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

3

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18 **ABSTRACT**

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

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

44 **1. Introduction**

45 Mesofauna represent a major component of soil biological communities and play a
46 critical role in maintaining soil quality and a range of ecosystem functions (Barrios, 2007).
47 Soil invertebrates support decomposition, nutrient cycling, and soil formation, which
48 facilitates water supply and regulates local erosion and climate (Lavelle et al., 2006; Barrios,
49 2007). Such functions are key components soil health (Doran and Zeiss, 2000). Acari
50 (Gulvik, 2007) and Collembola (Rusek, 1998) are the most abundant groups of mesofauna.
51 Collembola in soils are important consumers of microbial films and fungal hyphae or larger
52 plant detritus, and can influence soil structure in some systems (Rusek, 1998). Important
53 Acari sub-orders include Oribatida and Mesostigmata. Oribatids are the most numerous and
54 diverse group in most undisturbed soils. They are slow moving, heavily armoured, with
55 comparatively low fecundity and relatively long lifespans to other mesofauna (Gulvik, 2007)
56 and consume organic matter as well as fungi (Schneider et al., 2005). Mesostigmatids are
57 commonly important predators within soils, consuming a wide range of invertebrate fauna
58 (Gulvik, 2007)

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

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

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

91 The effectiveness of mesofauna as indicators of soil health at a national-scale is
92 unclear, since contemporary surveys to date lack extensive detail on mesofauna trends. Of

93 particular concern is whether differences amongst mesofauna communities are indicative of
94 functional processes at the level of habitat or soil type. However, identifying mesofauna to
95 species-level can present a significant impediment to researchers. Understanding if higher-
96 level taxonomic groups of mesofauna can show consistent nationwide trends or highlight
97 important environmental characteristics is needed to realise their application as effective
98 bioindicators of soil quality.

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

112

113 **2. Materials and methods**

114 *2.1. Study design*

115 In Wales, UK, Glastir is a national-level agri-environment scheme, involving 4,911
116 landowners with an area of 3,263 km². It is the main way that the Welsh Government and the
117 European Union (EU) pays for environmental goods and services. The Glastir Monitoring

118 and Evaluation Programme (GMEP) was established to evaluate the scheme's effectiveness.
119 GMEP collected evidence for six intended outcomes from the Glastir scheme; climate change
120 mitigation, improvement to soil and water quality, a halt in the decline of biodiversity,
121 improved woodland management and greater access to the welsh landscape and condition of
122 historic features (Emmett and the GMEP Team, 2015). From 2013 to 2016, GMEP was the
123 largest and most in-depth active soil monitoring programme measuring environmental state
124 and change in the EU (Emmett and the GMEP Team, 2014). For a detailed description of
125 GMEP see Supplementary Material.

126 As part of GMEP, survey teams travelled across Wales taking soil samples. The
127 methodology used was established previously in the Countryside Survey (Emmett et al.,
128 2010). Briefly, randomly allocated 1 km² squares, each containing 5 plot locations, were
129 monitored across Wales. The habitat of each plot was classified using an Aggregate
130 Vegetation Class (AVC) based on a high-level aggregation of vegetation types derived from
131 plant species data in each plot. There are eight categories of AVC: Crops/weeds, Tall
132 grassland/herb, Fertile grassland, Infertile grassland, Lowland wood, Upland wood,
133 Moorland-grass mosaic, and Heath/bog (Bunce et al., 1999; for detailed description see Table
134 S1). Soil type was categorised following the Main Group classifications of the National Soil
135 Map (Avery, 1990; for detailed description see Table S2). In addition, an organic matter
136 classification was used based on three loss-on-ignition (LOI) categories: mineral (0-8% LOI),
137 humus-mineral (8-30% LOI), organo-mineral (30-60% LOI), and organic (60-100% LOI) as
138 used in the Countryside Survey (Emmett et al., 2010).

139 Soils were sampled from late spring until early autumn in 2013 and 2014, with cores
140 taken at each plot (8 cm depth, 4 cm diameter) for subsequent mesofauna extraction, co-
141 located with cores for soil chemical and physical parameters. These were taken from 60 x 1
142 km² squares in 2013 and 90 x 1 km² in 2014 (Fig. 1), with 684 samples included in analyses.

