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Evaluation of mesofauna communities as soil quality indicators in a national-level monitoring programme

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ABSTRACT

Mesofauna underpin many ecosystem functions in soils. However, mesofauna communities are often overlooked when discussing these functions on large scales. They have been proposed as bioindicators of soil quality and ecosystem health. This study aimed to evaluate differences amongst mesofauna communities, particularly Acari and Collembola, across multiple habitat and soil types, as well as organic matter levels, and their relationships with soil characteristics, on a national-scale. Soil cores were collected from 685 locations as part of a nationwide soil monitoring programme of Wales. Plant community composition, soil type, as well as physical and chemical variables, including pH, total C and N, were measured at these locations. Mesofauna were extracted from soil cores and identified using a Tullgren funnel technique. Acari were sorted to Order; Collembola were sorted according to Super-family. Abundances of mesofauna were consistently lowest in arable sites and highest in lowland woodlands, except for Mesostigmata. Differences between similar habitat types (e.g. Fertile and Infertile grasslands) were not detected using the national-level dataset and differences in mesofauna communities amongst soil types were unclear. Relationships between mesofauna groups and soil organic matter class, however, were much more informative. Oribatid abundances were lowest in mineral soils and correlated with all soil properties except moisture content. Collembola and Mesostigmata abundances were likely negatively influenced by increased moisture levels in upland peat habitats where their abundances were lowest. These groups also had low abundances in heathlands and this was reflected in low diversity values. Together, these findings show that this national-level soil survey can effectively identify differences in mesofauna community structure and correlations with soil properties. Identification of mesofauna at high taxonomic levels in national-level soil monitoring is encouraged to better understand the ecological context of changes in soil properties.

Key words: *Soil biodiversity; Vegetation class; Hydrophobicity; Wales; Mites; Springtails*

1. Introduction

Mesofauna represent a major component of soil biological communities and play a critical role in maintaining soil quality and a range of ecosystem functions (Barrios, 2007). Soil invertebrates support decomposition, nutrient cycling, and soil formation, which facilitates water supply and regulates local erosion and climate (Lavelle et al., 2006: Barrios, 2007). Such functions are key components soil health (Doran and Zeiss, 2000). Acari (Gulvik, 2007) and Collembola (Rusek, 1998) are the most abundant groups of mesofauna. Collembola in soils are important consumers of microbial films and fungal hyphae or larger plant detritus, and can influence soil structure in some systems (Rusek, 1998). Important Acari sub-orders include Oribatida and Mesostigmata. Oribatids are the most numerous and diverse group in most undisturbed soils. They are slow moving, heavily armoured, with comparatively low fecundity and relatively long lifespans to other mesofauna (Gulvik, 2007) and consume organic matter as well as fungi (Schneider et al., 2005). Mesostigmatids are commonly important predators within soils, consuming a wide range of invertebrate fauna (Gulvik, 2007)

With such life-history characteristics as well as their small size, varied ecological preferences, relatively high fecundity, and ease of sampling, mesofauna may serve as bioindicators of soil quality and ecosystem health (Gerlach et al., 2013). At the broad level, abundances of Acari and Collembola are useful for understanding how biota respond to the impacts and intensity of land-use on ecosystems (Black et al., 2003; Rutgers et al. 2009; Nielsen et al., 2010a; Arroyo et al., 2013), as well as the effects of anthropogenic disturbance (Tsiafouli et al., 2015). While mesofauna are often overlooked, studies of mesofauna as bioindicators have been implemented in a number of large-scale soil assessment and ecosystem monitoring programmes across Europe.

In the Netherlands, abundances of mesofauna, specifically in agricultural and horticultural sites, declined in areas with high disturbance and increased in areas where disturbance was minimal (Rutger et al., 2009). Cluzeau et al. (2012) suggested that greater abundances of Collembola indicated the use of organic fertilisers and high-level of agricultural management. Ireland's Crébeo soil biodiversity assessment found indicator species that differentiated agricultural land uses (Keith et al., 2012). Soil invertebrate measures were added as bioindicator metrics to the UK Countryside Survey in 1998. Black et al. (2003) found Acari, especially oribatids, preferred highly organic, moist soils as well as undisturbed upland habitats including moors, heaths, bogs, and woods, whereas Collembola made up a greater proportion of mesofauna communities in grasslands and deciduous woodlands.

