5), 19% silt (SD 3.9) and 59% sand (SD 4.2) and thus classifies as a loamy sand soil with high SOM content (USDA soil classification; Rhei-Sapric Histosol). All three peat meadows have a history as high-productive agricultural grasslands, but at the time of this study, only one meadow (NVV) was used as a high-productive grassland with 5–6 cuts of grass per year. None of the meadows had experienced tilling, other cultivations or use of pesticides, at least not in the past 50 years. Meadow BHP switched to organic farming around 2010, with extensive levels of grazing by cows (1.5 LSU ha-1) instead of mowing. Meadow LP was the most regenerative: it was managed similarly to BHP and NVV up until 1990, after which no more manure or artificial fertilizer was applied and mowing frequency was strongly reduced to once per year (1–2 cuts of grass per year). Consequently, it was also the most diverse meadow in terms of vegetation composition and aboveground fauna (i.e. birds and insects) composition (Marselis et al., 2024).

Soil mesofauna was sampled in the three meadows on five evenly spread sampling points across 100-m-long transects running from ditch to ditch, on 20 and 21 September 2021. Prior to sampling, the weather conditions were optimal to sample small soil fauna and all fields were sampled within 2 days. The first and last sample of each transect were taken from ditch banks <1 m distance from the ditch. In total, 14 transects were sampled in NVV, along with eight transects in BHP and LP

each. Soil samples with a diameter of 10 cm and a depth of 5 cm were manually collected using a soil corer from which soil biota was extracted using a Tullgren funnel (Macfadyen, 1961; van Straalen & Rijninks, 1982). All specimens were identified to order level and counted using a microscope. Coleoptera were determined further to family level, due to their high anticipated abundance and wide variety of functions within ecosystems. The samples for soil parameters were collected from the top 10 cm and were only available for the field plots, not for the plots on the ditch banks. Soil SOM content and C:N ratio were measured using NIR in a commercial lab (Eurofins).

Abundance of soil organisms was adjusted according to the dry weight of each sample as there was large variability in the amount of soil collected and its dry weight (ranging from 91 to 541 g with median at 268 g). Shannon diversity index was calculated and used to evaluate the diversity of soil fauna. Acari-Collembola ratio was calculated using the abundances of the organism groups. The effect of meadows (with different management intensities) on SOM content, C:N ratio, abundance per kg of soil, diversity and Acari-Collembola ratio were evaluated using linear mixed-effect models (package 'nlme' in R v. 4.3.3), and Tukey test was used (using 'emmeans') to test post hoc differences between individual meadows. The data on Acari-Collembola ratio were log transformed to fulfil requirements of the model. To create co-occurrence networks, correlation matrices were constructed in R, with the resulting p-values corrected according to the Benjamini-Hochberg procedure. Correlations with a p-value lower than 0.05 were selected, conform to scientific standard and processed in Cytoscape (v.3.10.2; Shannon et al., 2003) to form co-occurrence networks. The network metrics of average number of neighbours of each node and network density were calculated in Cytoscape.