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

145 Soil physical and chemical characteristics were assessed on the additional soil cores
146 from each site. We chose standard soil quality indicators including bulk density (g/cm³), pH
147 (measured in 0.01 M CaCl₂), volumetric water content (m³/m³), total phosphorus (P) (mg/kg),
148 total C (%), total nitrogen (N) (%), and soil water repellency (as water drop penetration time
149 in seconds). Mean values of each variable are presented in the Supplementary Material for
150 each AVC (Table S3). These analyses were conducted following Countryside Survey
151 protocols (Emmett et al., 2010).

152

153 *2.2. Mesofauna extraction and identification*

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

168

169 *2.3. Statistical analyses*

170 Differences in community composition were assessed using non-metric dimensional
171 scaling (NMDS) with subsequent analysis of multivariate homogeneity of group variances
172 (*betadisper* function), followed by ANOVA with Tukey's HSD *post-hoc* tests, and similarity
173 percentages (SIMPER), using the R software package "vegan" (Oksanen et al., 2016).
174 Significant changes in mesofauna abundances, total catch, and diversity were tested with
175 linear mixed models using the "nlme" package (Pinheiro et al., 2016) with R version 3.1.1 (R
176 Core Team, 2016) following $\log_{10} + 1$ transformations to normalise data. The terms
177 "identifier" (to denote who identified the mesofauna) and "square" (the 1 km² square from
178 which each sample was taken) were included as random-effects in the models. Where
179 significant, data were subjected to Tukey's HSD *post-hoc* testing to determine where
180 differences in mesofauna metrics amongst individual AVCs, soil types, and LOI classes were
181 significant. Correlations between mesofauna abundance and soil properties were determined
182 using Spearman's rank correlation coefficient and modified versions of the previously
183 described linear mixed models with pseudo-R² values calculated with the "piecewiseSEM"
184 package (Lefcheck, 2015).

185

186 **3. Results**

187 *3.1. Mesofauna composition*

188 Oribatids were generally the most common mesofauna group accounting for between
189 20 and 44% of the individuals recorded across all AVCs. Entomobryoidea were the most
190 common group of Collembola encountered, especially in Upland and Lowland Woods, where
191 they accounted for approximately 15-25% of mesofauna in each AVC. Symphypleona
192 (Collembola) were the rarest mesofauna group in all AVCs, representing less than 4% of all

193 individuals recorded. While NMDS analysis revealed no distinct clusters of community
194 composition (Fig. S1), significant differences in homogeneity of variance across AVC types
195 ($F_{7,677} = 3.11$, $p = 0.003$) were reflected through differences in the variation in mesofauna
196 composition between Fertile grasslands and both Upland wood ($p = 0.04$) and Heath/bog ($p =$
197 0.02). Based on SIMPER analysis, this was likely driven by differences in proportional
198 abundances of total Collembola and Mesostigmata. Mesostigmata accounted for
199 approximately 21% and 18% of the dissimilarity when Fertile grassland was compared to
200 Heath/bog and Upland wood, respectively. Collembola accounted for approximately 33% and
201 36% of the dissimilarities between these same groups.

202

203 *3.2. Abundance and diversity measures*

204 *3.2.1. Differences amongst AVC types*

205 Total mesofauna abundances differed significantly amongst AVCs ($F_{7, 515} = 5.65$, $p <$
206 0.001). Abundances were three times higher (Table S4) in Lowland wood than in
207 Crops/weeds, where abundances were lowest (Fig. 2A). Total mesofauna abundances in
208 Crops/weeds were significantly lower than in Lowland ($p < 0.001$) and Upland wood ($p =$
209 0.004), Infertile grassland ($p < 0.001$), and Moorland-grass mosaic ($p = 0.028$). Total
210 mesofauna abundance in Lowland wood abundances was also significantly greater than
211 Heath/bog ($p = 0.038$; Fig. 2A). The effect of AVC on total invertebrate catch (mesofauna
212 plus others) was also highly significant ($F_{7, 515} = 5.49$, $p < 0.001$), following the same trends
213 previously mentioned.

214 As with total mesofauna, AVC had a significant effect on oribatid abundance ($F_{7, 515} =$
215 13.35 , $p < 0.001$). Again, abundances of oribatids were highest in Lowland wood, and lowest
216 in Crops/weeds. Abundances were significantly lower in Crops/weeds and Fertile grassland
217 than all other AVCs except Tall grass and herb ($p = 0.973$; $p = 0.995$, respectively).