The fact that such monitoring programmes are undertaken at a national-scale means that trends can be observed for wide geographic areas, offering a range of benefits for ecological synthesis. Firstly, broad, intensive sampling contributes to a national taxonomic inventory for soil biota including information of diversity and distribution. Secondly, large-scale soil monitoring programmes provide a spatially varied dataset, ideal for linking biological indicators to ecosystem health/functions. Thirdly, such datasets also offer an opportunity to develop and test large-scale hypotheses on, agricultural practices, land remediation, and soil pollution in relation to ecosystem services and health. Finally, soils have been described as a critical resource for sustaining human life, similar to air and water (Havlicek, 2010). The importance of soil is slowly becoming recognised through policy, with, the government of Wales adopting soil carbon (C) as a national status indicator of progress under the Well-being of Future Generations (Wales) Act 2015 (Welsh Government, 2016).

The effectiveness of mesofauna as indicators of soil health at a national-scale is unclear, since contemporary surveys to date lack extensive detail on mesofauna trends. Of particular concern is whether differences amongst mesofauna communities are indicative of functional processes at the level of habitat or soil type. However, identifying mesofauna to species-level can present a significant impediment to researchers. Understanding if higher-level taxonomic groups of mesofauna can show consistent nationwide trends or highlight important environmental characteristics is needed to realise their application as effective bioindicators of soil quality.

Here, we present findings of mesofauna community metrics collected over a 2-year period as part of a nation-wide soil monitoring programme. Specifically, we aim to evaluate how mesofauna communities, including abundances of various groups of Acari and Collembola, differ amongst habitats and soils with diverse physico-chemical properties across an intensively sampled national landscape including many diverging habitats. We hypothesise that mesofauna will be more abundant and diverse with decreasing disturbance and specifically, that biodiversity will be lowest in frequently disturbed agricultural soils and highest in less-disturbed sites like woodland soils. We also explore relationships between various mesofaunal groups and several, pre-selected soil physical and chemical parameters. We expect organic matter (positive), pH, (positive) and moisture content (negative) to be most strongly correlated with mesofauna abundances. The ultimate aim of the work was to establish whether important mesofauna groups effectively delineate habitat and environmental differences amongst sites for a national-scale assessment of soil quality.

2. Materials and methods

2.1. Study design

In Wales, UK, Glastir is a national-level agri-environment scheme, involving 4,911 landowners with an area of 3,263 km^2. It is the main way that the Welsh Government and the European Union (EU) pays for environmental goods and services. The Glastir Monitoring and Evaluation Programme (GMEP) was established to evaluate the scheme's effectiveness. GMEP collected evidence for six intended outcomes from the Glastir scheme; climate change mitigation, improvement to soil and water quality, a halt in the decline of biodiversity, improved woodland management and greater access to the welsh landscape and condition of historic features (Emmett and the GMEP Team, 2015). From 2013 to 2016, GMEP was the largest and most in-depth active soil monitoring programme measuring environmental state and change in the EU (Emmett and the GMEP Team, 2014). For a detailed description of GMEP see Supplementary Material.

