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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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17

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 km<sup>2</sup>. 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 km<sup>2</sup> 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 km<sup>2</sup> squares in 2013 and 90 x 1 km<sup>2</sup> 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 ( $\text{g/cm}^3$ ), pH  
147 (measured in 0.01 M  $\text{CaCl}_2$ ), volumetric water content ( $\text{m}^3/\text{m}^3$ ), 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 km<sup>2</sup> 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-R<sup>2</sup> 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

#### 441 **References**

442 Arroyo, J., Keith, A.M., Schmidt, O., Bolger, T., 2013. Mite abundance and richness in an Irish  
443 survey of soil biodiversity with comments on some newly recorded species. Irish Naturalists'  
444 Journal 33, 19-27.

445 Avery, B.W., 1990. Soils of the British Isles. CAB International, Wallingford.

446 Barrios, E., 2007. Soil biota, ecosystem services and land productivity. Ecological Economics 64,  
447 269-285.

448 Battigelli, J.P., Spence, J.R., Langor, D.W., Berch, S.M., 2004. Short-term impact of forest soil  
449 compaction and organic matter removal on soil mesofauna density and oribatid mite diversity.  
450 Canadian Journal of Forest Research 34, 1136-1149.

451 Behan-Pelletier, V.M., 1999. Oribatid mite biodiversity in agroecosystems: role for bioindication.  
452 Agriculture, Ecosystems and Environment 74, 411-423.

453 Behan-Pelletier, V.M., 2003. Acari and Collembola biodiversity in Canadian agricultural soils.  
454 Canadian Journal Soil Science 83, 279-288.

455 Black, H.I.J., Parekh, N.R., Chaplow, J.S., Monson, F., Watkins, J., Creamer, R., Potter, E.D., Poskitt,  
456 J.M., Rowland, P., Ainsworth, G., Hornung, M., 2003. Assessing soil biodiversity across Great  
457 Britain: national trends in the occurrence of heterotrophic bacteria and invertebrates in soil. Journal  
458 of Environmental Management 67, 255-266.

459 Bunce, R.G.H., Barr, C.J., Gillespie, M.K., Howard, D.C.H., Scott, W.A., Smart, S.M., van der Poll,  
460 H.M., Watkins, J.W., 1999. Vegetation of the British countryside – the Countryside Vegetation  
461 System. ECOFACT Volume 1. DETR, London, 224 pp.

462 Choi, W.I., Ryoo, M.I., Kim, J.-G., 2002. Biology of *Paronychiurus kimi* (Collembola:  
463 Onychiuridae) under the influence of temperature, humidity and nutrition. Pedobiologia 46, 548-  
464 577.

465 Cole, L., Buckland, S.M., Bardgett, R.D., 2008. Influence of disturbance and nitrogen addition on  
466 plant and soil animal diversity in grassland. Soil Biology & Biochemistry 40, 505-514.

467 Cluzeau, D., Guernion, M., Chaussod, R., Martin-Laurent, F., Villenave, C., Cortet, J., Ruiz-  
468 Camacho, N., Pernin, C., Mateille, T., Philippot, L., Bellido, A., Rougé, L., Arrouays, D., Bispo,

469 A., Pérès, G., 2012. Integration of biodiversity in soil quality monitoring: baselines for microbial  
470 and soil fauna parameters for different land-use types. *European Journal of Soil Biology* 49, 63-72.

471 Creer, S., Deiner, K., Frey, S., Porazinska, D., Taberlet, P., Thomas, W.K., Potter, C., Bik, H.M.,  
472 2016. The ecologist's field guide to sequence-based identification of biodiversity. *Methods in*  
473 *Ecology and Evolution* 7, 1008-1018.

474 Crotty, F.V., Shepherd, M., 2014. A Key to the Soil Mites of Britain and Ireland (Test Version 5).  
475 Field Studies Council, Telford.

476 Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil  
477 quality. *Applied Soil Ecology* 15, 3-11.

478 Emmett, B.A., the GMEP team, 2014. Glastir Monitoring & Evaluation Programme. First Year  
479 Annual Report to Welsh Government (Contract reference: C174/2010/11). NERC/Centre for  
480 Ecology & Hydrology (CEH Project: NEC04780), pp. 442.

481 Emmett, B.A., the GMEP team, 2015. Glastir Monitoring & Evaluation Programme, Second Year  
482 Annual Report to Welsh Government (Contract Reference: C147/2010/11). NERC/Centre for  
483 Ecology & Hydrology (CEH Project: NEC04780), pp 316.