218 Additionally, oribatid abundances were significantly greater in Lowland wood than in Tall
219 grass and herb ($p = 0.025$) and Infertile grassland ($p = 0.004$) AVCs (Fig. 2B). Though
220 abundances of Mesostigmata differed significantly by AVC ($F_{7, 515} = 8.874$, $p < 0.001$), such
221 differences were not consistent with the overall trend (Fig. 2C). Numbers of Mesostigmata
222 were significantly lower in Moorland-grass mosaic and Heath/bog than Fertile (both $p <$
223 0.001) and Infertile grassland (both $p < 0.001$), as well as Upland wood ($p = 0.023$, $p < 0.001$,
224 respectively). Abundances in Heath/bog were nearly four times (Table S4) lower than in
225 Lowland wood ($p = 0.014$).

226 Abundances of Collembola did not follow the same overall pattern. Abundances of
227 Symphypleona were negligible across all AVC's. Entomobryoidea and Poduroidea
228 abundances showed similar differences between AVCs ($F_{7, 515} = 5.72$, $p < 0.001$; $F_{7, 515} =$
229 5.97 , $p < 0.001$, respectively). Entomobryoidea abundances were significantly greater in
230 Lowland wood than in Fertile ($p = 0.036$) and Infertile grassland ($p = 0.047$), Moorland-grass
231 mosaic ($p = 0.018$), Crops/weeds ($p = 0.002$), and Heath/bog ($p < 0.001$). Abundances in
232 Crops/weeds ($p = 0.028$) and Heath/bog ($p < 0.001$) were significantly lower than in Upland
233 wood by approximately six and seven times, respectively (Table S4). Additionally,
234 abundances in Heath/bog were also significantly lower than Infertile ($p = 0.006$), and Fertile
235 grassland ($p = 0.041$; Fig. 2D). Abundances of Poduroidea were significantly lower in
236 Crops/Weeds ($p = 0.009$), Moorland-grass mosaic ($p = 0.017$), and Heath/bog ($p < 0.001$)
237 AVCs than Lowland wood. Abundances in Heath/bog were also significantly lower than both
238 grasslands (both $p < 0.001$), Moorland-grass mosaic ($p = 0.01$), and Upland wood ($p = 0.001$;
239 Fig. 2E).

240 AVC had a significant ($F_{7, 515} = 13.90$, $p < 0.001$) effect on H' diversity values (Fig.
241 2F), possibly influenced by changes in Collembola and mesostigmatid abundances. Diversity
242 values were significantly lower in Crops/weeds and Heath/bog when compared with both

243 Fertile ($p = 0.022$; $p < 0.001$, respectively) and Infertile grassland ($p = 0.027$; $p < 0.001$,
244 respectively). Additionally, H' values in Infertile grassland were significantly greater than in
245 Moorland-grass mosaic ($p < 0.001$). Lowland wood diversity values were significantly
246 greater than Heath/bog ($p < 0.001$) and Moorland-grass mosaic (0.014). Heath/bog H' values
247 were also significantly lower than Moorland-grass mosaic ($p = 0.009$) and Upland wood ($p <$
248 0.001).

249

250 3.2.2. Differences between soil types and LOI classes

251 Soil type had detectable effects on Mesostigmata ($F_{6, 516} = 4.34$, $p < 0.001$),
252 Entomobryoidea ($F_{6, 516} = 3.10$, $p = 0.006$), and Poduroidea ($F_{6, 516} = 2.34$, $p = 0.031$; Fig. 3).
253 Mesostigmata abundances were three times greater in brown soils than peat ($p < 0.001$) and
254 nearly twice greater than in surface-water gley soils ($p = 0.005$; Fig. 3C; Table S5).
255 Entomobryidea and Poduroidea abundances were also significantly higher in brown soils than
256 in peats ($p = 0.009$; $p = 0.043$, respectively; Fig 3D, 3E). These differences are reflected in H'
257 values ($F_{6, 516} = 6.16$, $p < 0.001$), where the same differences can be seen (brown soils-peats:
258 $p < 0.001$; brown soils-surface-water gleys: $p = 0.002$), in addition to a significant difference
259 between podzolic and peat soils ($p = 0.002$) (Fig. 3F).

260 Differences in mesofauna abundance amongst LOI classes were more informative.
261 Significant differences were observed for total mesofauna ($F_{3, 518} = 3.97$, $p = 0.008$; Fig. 4A),
262 total invertebrates ($F_{3, 518} = 3.99$, $p = 0.008$), and oribatid abundances $F_{3, 518} = 7.74$, $p <$
263 0.001). Here, abundances were significantly higher in humus-mineral than in mineral soils (p
264 $= 0.026$; $p = 0.030$; $p < 0.001$, respectively). Oribatid abundances were also significantly
265 greater in organo-mineral soils than mineral soils ($p = 0.007$) and in lower organic than
266 mineral soils ($p < 0.001$; Fig. 4B).