As part of GMEP, survey teams travelled across Wales taking soil samples. The methodology used was established previously in the Countryside Survey (Emmett et al., 2010). Briefly, randomly allocated 1 km^2 squares, each containing 5 plot locations, were monitored across Wales. The habitat of each plot was classified using an Aggregate Vegetation Class (AVC) based on a high-level aggregation of vegetation types derived from plant species data in each plot. There are eight categories of AVC: Crops/weeds, Tall grassland/herb, Fertile grassland, Infertile grassland, Lowland wood, Upland wood, Moorland-grass mosaic, and Heath/bog (Bunce et al., 1999; for detailed description see Table S1). Soil type was categorised following the Main Group classifications of the National Soil Map (Avery, 1990; for detailed description see Table S2). In addition, an organic matter classification was used based on three loss-on-ignition (LOI) categories: mineral (0-8% LOI), humus-mineral (8-30% LOI), organo-mineral (30-60% LOI), and organic (60-100% LOI) as used in the Countryside Survey (Emmett et al., 2010).

Soils were sampled from late spring until early autumn in 2013 and 2014, with cores taken at each plot (8 cm depth, 4 cm diameter) for subsequent mesofauna extraction, co-located with cores for soil chemical and physical parameters. These were taken from 60 x 1 km^2 squares in 2013 and 90 x 1 km^2 in 2014 (Fig. 1), with 684 samples included in analyses.

Cores were kept in cool boxes or fridges at 4ºC and then posted overnight to the Centre for Ecology and Hydrology, Lancaster for mesofauna extraction.

Soil physical and chemical characteristics were assessed on the additional soil cores from each site. We chose standard soil quality indicators including bulk density (g/cm^3), pH (measured in 0.01 M $CaCl_2$), volumetric water content (m^3/m^3), total phosphorus (P) (mg/kg), total C (%), total nitrogen (N) (%), and soil water repellency (as water drop penetration time in seconds). Mean values of each variable are presented in the Supplementary Material for each AVC (Table S3). These analyses were conducted following Countryside Survey protocols (Emmett et al., 2010).

2.2. Mesofauna extraction and identification

Mesofauna were extracted from soil cores using a Tullgren funnel technique over five days and collected in tubes containing 70% ethanol (Winter and Behan-Pelletier, 2007). Specimens were sorted for identification and enumerated. Due to their importance and proportional dominance in soils, Acari and Collembola were of primary interest. Acari were identified to Order (Mesostigmata) and Sub-order (Oribatida or Prostigmata) following Crotty and Shepherd (2014). Collembola were identified to Order (Symphypleona) or Superfamily (Entobryoidea or Poduroidea) following Hopkin (2007). Other animals identified included Araneae, Chilopoda, Coleoptera, Dermaptera, Diplura, Diptera, Hemiptera, Hymenoptera, Isopoda, Oligochaeta, Protura, Pseudoscorpiones, and Thysanoptera. For each sample, abundances of all mesofauna groups (Oribatida, Mesostrigmata, Entomobryoidea, Poduroidea, and Symphypleona) were enumerated, as well as their combined abundance (=total mesofauna) and the abundance of all invertebrates extracted (=total invertebrate catch). Shannon's diversity (H') was calculated on abundance data of the five mesofauna groups.

2.3. Statistical analyses

Differences in community composition were assessed using non-metric dimensional scaling (NMDS) with subsequent analysis of multivariate homogeneity of group variances (*betadisper* function), followed by ANOVA with Tukey's HSD *post-hoc* tests, and similarity percentages (SIMPER), using the R software package "vegan" (Oksansen et al., 2016). Significant changes in mesofauna abundances, total catch, and diversity were tested with linear mixed models using the "nlme" package (Pinheiro et al., 2016) with R version 3.1.1 (R Core Team, 2016) following $\log_{10}$ +1 transformations to normalise data. The terms "identifier" (to denote who identified the mesofauna) and "square" (the 1 km^2 square from which each sample was taken) were included as random-effects in the models. Where significant, data were subjected to Tukey's HSD *post-hoc* testing to determine where differences in mesofauna metrics amongst individual AVCs, soil types, and LOI classes were significant. Correlations between mesofauna abundance and soil properties were determined using Spearmann's rank correlation coefficient and modified versions of the previously described linear mixed models with pseudo-R^2 values calculated with the "piecewiseSEM" package (Lefcheck, 2015).