484 Emmett, B.A., Reynolds, B., Chamberlain, P.M., Rowe, E., Spurgeon, D., Brittain, S.A., Frogbrook,  
485 Z., Hughes, S., Lawlor, A.J., Poskitt, J., Potter, E., Robinson, D.A., Scott, A., Wood, C., Woods,  
486 C., 2010. Countryside Survey: Soils Report from 2007. NERC/Centre for Ecology and Hydrology,  
487 192 pp. (CS Technical Report No. 9/07, CEH Project Number: C03259).

488 Gan, H., Zak, D.R., Hunter, M.D., 2013. Chronic nitrogen deposition alters the structure and function  
489 of detrital food webs in a northern hardwood ecosystem. *Ecological Applications* 23, 1311-1321.

490 Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of  
491 available taxonomic groups. *Journal of Insect Conservation* 17, 831-850.

492 Graham, E.B., Knelman, J.E., Schindlbacher, A., Siciliano, S., Breulmann, M., Yannarell, A., Beman,  
493 J.M., Abell, G., Philippot, L., Prosser, J., Foulquier A., Yuste, J.C., Glanville, H.C., Jones, D.L.,  
494 Angel, R., Salminen, J., Newton, R.J., Bürgmann, H., Ingram, L.J., Hamer, U., Siljanen, H.M.P.,  
495 Peltoniemi, Potthast, K., Bañeras, L. Hartmann, M., Banerjee, S., Y. Yu R.-Q., Nogaro, G.,  
496 Richter, A., Koranda, M., Castle, S.C., Goberna, M., Song, B., Chatterjee, A., Nunes, O.C., Lopes,

497 A.R., Cao, Y., Kaisermann, A., Hallin, S., Strickland, M.S., G.-P., J., Barba, J., Kang, H., Isobe,  
498 K., Papaspyrou, S., Pastorelli, R., Lagomarsino, A., Lindström, E.S., Basiliko, N., Nemergut, D.R.,  
499 2016. Microbes as engines of ecosystem function: when does community structure enhance  
500 predictions of ecosystem processes? *Frontiers in Microbiology* 7, 214.

501 Gulvik, M.E., 2007. Mites (Acari) as indicators of soil biodiversity and land use monitoring: a review.  
502 *Polish Journal of Ecology* 55, 415-440.

503 Hallett, P.D., Ritz, K., Wheatley, R.E., 2001. Microbial derived water repellency in golf course soil.  
504 *International Turfgrass Society Research Journal* 9, 518-524.

505 Havlicek, E., 2012. Soil biodiversity and bioindication: from complex thinking to simple acting.  
506 *European Journal of Soil Biology* 49, 80-84.

507 Keith, A.M., Boots, B., Hazard, C., Niechoj, R., Arroyo, J., Bending, G.D., Bolger, T., Breen, J.,  
508 Clipson, N., Doohan, F.M., Griffin, C.T., Schmidt, O., 2012. Cross-taxa congruence, indicators  
509 and environmental gradients in soils under agricultural and extensive land management. *European*  
510 *Journal of Soil Biology* 49, 55-62.

511 Keith, A.M., Griffiths, R.I., Henrys, P.A., Hughes, S., Lebron, I., Maskell, L.C., Ogle, S.M.,  
512 Robinson, D.A., Rowe, E.C., Smart, S.M., Spurgeon, D., Wood, C.M., Emmett, B.E., 2015.  
513 Monitoring Soil Natural Capital and Ecosystem Services by Using Large-Scale Survey Data. In  
514 Stormberger, M., Cornerford, N., Lindbo, D. (Eds.), *Soil Ecosystem Services*. SSSA, Madison,  
515 WI. doi:10.2136/2015.soilecosystemservices.2014.0070.

516 Kirkham, F.W., 2001. Nitrogen uptake and nutrient limitation in six hill moorland species in relation  
517 to atmospheric nitrogen deposition in England and Wales. *Journal of Ecology* 89, 1041-1053.

518 Koehler, H.H., 1997. Mesostigmata (Gamasina, Uropodina), efficient predators in agroecosystems.  
519 *Agriculture, Ecosystems and Environment* 62, 105-117.

520 Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi,  
521 J.-P., 2006. Soil invertebrates and ecosystem services. *European Journal of Soil Biology* 42, S3-  
522 S15.

523 Lefcheck, J.S., 2015. piecewiseSEM: piecewise structural equation modelling in R for ecology,  
524 evolution, and systematics. *Methods in Ecology and Evolution* 7, 573-579.

525 Nielsen, U.N., Osler, G.H.R., Campbell, C.D., Neilson, R., Burslem, D.F.R.P., van der Wal, R.,  
526 2010a. The influence of vegetation type, soil properties and precipitation on the composition of  
527 soil mite and microbial communities at the landscape scale. *Journal of Biogeography* 37, 1317-  
528 1328.