267 The effect of LOI class on abundance was the same for Mesostigmata ($F_{3, 518} = 11.97$,
268 $p < 0.001$) and Entomobryoidea ($F_{3, 518} = 7.36$, $p < 0.001$). Here, abundances of both were
269 significantly lower in organic soils than humus-mineral, mineral (all $p < 0.001$), and organo-
270 mineral ($p = 0.023$, $p = 0.037$, respectively) soils (Fig. 4B, 4C) by orders of four to five times
271 respectively (Table S6). A similar trend was observed in Poduroidea abundances ($F_{3, 518} =$
272 9.96 , $p < 0.001$). However, in this case, abundances were significantly lower in organic soils
273 than humus-mineral ($p < 0.001$) and mineral ($p = 0.01$) soils (Fig. 4E). LOI class significantly
274 ($F_{3, 518} = 28.67$, $p < 0.001$) affected diversity values, being significantly greater in humus-
275 mineral ($p < 0.001$), mineral, ($p < 0.001$) and organo-mineral ($p = 0.007$) soils than in organic
276 soils. There were also significant differences between organo-mineral soils and both mineral
277 ($p = 0.028$) and humus-mineral soils ($p = 0.001$; Fig. 4F).

278

279 *3.3. Correlates with soil physical and chemical variables*

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

291

292 **4. Discussion**

293 *4.1. Trends in mesofauna communities*

294 Total abundance and diversity values were consistently lower in arable sites. These
295 results support those of other studies that have shown Acari and Collembola abundances
296 decline in agricultural habitats when compared to more extensive habitats (de Vries et al.,
297 2013; Arroyo et al., 2013; Tsiafouli et al., 2015). For example, Tsiafouli et al. (2015) found
298 Acari and Collembola diversity and biomass declined with increasing agricultural land-use
299 intensity across a range of European sites. These groups (Behan-Pelletier, 2003; Tsiafouli et
300 al., 2015) are generally susceptible to disturbance, which has been seen across Europe
301 (Postma-Blaauw et al., 2010; de Vries et al., 2013), North America (Behan-Pelletier, 2003),
302 and Australia (Osler and Murphy, 2005).

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

310

311 *4.2. Soil properties and oribatids*

312 The negative correlation of oribatid mite abundance with pH and bulk density, in
313 addition to the positive relationship with soil organic matter observed in the present study is
314 consistent with results from Ireland (Arroyo et al., 2013). Oribatids are sensitive to
315 agricultural practices, primarily due to life-history characteristics such as low fecundity and
316 relatively long generation times (Behan-Pelletier, 1999). Soil compaction and litter removal

317 have been shown to lower oribatid densities in forest plantations (Battigelli et al., 2004) and
318 both processes commonly occur under conventional agricultural management.

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

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

336

337 *4.3 Trends in Mesostigmata and Collembola populations*

338 Interestingly, Collembola abundances were as low in Heath/bog sites as they were in
339 Crops/weeds. Most Heath/bog sites were located in upland regions. The Welsh uplands
340 include at-risk habitats such as peatlands, which are sensitive to disturbance (Reed et al.,
341 2009), tend to be colder and have a higher levels of C, more frequent of precipitation as well

342 as greater N deposition than lowland habitats (Kirkham, 2001). Temperature and moisture
343 level has been identified as stressors for Collembola communities. Choi and colleagues
344 (2002) found development of temperate Collembola can be halted by temperatures lower than
345 5 °C. Sustained elevated N deposition in American forest soils has been shown to reduce
346 Collembola densities (Gan et al., 2013). Increased frequency and severity of precipitation
347 also reduce Collembola richness and abundance in both mesocosm (Turnbull and Lindo,
348 2015) and *in situ* experiments (Tsiafouli et al., 2005). Furthermore, increases in peatland
349 Collembola populations have been documented when peatlands are drained for forestry
350 (Silvan et al., 2000). Total C and N, as well as C: N ratio, were highest in upland habitats
351 (Table S3); therefore, the negative relationships between Collembola and these variables
352 were likely artefacts of the strong effect of moisture levels in upland, peat-rich sites.