3. Results

3.1. Mesofauna composition

Oribatids were generally the most common mesofauna group accounting for between 20 and 44% of the individuals recorded across all AVCs. Entomobryoidea were the most common group of Collembola encountered, especially in Upland and Lowland Woods, where they accounted for approximately 15-25% of mesofauna in each AVC. Symphypleona (Collembola) were the rarest mesofauna group in all AVCs, representing less than 4% of all individuals recorded. While NMDS analysis revealed no distinct clusters of community composition (Fig. S1), significant differences in homogeneity of variance across AVC types ($F_{7,677}$ = 3.11, p = 0.003) were reflected through differences in the variation in mesofauna composition between Fertile grasslands and both Upland wood (p = 0.04) and Heath/bog (p = 0.02). Based on SIMPER analysis, this was likely driven by differences in proportional abundances of total Collembola and Mesostigmata. Mesostigmata accounted for approximately 21% and 18% of the dissimilarity when Fertile grassland was compared to Heath/bog and Upland wood, respectively. Collembola accounted for approximately 33% and 36% of the dissimilarities between these same groups.

3.2. Abundance and diversity measures

3.2.1. Differences amongst AVC types

Total mesofauna abundances differed significantly amongst AVCs ($F_{7, 515}$ = 5.65, p < 0.001). Abundances were three times higher (Table S4) in Lowland wood than in Crops/weeds, where abundances were lowest (Fig. 2A). Total mesofauna abundances in Crops/weeds were significantly lower than in Lowland (p < 0.001) and Upland wood (p = 0.004), Infertile grassland (p < 0.001), and Moorland-grass mosaic (p = 0.028). Total mesofauna abundance in Lowland wood abundances was also significantly greater than Heath/bog (p = 0.038; Fig. 2A). The effect of AVC on total invertebrate catch (mesofauna plus others) was also highly significant ($F_{7, 515}$ = 5.49, p < 0.001), following the same trends previously mentioned.

As with total mesofauna, AVC had a significant effect on oribatid abundance ($F_{7, 515}$ = 13.35, p < 0.001). Again, abundances of oribatids were highest in Lowland wood, and lowest in Crops/weeds. Abundances were significantly lower in Crops/weeds and Fertile grassland than all other AVCs except Tall grass and herb (p = 0.973; p = 0.995, respectively).

Additionally, oribatid abundances were significantly greater in Lowland wood than in Tall grass and herb ($p = 0.025$) and Infertile grassland ($p = 0.004$) AVCs (Fig. 2B). Though abundances of Mesostigmata differed significantly by AVC ($F_{7, 515} = 8.874$, $p < 0.001$), such differences were not consistent with the overall trend (Fig. 2C). Numbers of Mesostigmata were significantly lower in Moorland-grass mosaic and Heath/bog than Fertile (both $p < 0.001$) and Infertile grassland (both $p < 0.001$), as well as Upland wood ($p = 0.023$, $p < 0.001$, respectively). Abundances in Heath/bog were nearly four times (Table S4) lower than in Lowland wood ($p = 0.014$).

Abundances of Collembola did not follow the same overall pattern. Abundances of Symphypleona were negligible across all AVC's. Entomobryoidea and Poduroidea abundances showed similar differences between AVCs ($F_{7, 515} = 5.72$, $p < 0.001$; $F_{7, 515} = 5.97$, $p < 0.001$, respectively). Entomobryoidea abundances were significantly greater in Lowland wood than in Fertile ($p = 0.036$) and Infertile grassland ($p = 0.047$), Moorland-grass mosaic ($p = 0.018$), Crops/weeds ($p = 0.002$), and Heath/bog ($p < 0.001$). Abundances in Crops/weeds ($p = 0.028$) and Heath/bog ($p < 0.001$) were significantly lower than in Upland wood by approximately six and seven times, respectively (Table S4). Additionally, abundances in Heath/bog were also significantly lower than Infertile ($p = 0.006$), and Fertile grassland ($p = 0.041$; Fig. 2D). Abundances of Poduroidea were significantly lower in Crops/Weeds ($p = 0.009$), Moorland-grass mosaic ($p = 0.017$), and Heath/bog ($p < 0.001$) AVCs than Lowland wood. Abundances in Heath/bog were also significantly lower than both grasslands (both $p < 0.001$), Moorland-grass mosaic ($p = 0.01$), and Upland wood ($p = 0.001$; Fig. 2E).