3 | RESULTS AND DISCUSSION

Most of the metrics evaluated showed differences between areas with different land use. Yet, all metrics analysed indicated different meadows to be the best performing ones (Figure 1). SOM content was affected by meadow ($F = 15.54$, $p < 0.001$) and significantly lower in BHP than both other meadows (Figure 1a), while the C:N ratio was significantly higher in LP, the most regenerative meadow ($F = 8.91$, $p < 0.005$, Figure 1b). Regarding the biotic factors, soil faunal abundance (as measured per kg of soil; $F = 3.88$, $p < 0.05$) differed significantly between meadows and adhered to the same ranking as both chemical metrics, with LP showing the highest abundance, followed by NVV (conventional) and BHP, respectively (Figure 1c). Diversity of organisms measured
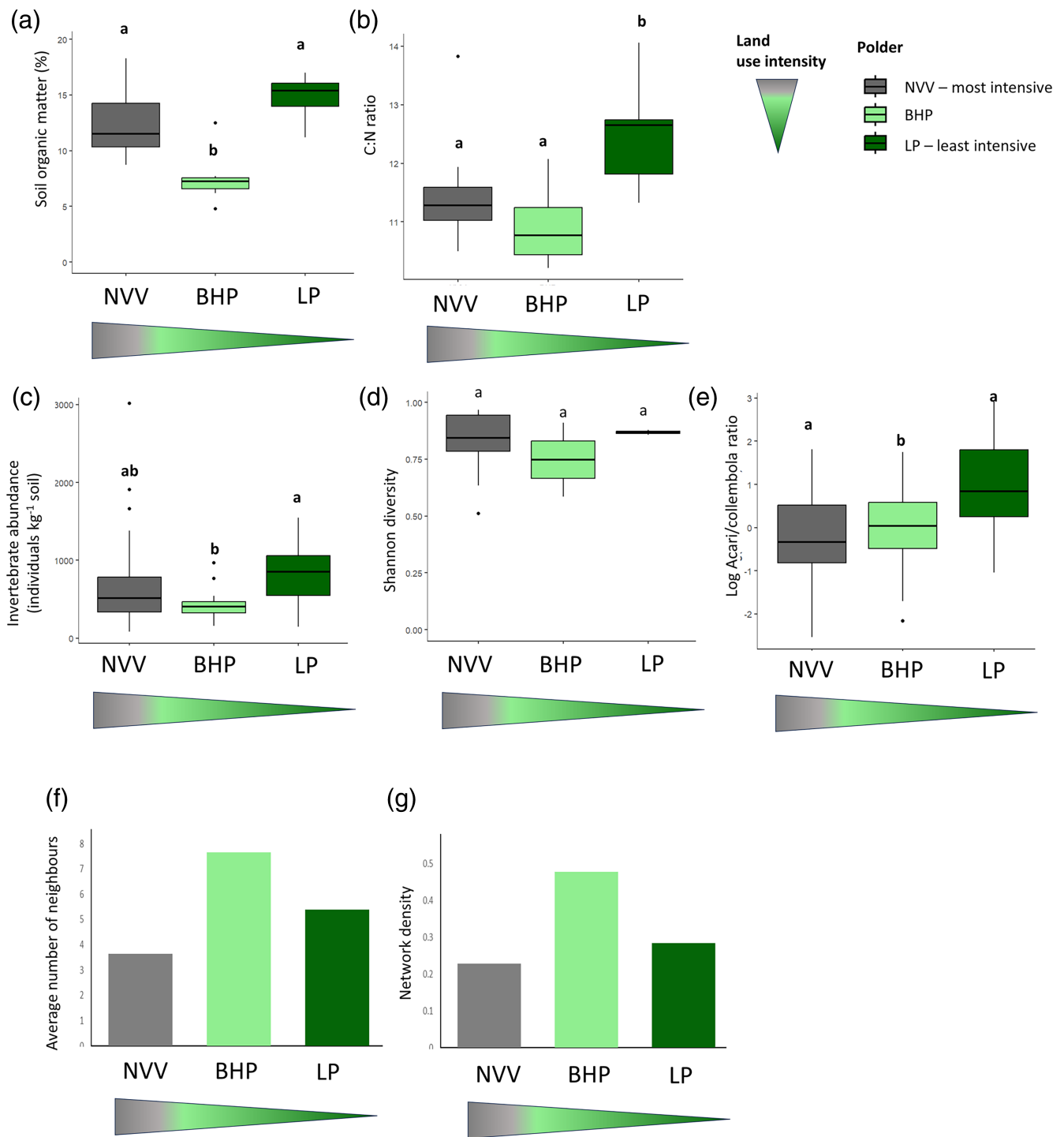
FIGURE 1 The examined metrics (y-axis) for each of the three meadows NVV, BHP and LP, respectively along the land-use intensity gradient. NVV has the highest land-use intensity (grey), BHP intermediate (light green) and LP the lowest (dark green). Each boxplot denotes the mean and variation, except for the network metrics which lack within-meadow variation. (a) Soil organic matter content as a percentage of the total soil weight. (b) The ratio of carbon to nitrogen in the top 5 cm of the soil. (c) Total soil faunal abundance per kilogram of dry soil. (d) Shannon's Diversity Index. (e). The logarithm of ratio of Acari to Collembola abundance. (f) The average number of neighbours per node in the network analysis. (g) Network density, the realized proportion of potential connections between nodes. The statistical significance based post-hoc test Tukey HSD is marked in the figure with letters and with confidence of $p < 0.05$.

by Shannon's diversity index, on the contrary, was not responding to land-use gradient ($F = 1.51$, $p = 0.23$) and showed no significant differences between any of the meadows (Figure 1d). The Acari-Collembola ratio was also significantly affected by the land-use intensity of meadows (log transformed; $F = 8.60$, $p < 0.001$) and was

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higher in meadow LP than in the other meadows (Figure 1e). Lastly, network metrics showed that BHP, the meadow with extensive grazing, had the highest network density and average number of neighbours, followed by LP and then NVV (Figures 1f,g and 2).