529 Nielsen, U.N., Osler, G.H.R., Campbell, C.D., Neilson, R., Burslem, D.F.R.P., van der Wal, R.,  
530 2010b. The enigma of soil animal species diversity revisited: the role small-scale heterogeneity.  
531 *PLoS One* 5, e11567.

532 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., MacGinn, D., Minchin, P.R.,  
533 O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2016.  
534 *vegan: Community Ecology Package*. R package version 2.4-0. URL: [https://CRAN.R-](https://CRAN.R-project.org/package=vegan)  
535 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan).

536 Osler, G.H.R., Murphy, D.V., 2005. Oribatid mite species richness and soil organic matter fractions in  
537 agricultural and native vegetation soils in Western Australia. *Applied Soil Ecology* 29, 93-98.

538 Osler, G.H.R., Sommerkorn, M., 2007. Towards a complete soil C and N cycle: incorporating the soil  
539 fauna. *Ecology* 88, 1611-1621.

540 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2016. *nlme: Linear and Nonlinear*  
541 *Mixed Effects Models*. R package version 3.1-128, URL: [http://CRAN.R-](http://CRAN.R-project.org/package=nlme)  
542 [project.org/package=nlme](http://CRAN.R-project.org/package=nlme).

543 Postma-Blaauw, M.B., de Goede, R.G.M., Bloem, J., Faber, J.H., Brussard, L., 2010. Soil biota  
544 community structure and abundance under agricultural intensification and extensification. *Ecology*  
545 91, 460-473.

546 R Core Team, 2016. *R: A language and environment for statistical computing*. R Foundation for  
547 Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.

548 Ratnasingham, S., Hebert, P.D.N., 2007. BOLD: the barcode of life data system  
549 ([www.barcodinglife.org](http://www.barcodinglife.org)). *Molecular Ecology Notes* 7, 355-364.

550 Reed, M.S., Bonn, A., Slee, W., Beharry-Borg, N., Birch, J., Burt, T.P., Chapman, D., Chapman, P.J.,  
551 Clay, G.D., Cornell, S.J., Fraser, E.D.G., Glass, J.H., Holden, J., Hodgson, J.A., Hubacek, K.,  
552 Irvine, B., Jin, N., Kirkby, M.J., Kunin, W.E., Moore, O., Moseley, D., Prell, C., Price, M.F.,

553 Quinn, C.H., Redpath, S., Reid, C., Stagl, S., Stringer, L.C., Termansen, M., Thorp, S., Towers,  
554 W., Worrall, F., 2009. The future of the uplands. *Land Use Policy* 265, S204-S216.

555 Rillig, M.C., 2005. A connection between fungal hydrophobins and soil water repellency?  
556 *Pedobiologia*, 49, 395-399.

557 Rillig, M.C., Mardatin, N.F., Leifheit, E.F., Antunes, P.M., 2010. Mycelium of arbuscular  
558 mycorrhizal fungi increases soil water repellency and is sufficient to maintain water-stable soil  
559 aggregates. *Soil Biology & Biochemistry* 42, 1189-1191.

560 Rutgers, M., Schouten, A.J., Bloem, J., van Eekeren, N., de Goede, R.G.M., Jagers op Akkerhuis,  
561 G.A.J.M., van der Wal, A., Mulder, C., Brussaard, L., Breure, A.M., 2009. Biological  
562 measurements in a nationwide soil monitoring network. *European Journal of Soil Science* 60, 820-  
563 832.

564 Rusek, J., 1998, Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity*  
565 *and Conservation* 7, 1207-1219.

566 Schon, N.L., Mackay, A.D., Gray, R.A.J., Minor, M.A., 2011. Influence of phosphorus inputs and  
567 sheep treading on soil macrofauna and mesofauna in hill pastures. *New Zealand Journal of*  
568 *Agricultural Research* 54, 83-96.

569 Schneider, K., Renker, C, Maraun, M., 2005. Oribaitd mite (Acari, Oribatida) feeding on  
570 ectomycorrhizal fungi. *Mycorrhiza* 16, 67-72.

571 Seniczak, S., Dabrowski, J., Klimek, A., Kaczmarek, S., 1998. Effects of air pollution produced by a  
572 nitrogen fertilizer factory on the mites (Acari) associated with young Scots pine forests in Poland.  
573 *Applied Soil Ecology* 9, 453-458.

574 Silvan, N., Laiho, R., Vasander, H., 2000. Changes in mesofauna abundance in peat soils drained for  
575 forestry. *Forest Ecology and Management* 133, 127-133.

576 Tsiafouli, M.A., Kallimanis, A.S., Katana, E., Stamou, G.P., Sgardelis, S.P., 2005. Responses of soil  
577 microarthropods to experimental short-term manipulations of soil moisture. *Applied Soil Ecology*  
578 29, 17-26.