AVC had a significant ($F_{7, 515} = 13.90$, $p < 0.001$) effect on H' diversity values (Fig. 2F), possibly influenced by changes in Collembola and mesostigmatid abundances. Diversity values were significantly lower in Crops/weeds and Heath/bog when compared with both

Fertile ($p = 0.022$; $p < 0.001$, respectively) and Infertile grassland ($p = 0.027$; $p < 0.001$, respectively). Additionally, H' values in Infertile grassland were significantly greater than in Moorland-grass mosaic ($p < 0.001$). Lowland wood diversity values were significantly greater than Heath/bog ($p < 0.001$) and Moorland-grass mosaic (0.014). Heath/bog H' values were also significantly lower than Moorland-grass mosaic ($p = 0.009$) and Upland wood ($p < 0.001$).

3.2.2. Differences between soil types and LOI classes

Soil type had detectable effects on Mesostigmata ($F_{6,\ 516} = 4.34$, $p < 0.001$), Entomobryoidea ($F_{6,\ 516} = 3.10$, $p = 0.006$), and Poduroidea ($F_{6,\ 516} = 2.34$, $p = 0.031$; Fig. 3). Mesostigmata abundances were three times greater in brown soils than peat ($p < 0.001$) and nearly twice greater than in surface-water gley soils ($p = 0.005$; Fig. 3C; Table S5). Entomobryidea and Poduroidea abundances were also significantly higher in brown soils than in peats ($p = 0.009$; $p = 0.043$, respectively; Fig 3D, 3E). These differences are reflected in H' values ($F_{6,\ 516} = 6.16$, $p < 0.001$), where the same differences can be seen (brown soils-peats: $p < 0.001$; brown soils-surface-water gleys: $p = 0.002$), in addition to a significant difference between podzolic and peat soils ($p = 0.002$) (Fig. 3F).

Differences in mesofauna abundance amongst LOI classes were more informative. Significant differences were observed for total mesofauna ($F_{3,\ 518} = 3.97$, $p = 0.008$; Fig. 4A), total invertebrates ($F_{3,\ 518} = 3.99$, $p = 0.008$), and oribatid abundances $F_{3,\ 518} = 7.74$, $p < 0.001$). Here, abundances were significantly higher in humus-mineral than in mineral soils ($p = 0.026$; $p = 0.030$; $p < 0.001$, respectively). Oribatid abundances were also significantly greater in organo-mineral soils than mineral soils ($p = 0.007$) and in lower organic than mineral soils ($p < 0.001$; Fig. 4B).

The effect of LOI class on abundance was the same for Mesostigmata ($F_{3,\ 518} = 11.97$, $p < 0.001$) and Entomobryoidea ($F_{3,\ 518} = 7.36$, $p < 0.001$). Here, abundances of both were significantly lower in organic soils than humus-mineral, mineral (all $p < 0.001$), and organo-mineral ($p = 0.023$, $p = 0.037$, respectively) soils (Fig. 4B, 4C) by orders of four to five times respectively (Table S6). A similar trend was observed in Poduroidea abundances ($F_{3,\ 518} = 9.96$, $p < 0.001$). However, in this case, abundances were significantly lower in organic soils than humus-mineral ($p < 0.001$) and mineral ($p = 0.01$) soils (Fig. 4E). LOI class significantly ($F_{3,\ 518} = 28.67$, $p < 0.001$) affected diversity values, being significantly greater in humus-mineral ($p < 0.001$), mineral, ($p < 0.001$) and organo-mineral ($p = 0.007$) soils than in organic soils. There were also significant differences between organo-mineral soils and both mineral ($p = 0.028$) and humus-mineral soils ($p = 0.001$; Fig. 4F).