To a certain extent, the different measured parameters showed similar pattern and were equally good in differentiating meadows of different land uses. SOM content and faunal abundance both showed highest values under regenerative management (Figure 1a,c), which was also observed in previous studies (Potapov et al., 2017). This is perhaps unsurprising, as an increase in SOM content results in an increase in microbes, which constitute the basis of the soil food web. The C:N ratio followed a similar pattern, and meadow LP had significantly higher C:N values indicating potentially of more fungal dominated food web and slower nutrient cycling (Figure 1b). However, in all meadows, the C:N values found (ranging from 10 to 12.5) were well below the range of 20–30:1 considered optimal to soil health and threshold for nutrient immobilization to occur (Biswas & Micallef, 2019). Hence, we expect that all of these meadows are still in stage of recovery from their past agricultural practices (Morriën et al., 2017) and expected future increase in C would possibly be reflected in an increase in faunal abundance. Site BHP was the only meadow that was grazed,

which is known to negatively impact many soil fauna due to soil compaction and reduced pore spaces and litter (van Klink et al., 2015), and could have contributed to the lower abundance of soil fauna in that meadow (Bardgett & Cook, 1998).

While our findings reveal clear differences between SOM content and C:N ratio in the different meadows, there were no significant differences in diversity of soil organisms (Figure 1d). One might expect a higher nutrient availability and abundance to result in more niches, thus enhancing diversity (Levine & Hillerislambers, 2009), but we did not find such an effect. This might imply that the additional resources disproportionately benefited a small group of taxa, without affecting total diversity levels. However, is important to note that organisms were only identified to order or family level, and that a more accurate determination process would maybe have given different results (Berg & Bengtsson, 2007).

The Acari-Collembola ratio (Figure 1e) was higher in the regenerative meadow (LP) compared with meadows that with a more conventional management (BHP & NVV). Moreover, oribatid mite abundance was highest in LP further indicating that the food-web structure in this meadow had changed from a Collembola dominated food web that is currently observed in conventional managed meadows. This shift might possibly following the
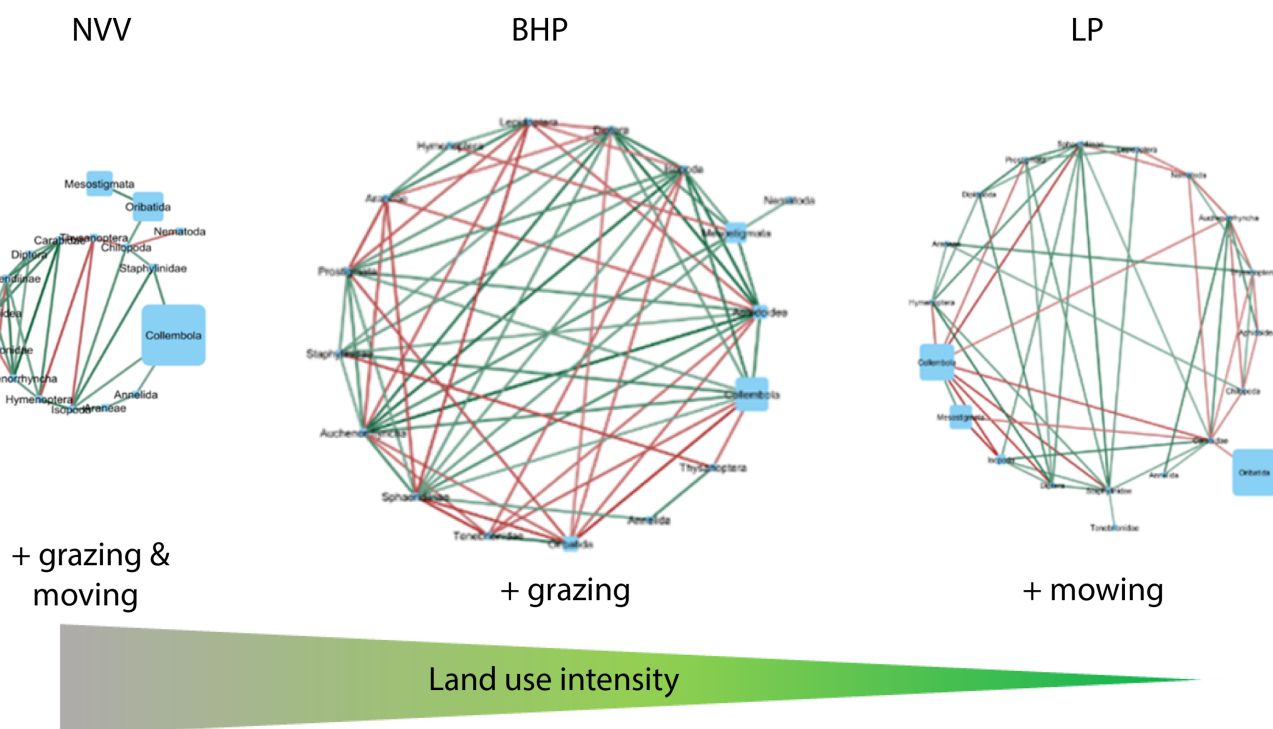