579 Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K.,  
580 Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L., Jørgensen, H.B.,



581 Christensen, S., d’Hertefeldt, T., Hotes, S., Hol, W.H. G., Frouz, J., Liiri, M., Mortimer, S.R.,  
582 Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V., Stray, J., Wolters, V., Hedlund, K., 2015.  
583 Intensive agriculture reduces soil biodiversity across Europe. *Global Change Biology* 21, 973-985.  
584 Turnbull, M.S., Lindo, Z., 2015. Combined effects of abiotic factors on Collembola communities  
585 reveal precipitation may act as a disturbance. *Soil Biology & Biochemistry* 82, 36-43.  
586 de Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Jørgensen, H.B.,  
587 Brady, M.V., Christensen, S., de Ruyter, P.C., d’Hertefeldt, T., Frouz, J., Hedlund, K., Hemerik,  
588 L., Hol., W.H.G., Hotes, S., Mortimer, S.R., Setälä, H., Sgardelis, S.P., Uteseny, K., van der  
589 Putten, W.H., Wolters, V., Bardgett, R.D., 2013. Soil food web properties explain ecosystem  
590 services across European land use systems. *Proceedings of the National Academy of Sciences* 110,  
591 14296-14301.  
592 Welsh Government, 2016. How to measure a nation’s progress? National indicators for Wales.  
593 Hawlfraint y Goron, WG26817, ISBN Digidol 978 1 4734 6309 7.  
594 Winter, J.P., Behan-Pelletier, V.M., 2007. Microarthropods In: Carter, M.R., Gregorich, E.G. (Eds.),  
595 Soil Sampling and Methods of Analysis 2<sup>nd</sup> edition. CRC press, Taylor & Francis Group LLC,  
596 Boca Raton, FL, pp. 399-414.

597

## 598 **Figure Captions**

599 **Fig. 1.** Map of 1 km<sup>2</sup> 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 log<sub>10</sub> 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).