3.3. Correlates with soil physical and chemical variables

Oribatid abundances significantly correlated with every soil property analysed except soil moisture content (Table 1). Positive relationships were found between oribatid abundance and total C, total N, C:N ratio, and soil water repellency; negative relationships were found between oribatid abundance and pH and total P (Table 1). Oribatids were the only group to have a significant relationship with soil water repellency (Fig. 5). Total mesofauna correlated negatively with moisture content and pH, and positively with soil water repellency. Mesostigmata had significant positive relationships with bulk density and pH, and had significant negative relationships for total C, total N, C:N ratio, and moisture content (Table 1). Entomobryoidea and Poduroidea displayed negative relationships with total C, total N, C:N ratio, and soil moisture content. Both groups only had significant positive correlations with bulk density (Table 1).

4. Discussion

4.1. Trends in mesofauna communities

Total abundance and diversity values were consistently lower in arable sites. These results support those of other studies that have shown Acari and Collembola abundances decline in agricultural habitats when compared to more extensive habitats (de Vries et al., 2013; Arroyo et al., 2013; Tsiafouli et al., 2015). For example, Tsiafouli et al. (2015) found Acari and Collembola diversity and biomass declined with increasing agricultural land-use intensity across a range of European sites. These groups (Behan-Pelletier, 2003; Tsiafouli et al., 2015) are generally susceptible to disturbance, which has been seen across Europe (Postma-Blaauw et al., 2010; de Vries et al., 2013), North America (Behan-Pelletier, 2003), and Australia (Osler and Murphy, 2005).

LOI classification was more informative than soil type when explaining differences in mesofauna abundance and diversity. This is likely an artefact of the resolution and accuracy of soil classification. Soil types were inferred from major groups defined by Avery (1990) associated with the series listed for each sample location on the National Soil Map (see Supplementary Material). In contrast, LOI classification was derived from co-located plot data and may provide more important ecological trends than traditional mapped soil taxonomy.

4.2. Soil properties and oribatids

The negative correlation of oribatid mite abundance with pH and bulk density, in addition to the positive relationship with soil organic matter observed in the present study is consistent with results from Ireland (Arroyo et al., 2013). Oribatids are sensitive to agricultural practices, primarily due to life-history characteristics such as low fecundity and relatively long generation times (Behan-Pelletier, 1999). Soil compaction and litter removal have been shown to lower oribatid densities in forest plantations (Battigelli et al., 2004) and both processes commonly occur under conventional agricultural management.

Oribatids were the only group to correlate with soil water repellency. Although soil water repellency is not commonly studied in relation to mesofauna, it is known that soils rich in fungi are often hydrophobic (Hallett et al., 2001; Rillig et al., 2010). Many species of Oribatida are fungivorous (Behan-Pelletier, 1999). We suspect that this relationship may be indicative of soils with high fungal abundance. Further research using microbial data could explore a similar correlation between soil hydrophobicity and fungi, likely to be driven by filamentous species (Rillig, 2005).

Abundances of Oribatida had significant, positive relationships with total N and C:N ratio. This is contrary to research by Cole et al. (2008), who found positive interactions with Collembola abundance and total N, and no relationship with oribatid abundance. However, many oribatid taxa may be tolerant of increased soil N addition, especially ammonium (Seniczak et al., 1998). The positive relationship with C:N ratio suggests that Welsh oribatid populations are predominantly fungivorous, whereas the other groups studied are either obviously predatory or might favour bacterivorous or omnivorous diets (Osler and Sommerkorn, 2007). Oribatids were negatively correlated with total P, which is consistent with a previous study by Schon et al. (2011), who found P additions decreased oribatid abundances. This relationship may be indicative of a shift towards intensive agriculture.