353 Mesostigmata abundances only declined in Moorland-grass mosaic and Heath/bog
354 sites. Mesostigmatids had the same trends with bulk density (positive), and moisture content
355 (negative) as Collembola, but were positively correlated with pH. Prey availability has been
356 shown to have a strong influence on mesostigmatid abundance (Nielsen et al., 2010a; Nielsen
357 et al., 2010b). Decreased prey abundance (i.e. Collembola, Nielson et al., 2010a) could limit
358 their populations in moist upland habitats. Higher abundances in agricultural areas may have
359 been maintained through consumption of unsurveyed prey such as nematodes (Koehler,
360 1997), as predatory Acari in arable habitats are often generalists or omnivores (Postma-
361 Bloouw et al., 2010).

362

363 *4.3. Implications for national-level soil monitoring*

364 The approach employed by GMEP is efficient and cost-effective and the collection of
365 a separate mesofauna core from each site does not add considerably to sampling effort of a
366 monitoring programme (Emmett and the GMEP Team, 2014; 2015). This study showed that

367 meaningful conclusions can be drawn from a nationwide mesofauna dataset collected using a
368 relatively simple, standardised methodology. Yet, trends observed in the present study
369 highlight some important shortcomings of using mesofauna as bioindicators of soil quality.

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

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

389 Higher taxonomic levels of mesofauna were however, informative of relationships
390 using locally derived soil data. Relationships of these groups with soil properties, though
391 potentially obscured when taken as a whole, allow for important insights into the ecological

392 implications of changes in the environment. Similarly, comparing mesofauna groups to soils
393 classified by LOI percentage on a national-level revealed trends that better inform us of the
394 ecological meaning behind distributions than traditional soil taxonomic classifications. It is
395 possible that further classification of mesofauna to species-level could be more informative.
396 We chose not to do this, and to instead use higher-level taxonomy following previous British
397 surveys (Black et al., 2003; Keith et al., 2015). National monitoring has an added benefit of
398 creating a national inventory of taxonomic specimens from which further research can be
399 conducted and from which more species may be described. Additionally, reference
400 collections of identified mesofauna species provide a strong starting-point for studies using
401 metabarcoding (Creer et al., 2016). Greater confidence can be given to database matches of
402 mesofauna from community and environmental DNA and DNA from identified specimens
403 can be uploaded to databases (Ratnasingham and Hebert, 2007) to build more complete
404 reference libraries. It is important to remember that comparisons of new molecular datasets
405 will require reference to historical taxonomic data, strengthening the case for acquiring new
406 reference materials as part of monitoring. Therefore, we suggest that the addition of surveys
407 of mesofauna identified at coarse taxonomic levels to any national soil monitoring
408 programme will be an important compliment to the assessments of soil properties and
409 biodiversity.

410 **5. Conclusions**

411 Our results show that at the national-level, mesofauna populations have the potential
412 to be effective environmental indicators, through their consistent sensitivity to differences in
413 habitat, plot-level soil class, and soil physical characteristics. This research represents an
414 important first step to assess agri-environment schemes and land-use change. The present
415 study was one of the most extensive nationwide surveys of mesofauna in Europe. Results
416 show that conventional stresses on soil mesofauna from agriculture can be observed across

417 the country with relatively low sampling effort. Additionally, it has revealed trends in
418 Collembola and Mesostigmata in highly sensitive upland areas. Such results may be of use to
419 policy-makers and land-managers actively trying to maintain a balance between rural
420 development and natural values. The sampling design used here has been effective for
421 analysis of disparate habitat types. However, further refinements are needed to separate
422 similar habitat types and to understand relationships with soil type as defined by the National
423 Soil Map using mesofauna communities. We encourage the use of mesofauna surveys in
424 regional- to national-level soil monitoring programmes to better inform researchers of the
425 ecological implications of changing soil properties. With the inclusion of mesofauna in soil
426 monitoring plans, a more complete picture of the potential of mesofauna as bioindicators of
427 soil quality will be made.

428

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440

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597

598 **Figure Captions**

599 **Fig. 1.** Map of 1 km² squares selected for GMEP monitoring. Sites are randomly offset by 10
600 km to protect landowner anonymity.

601

602 **Fig. 2.** Boxplots of **A)** total mesofauna; **B)** Oribatida; **C)** Mesostigmata; **D)** Entomobryoidea;
603 **E)** Poduroidea; **F)** Shannon's diversity plotted against Aggregate Vegetation Class. All
604 abundances are log₁₀ plus one transformed. Notches indicate confidence interval around the
605 median. Overlapping notches are a proxy for non-significant differences between medians.

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

608

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

615

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

622

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

627