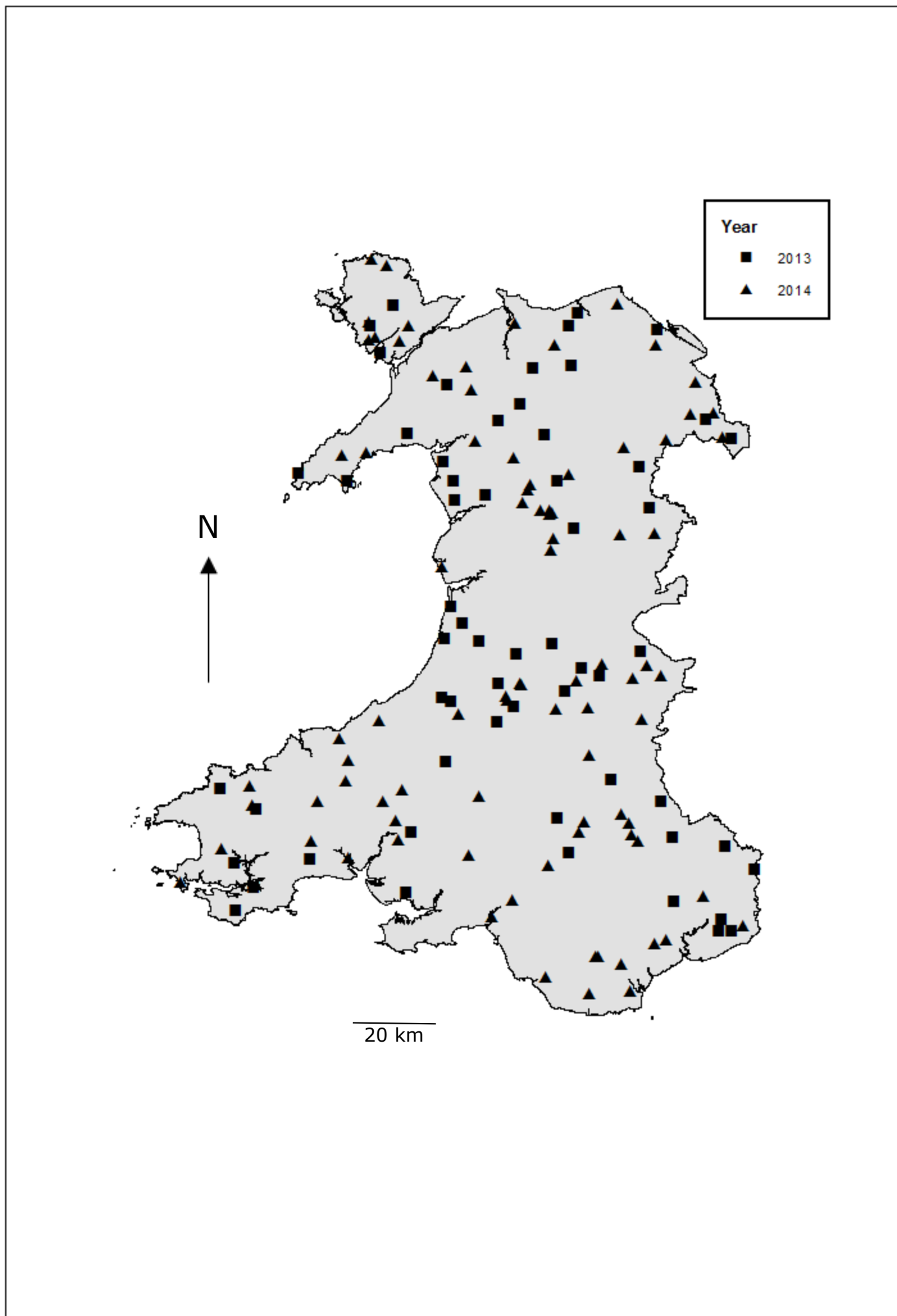
627

**Table 1.** Spearman correlations rho ( $\rho$ ) values for correlations with abundance of mesofauna groups with soil physical and chemical variables. \*\*\* indicates  $P < 0.001$ , \*\*  $0.001 > P < 0.01$ , \*  $0.01 > P < 0.05$ , blank indicates  $P > 0.05$ .

Soil variable	Total mesofauna	Oribatida	Mesostigmata	Entomobryoidea	Poduroidea
Total C	0.018	0.190***	-0.244***	-0.151***	-0.123***
Total N	-0.007	0.144***	-0.233***	-0.152***	-0.123***
C:N ratio	0.051	0.244***	-0.256***	-0.120***	-0.132***
pH (CaCl <sub>2</sub> )	-0.122***	-0.317***	0.118***	0.043	0.024
Bulk density	-0.056	-0.233***	0.216***	0.126***	0.089*
Soil water repellency <sup>a</sup>	0.142***	0.267***	-0.060	-0.48	-0.029
Volumetric water content	-0.175***	0.006	-0.381***	-0.235***	-0.286***
Total P	-0.054	-0.127***	0.054	0.001	0.022

<sup>a</sup> Soil water repellency was derived from median water drop penetration times (s) and log transformed