4.3 Trends in Mesostigmata and Collembola populations

Interestingly, Collembola abundances were as low in Heath/bog sites as they were in Crops/weeds. Most Heath/bog sites were located in upland regions. The Welsh uplands include at-risk habitats such as peatlands, which are sensitive to disturbance (Reed et al., 2009), tend to be colder and have a higher levels of C, more frequent of precipitation as well as greater N deposition than lowland habitats (Kirkham, 2001). Temperature and moisture level has been identified as stressors for Collembola communities. Choi and colleagues (2002) found development of temperate Collembola can be halted by temperatures lower than 5 °C. Sustained elevated N deposition in American forest soils has been shown to reduce Collembola densities (Gan et al., 2013). Increased frequency and severity of precipitation also reduce Collembola richness and abundance in both mesocosm (Turnbull and Lindo, 2015) and *in situ* experiments (Tsiafouli et al., 2005). Furthermore, increases in peatland Collembola populations have been documented when peatlands are drained for forestry (Silvan et al., 2000). Total C and N, as well as C: N ratio, were highest in upland habitats (Table S3); therefore, the negative relationships between Collembola and these variables were likely artefacts of the strong effect of moisture levels in upland, peat-rich sites.

Mesostigmata abundances only declined in Moorland-grass mosaic and Heath/bog sites. Mesostigmatids had the same trends with bulk density (positive), and moisture content (negative) as Collembola, but were positively correlated with pH. Prey availability has been shown to have a strong influence on mesostigmatid abundance (Nielsen et al., 2010a; Nielsen et al., 2010b). Decreased prey abundance (i.e. Collembola, Nielson et al., 2010a) could limit their populations in moist upland habitats. Higher abundances in agricultural areas may have been maintained through consumption of unsurveyed prey such as nematodes (Koehler, 1997), as predatory Acari in arable habitats are often generalists or omnivores (Postma-Bloouw et al., 2010).

4.3. Implications for national-level soil monitoring

The approach employed by GMEP is efficient and cost-effective and the collection of a separate mesofauna core from each site does not add considerably to sampling effort of a monitoring programme (Emmett and the GMEP Team, 2014; 2015). This study showed that meaningful conclusions can be drawn from a nationwide mesofauna dataset collected using a relatively simple, standardised methodology. Yet, trends observed in the present study highlight some important shortcomings of using mesofauna as bioindicators of soil quality.

Differences amongst AVCs were most commonly observed in those with extreme differences in disturbance levels or plant communities, such as Crops/weeds, Lowland wood, and Heath/bog. Using small, subterranean fauna to inform habitat classifications is likely an over-complicated methodology, when aboveground plant community assessments are easier and more informative. Indeed, our methodology could not consistently detect community changes amongst grassland and agricultural AVCs. This means that results of agricultural interventions focused on conversion to semi-natural grassland or extensification may not be evident in national soil surveys. Furthermore, the relationships between abundances and soil type were not clear and challenging to interpret.

Comparing trends amongst nationwide data sets to the literature also presents challenges. The majority of research published on the interaction of mesofauna and soil properties focuses on the habitat or microhabitat scale. Trends presented here represent an entire habitat gradient that may be driven by specific AVCs. For instance, the relationship between soil water repellency and oribatid mite abundance is driven by grassland AVCs. It should also be noted that working on a national-scale leads to discrepancies in replication. For example, in our dataset, the Tall grass/herb AVC was only represented by three samples, making any trends in this habitat unreliable. Conversely, an overabundance of habitat types in a national survey may obscure interesting trends in unique or rare systems. Thus, it may be necessary to subsample data from national surveys by habitat to find comparable data.