FIGURE 2 Co-occurrence networks for each of the three meadows NVV, BHP and LP, respectively, along the land-use intensity gradient. Green lines represents positive correlations between two species groups, while red lines indicates negative correlations between two species groups. Node size (blue squares) is scaled to the abundance within each respective meadow.

observed shift in C:N ratio in literature (Hasegawa & Takeda, 1996; McLean & Parkinson, 2000). Despite the major differences in land use between BHP and NVV over the past decade, there was no significant difference in Acari-Collembola ratio between the two meadows. This suggests that the Acari-Collembola-ratio is likely a rather ill-suited measure to determine the effect of more subtle agricultural practices (Menta & Remelli, 2020). Grazing in BHP (as compared to mowing in NVV) could have functioned as an additional source of agricultural disturbance (Bardgett & Cook, 1998), lowering the Acari-Collembola ratio and potentially undoing any effect of the organic management regime in BHP on the A-C ratio. Yet, the Acari-Collembola ratio was not sufficiently sensitive to pick up this long-term management shift, possibly due to its inherent multifactorial nature: it only measures the ratio in numbers of organisms and not the species diversity nor interactions between them covered in Shannon index and network analyses.

Network metrics were the most advanced metrics used in this study, which also makes them the most complex to interpret (Freilich et al., 2018). Our findings (Figure 2) show that only these network-based metrics showed striking differences between meadows BHP and NVV while the other metrics were mainly indicating differences between the regenerative land-use meadow (LP) and the two other meadows. Although we observed negative effects of grazing on bioindicator species and total soil fauna abundance, it is possible that the effect of grazing on network connectivity is caused by an increase in small scale spatial heterogeneity in grazed grasslands (Adler et al., 2001; Plue et al., 2018). Heterogeneity in vegetation height due to grazing, in combination with heterogeneity in cattle dung patches creates 'hot spots', described as crucial to ecologically relevant processes by Blagodatskaya and Kuzyakov (2013). However, such small scale heterogeneity might be too local and temporary to be detected in the soil chemical measurements but could have had a great impact on the soil fauna community which operate over larger spatiotemporal scales. Alternatively, a higher degree of compartmentalization in ecosystems (i.e. species co-existing in local microhabitats) has been proposed to inhibit co-occurrence strength (Montoya-Sánchez et al., 2023; Stouffer & Bascompte, 2011). The LP meadow was the area with the highest level of heterogeneity in terms of vegetational diversity (Marselis et al., 2024), and if this translated into differences in soil faunal distribution, it could have weakened network connectivity. As there are different forms of heterogeneity, both possible explanations (heterogeneity in local and regional levels) could be true simultaneously to varying degrees, resulting in BHP having a more connected ecological network than LP.

In any case, using co-occurrence network analysis, we were able to capture significant shifts in soil fauna communities undetected by traditionally used chemical and biological metrics. More research is needed to understand what implications of observed network structures are for key ecosystem functions (e.g. nutrient cycling, resilience) and how structure and connectivity within networks are affected by environmental spatial heterogeneity. As such, we deem it a valuable addition to the metrics currently used to evaluate soil quality. While generally cheaper and easier to interpret than eDNA based methods, all metrics used here are based on counts of soil fauna extracted from soils and identification using specialized (yet, teachable) identification skills, and are hence not particularly high-throughput or user-friendly needing specialized expertise (Griffiths et al., 2016). The network metrics are at the beginning most difficult to interpret (Freilich et al., 2018), yet we propose they are inherently more tangible to farmers and land-managers as they encompass both information on species and their potential interactions (Marselis et al., 2024).

In conclusion, we show that large differences in soil health as a result of land use can be captured in chemical and biological indicators, while more subtle differences (biological vs. conventional farming; grazing vs. mowing) might be best captured using network analysis.

AUTHOR CONTRIBUTIONS

Charlie Mioulet: Investigation; writing – original draft; methodology; conceptualization; formal analysis. **Maarten Schrama:** Conceptualization; writing – review and editing; project administration; supervision. **Matty P. Berg:** Conceptualization; writing – review and editing; methodology; supervision. **S. Emilia Hannula:** Supervision; project administration; formal analysis; writing – review and editing; conceptualization.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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