Figure1



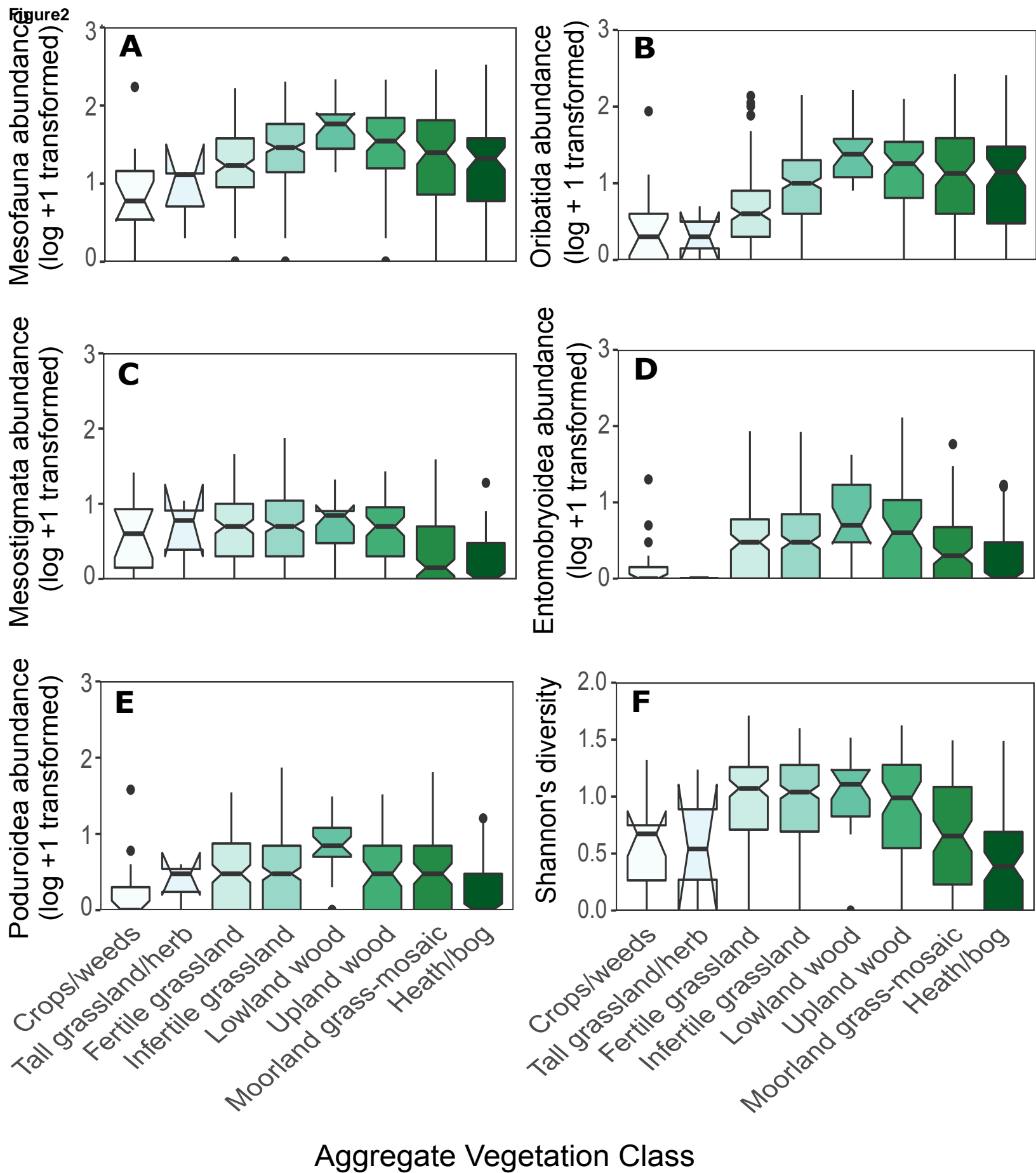
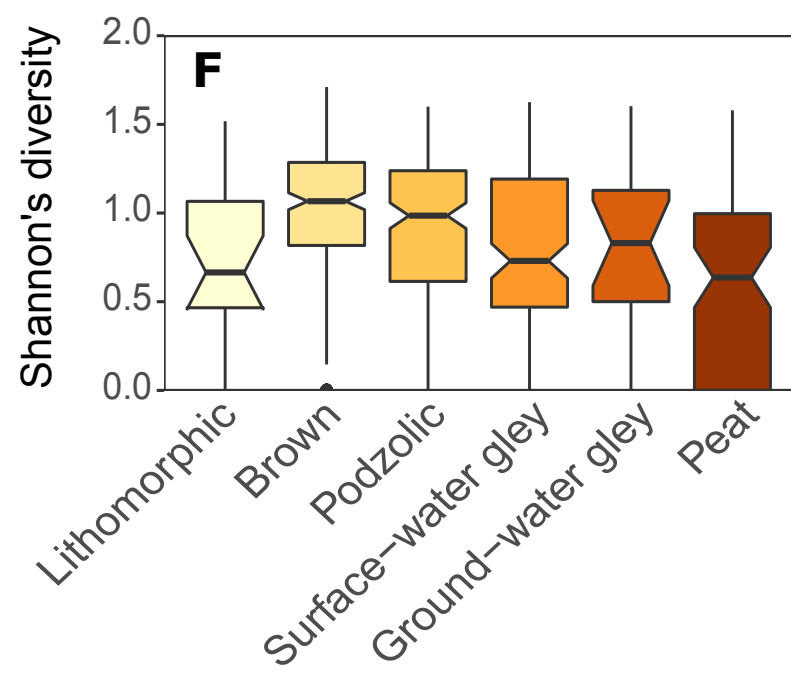
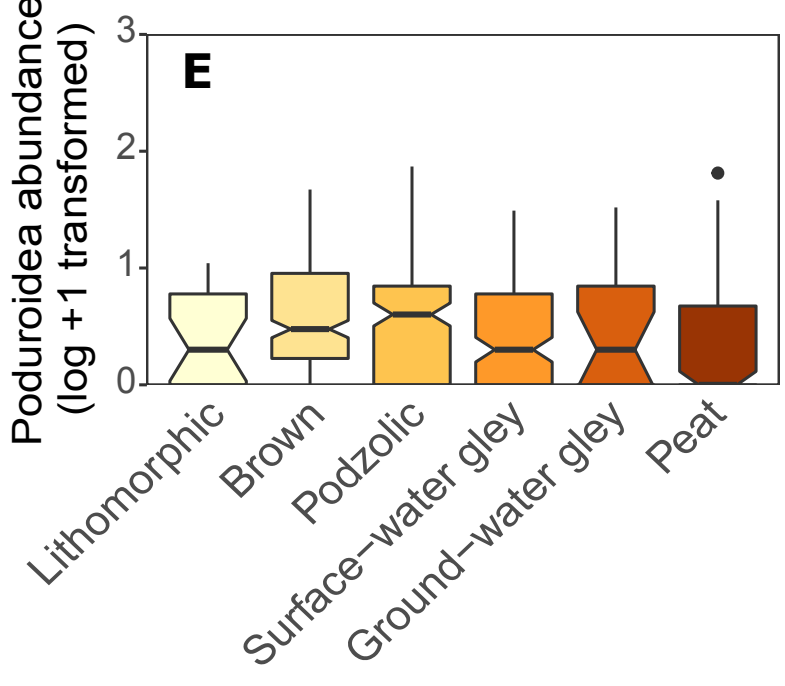