Higher taxonomic levels of mesofauna were however, informative of relationships using locally derived soil data. Relationships of these groups with soil properties, though potentially obscured when taken as a whole, allow for important insights into the ecological implications of changes in the environment. Similarly, comparing mesofauna groups to soils classified by LOI percentage on a national-level revealed trends that better inform us of the ecological meaning behind distributions that traditional soil taxonomic classifications. It is possible that further classification of mesofauna to species-level could be more informative. We chose not to do this, and to instead use higher-level taxonomy following previous British surveys (Black et al., 2003; Keith et al., 2015). National monitoring has an added benefit of creating a national inventory of taxonomic specimens from which further research can be conducted and from which more species may be described. Additionally, reference collections of identified mesofauna species provide a strong starting-point for studies using metabarcoding (Creer et al., 2016). Greater confidence can be given to database matches of mesofauna from community and environmental DNA and DNA from identified specimens can be uploaded to databases (Ratnasingham and Hebert, 2007) to build more complete reference libraries. It is important to remember that comparisons of new molecular datasets will require reference to historical taxonomic data, strengthening the case for acquiring new reference materials as part of monitoring. Therefore, we suggest that the addition of surveys of mesofauna identified at coarse taxonomic levels to any national soil monitoring programme will be an important compliment to the assessments of soil properties and biodiversity.

5. Conclusions

Our results show that at the national-level, mesofauna populations have the potential to be effective environmental indicators, through their consistent sensitivity to differences in habitat, plot-level soil class, and soil physical characteristics. This research represents an important first step to assess agri-environment schemes and land-use change. The present study was one of the most extensive nationwide surveys of mesofauna in Europe. Results show that conventional stresses on soil mesofauna from agriculture can be observed across the country with relatively low sampling effort. Additionally, it has revealed trends in Collembola and Mesostigmata in highly sensitive upland areas. Such results may be of use to policy-makers and land-managers actively trying to maintain a balance between rural development and natural values. The sampling design used here has been effective for analysis of disparate habitat types. However, further refinements are needed to separate similar habitat types and to understand relationships with soil type as defined by the National Soil Map using mesofauna communities. We encourage the use of mesofauna surveys in regional- to national-level soil monitoring programmes to better inform researchers of the ecological implications of changing soil properties. With the inclusion of mesofauna in soil monitoring plans, a more complete picture of the potential of mesofauna as bioindicators of soil quality will be made.

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Figure Captions

Fig. 1. Map of 1 km^2 squares selected for GMEP monitoring. Sites are randomly offset by 10 km to protect landowner anonymity.

Fig. 2. Boxplots of **A)** total mesofauna; **B)** Oribatida; **C)** Mesostigmata; **D)** Entomobryoidea; **E)** Poduroidea; **F)** Shannon's diversity plotted against Aggregate Vegetation Class. All abundances are $\log_{10}$ plus one transformed. Notches indicate confidence interval around the median. Overlapping notches are a proxy for non-significant differences between medians.

Black dots are outliers. AVC's are ordered from most (Crops and weeds) to least (Heath and bog) productive.

Fig. 3. Boxplots of **A)** total mesofauna; **B)** Oribatid mites; **C)** Mesostigmatid mites; **D)** Entomobryoidea; **E)** Poduroidea; **F)** Shannon's diversity plotted against soil type. All abundances are $\log_{10}$ plus one transformed. Notches indicate confidence interval around the median. Overlapping notches are a proxy for non-significant differences between medians. Black dots are outliers. Soils are listed in approximate order of increasing soil moisture content.

Fig. 4. Boxplots of **A)** mesofauna; **B)** Oribatid mites; **C)** Mesostigmatid mites; **D)** Entomobryoidea; **E)** Poduroidea; **F)** Shannon's diversity for each loss-on-ignition (LOI) class. All abundances are $\log_{10}$ plus one transformed. Notches indicate confidence interval around the median. Black dots are outliers. Overlapping notches are a proxy for non-significant differences between medians. LOI classes are listed in order of increasing soil organic matter content.

Fig. 5. Scatterplot and linear regression line of $\log_{10}$ plus one transformed oribatid abundances versus log-transformed soil water repellency ($\log_{10}(s)$) from all sample sites. Grey area around regression line represents 95% confidence interval. Pseudo-R^2 value was calculated using the R package "Piecewise SEM" (Lefcheck, 2015).