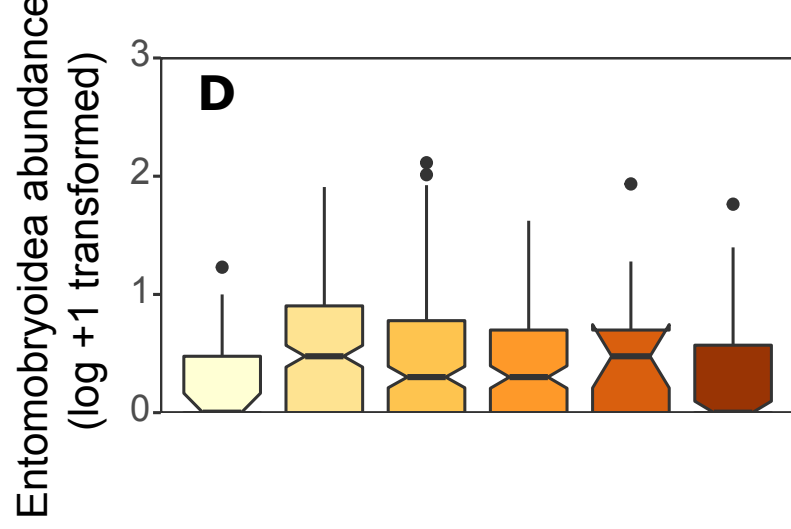
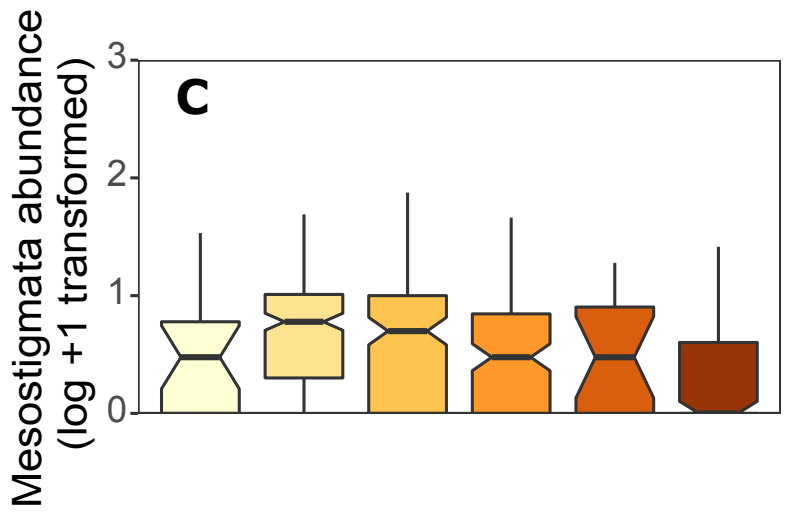
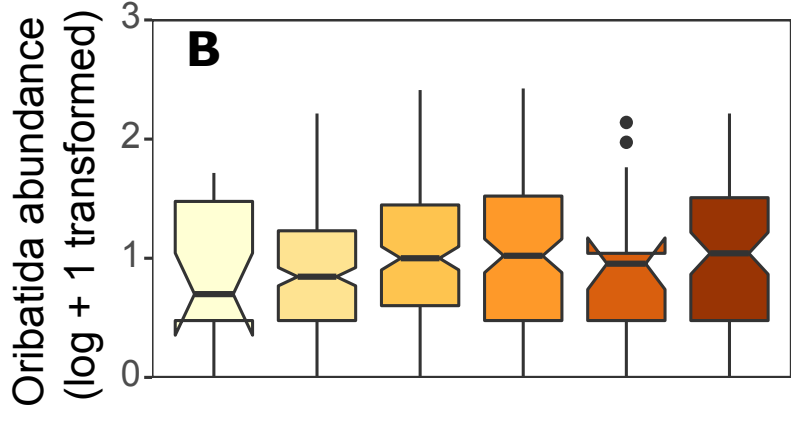
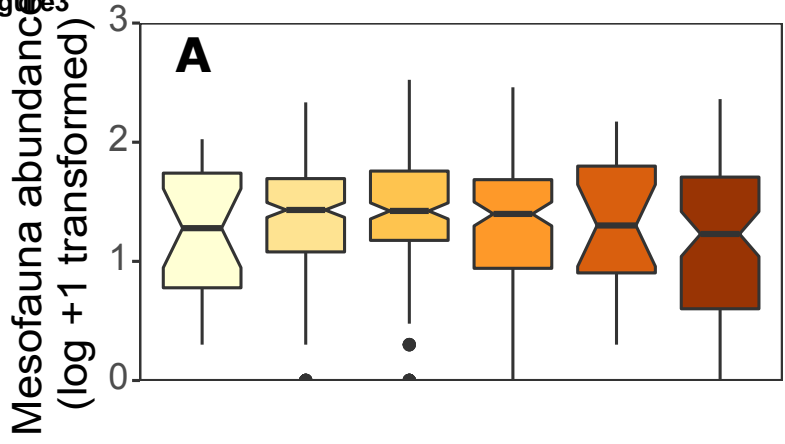


Fig 63



Soil Type

Figure 4

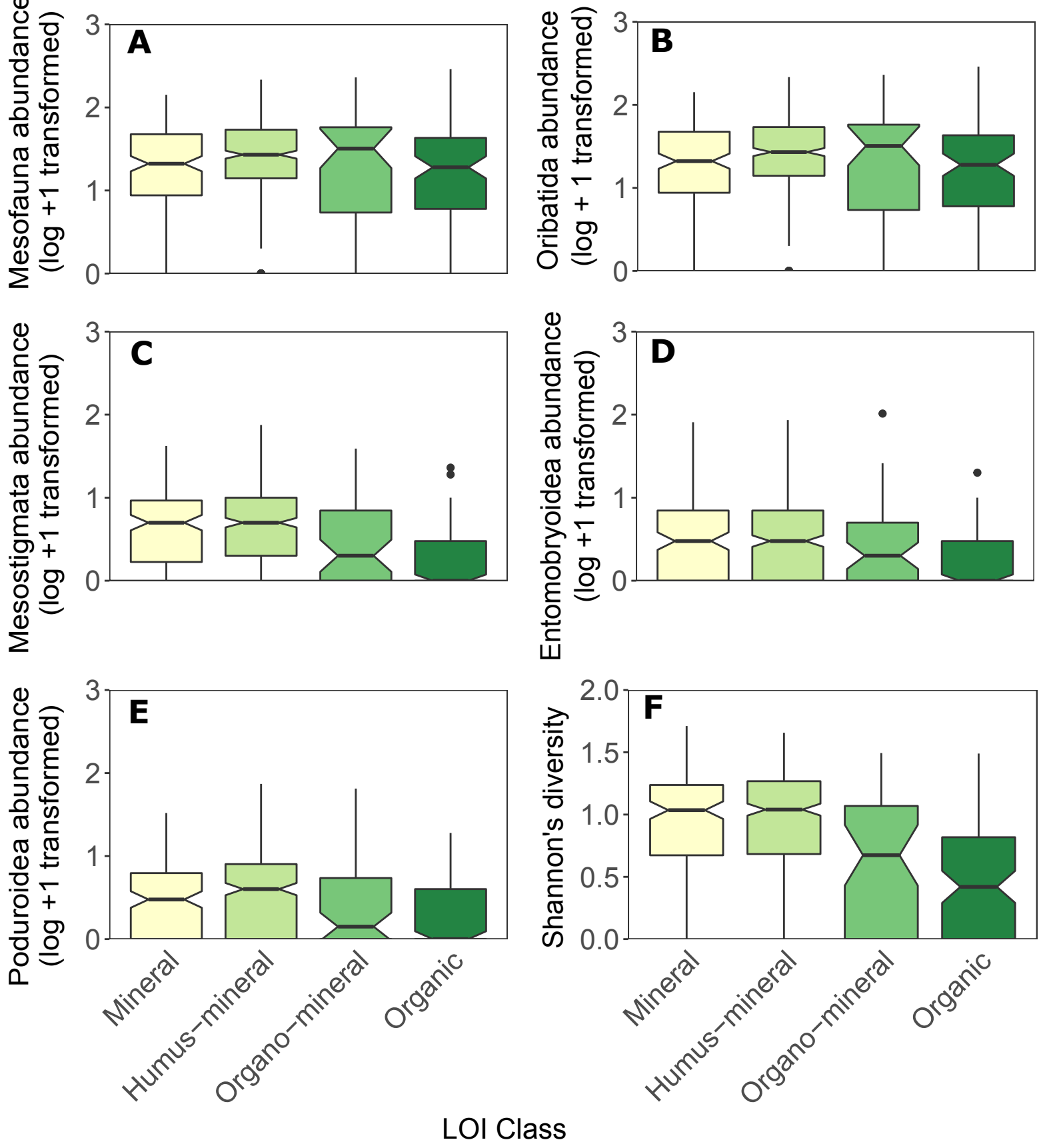


Figure5

